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RESEARCH ARTICLE

Physiological responses of four herbaceous plants to aluminum stress in South China

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Abstract Different plants have physiological responses under Al stress, but there is no systematic study to examine physiological responses of herbaceous plants under Al stress. The aim of this study is to investigate the effect of Al on physiological characteristics of four herbaceous plants, which distributed in red soil area in South China, and to analyze the differences in physiological responses to Al stress between the four herbaceous plants. Four herbaceous plants (*Pharbitis nil*, *Cassia occidentlis*, *Echinochloa colonum* and *Aeschynomene indica*) were used, and the seed germination percentage, the contents of chlorophyll, proline, and malondialdehyde (MDA), membrane permeability (MP), soluble sugar, and activities of peroxides (POD) and catalase (CAT) in leaves under five Al^{3+} treatments (0, 80, 400, 2 000, and 10 000 mg/L) were assayed with the sand culture method. The results showed remarkable effects of Al^{3+} on physiological characteristics of these four herbaceous plants. The seeds of all the four species could not germinate at 10 000 mg/L, and the growth of all plants were retarded under the 2 000 mg/L Al^{3+} treatment. Compared with the control, 2 000 mg/L Al^{3+} significantly ($P < 0.05$) reduced the contents of chlorophyll a and chlorophyll a + b, and increased the contents of MDA and MP. The content of proline increased very significantly ($P < 0.01$) and activities of POD and CAT were depressed. The contents of MDA and MP in leaves of *P. nil* and *A. indica* decreased, and the activities of POD and CAT in leaves of the two plants increased under 80 mg/L and 400 mg/L. However, the changes in *C. occidentlis* leaves were opposite to those of the above two plants. The changes in leaves of *E. colonum* were similar to those of *P. nil* and *A. indica* at 80 mg/L, but were opposite to those at 400 mg/L Al^{3+}. It is suggested that plants with higher activities of POD and CAT, more contents of chlorophyll and proline, and lower contents of MDA and MP consequently improve the tolerance to Al stress under low and middle Al treatments.

Keywords aluminium stress, physiological and ecological response, tolerance, seed germination, herbaceous plants

1 Introduction

Aluminum (Al) is one of the most abundant elements, makes up 8% of the earth's crust, and obtained as harmless oxides and aluminosilicates. Nevertheless, under acidic conditions (pH < 5), as is now the case in 21% of the arable lands in China, Al is solubilized into toxic forms (generally Al^{3+}), which threaten plants and environments (Rout et al., 2001; Ying et al., 2006).The recent increase of acid rain in most of the areas of South China accelerates the solubilization of Al and causes increasing trend of the soluble aluminum in soil and other relevant environments (Liu et al., 2004). The soluble aluminum phytotoxicity exists in most plants becomes a major threat to crop growth and productivity on acid soils (Kochian, 1995; Ermolayev et al., 2003).

Many investigations indicated that Al stress induced the formation of reactive oxygen species (ROS) and generation of peroxidants in membrane lipids, proteins and nucleic acids, thereby destroyed metabolism in plant cells (Kochian and Jones, 1997; Guo et al., 2004; Yang et al., 2005). Responses to Al stress vary with different plants and species. There are natural plants with high tolerance to Al stress (Wagatsuma and Akiba, 1989; Ma et al., 1997), and some plant species might be more tolerant than the others (Guo et al., 2004; Meriga et al., 2004). Although mechanisms involved in both phytotoxicity caused by aluminum and tolerance to aluminum in plants have not been clearly elucidated, there were evidences suggesting that the primary effect of Al toxicity was first detected on the cellular membrane, and thus the degree of lipid peroxidation under Al stress had a close relation to tolerance to Al stress in plants

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(Oteiza, 1994; Zhang et al., 1996; Yamamoto et al., 2001; Ahn et al., 2004).

In contrast, plants under Al stress may mobilize a variety of antioxidant enzymes such as superoxide dismutases (SODs), peroxidases (PODs) and catalases (CATs), and some other antioxidant compounds, such as proline and ascorbate, to scavenge peroxides (Kochian and Jones, 1997; Čiamporová, 2002; Devi et al., 2003). Therefore, antioxidant enzymes and other antioxidant compounds play an important role in resisting aluminum stress. There is a close relation between antioxidant activity and tolerance to Al stress in plants (Bowler et al., 1992; Foyer et al., 1994; Guo et al., 2004). Tolerance of plants to Al stress is revealed through investigating changes of lipid peroxidation, antioxidant enzymes, and other antioxidant compounds in response to Al stress.

Herbaceous plants show strong adaptability and competitiveness in nature, many of which must have some physiological and ecological mechanisms because they grown and distributed widely on acid soils. In recent decades, many researches have done in wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*), soybean (*Glycine max*), cotton (*Gossypium hirsutum*), Largeleaf Hydrangea (*Hydrangea macrophylla*) and buckwheat (*Fagopyrum esculentum*) (Zhang et al., 1996; Kong et al., 2000; Deborah and Tesfaye, 2003; Naumann and Horst, 2003; Peng et al., 2003) to find their physiological and ecological tolerances to Al stress. However, only few studies have been reported on physiological responses and tolerance to Al stress with wild herbaceous plants. Herbaceous plants can grow rapidly, have strong progenitive power and large biomass. Using some tolerant herbaceous plants to process highly efficient, non-contaminative bioremediation on acid soils polluted by Al can provide basis for crop production. Hence, investigating mechanism of physiological responses and tolerance to Al stress in different herbaceous plants can provide theoretical basis for revealing Al-resistant mechanism and preventing Al toxicity.

2 Materials and methods

2.1 Materials

Four herbaceous plants *Pharbitis nil*, *Cassia occidentlis*, *Echinochloa colonum,* and *Aeschynomene indica* were selected because of their wide distribution and well growth on acid red soils of South China.

2.2 Experimental methods

The plants were cultured with sand, and were disinfected, soaked in distilled water, and then dried. Five treatments were carried out with various amounts of Al, which was added by aluminum sulfate ($Al_2(SO_4)_3 \cdot 18H_2O$) to made the Al^{3+} concentration to 0, 80, 400, 2000 and 10 000 mg/L. Fullstrength Hoagland's solution was used to maintain plant nutrition. Thousand seeds of each plant were sowed on bourgeon bed (five treatments were applied conducted on sand) for germination. The number of germinated seeds was observed and recorded everyday. After germination, plants of similar size were selected and transferred to plastic pots (500mL). Each pot had five plants and each treatment repeated four times.

2.3 Sampling

Leaves were sampled on the 60th day after sowing for measuring contents of chlorophyll (Chl), malondialdehyde (MDA), proline, and soluble sugar (SS) and activities of catalase (CAT) and peroxides (POD). Roots were sampled for measuring membrane permeability (MP).

2.4 Measurement

The contents of chlorophyll were determined using mixed extraction (Liu and Yang, 2000), and activities of CAT were determined using guaiacol (Zheng et al., 1991). The contents of proline, MDA, MP, and SS, and activities of POD were measured using methods based on Institute of Plant Physiology of Shanghai (1999).

2.5 Data analysis

GLMANOVA was used to analyze the data using Statistical Program for Social Sciences (SPSS) software. All values except seed germination percentage were shown in the tables and figures.

3 Results

3.1 Effect of Al on the germination percentage of the four herbaceous plants

At high concentration (10 000 mg/L), Al can thoroughly inhibit seed germination. All the four plants could not germinate (Table1), which indicated that this concentration exceeded the tolerance for seed germination. All the four plants could germinate at other Al concentrations, but varied in germination percentage and trends. For 0~400 mg/L Al^{3+} treatment, the highest germination percentage was in *C. occidentlis* and the lowest was in *A. indica*. For 2 000 mg/L Al^{3+} treatment, the highest germination percentage was in *P. nil*. The germination percentage in *C. occidentlis* and *E. colonum* reduced as the Al concentration increased. The highest germination percentage was at 0 mg/L $Al^{3+}$and the lowest was at 2 000 mg/L Al^{3+}. The germination percentage increased and then decreased in *I. pharbitisnil* and *A. indica* with increasing Al^{3+}. It seemed that low concentration

Al^{3+}（80 and 400 mg/L Al^{3+}）facilitated seed germination, and hence the highest germination percentage was at 400 mg/L Al^{3+}, and the lowest at 2 000 mg/L Al^{3+}.

Table 1 Effect of Al on the germination percentage of the four herbaceous plants

Species	Treatment concentration of Al^{3+}/(mg·L^{-1})				
	0	80	400	2 000	10 000
Pharbitis nil /%	13.3	21.3	24.0	17.3	0
Cassia occidentlis /%	58.05	45.2	46.4	6.0	0
Echinochloa colonum /%	36.7	19.8	20.1	7.3	0
Aeschynomene indica /%	7.0	6.6	10.2	3.1	0

3.2 Effect of Al on leaf chlorophyll content of the four herbaceous plants

Results indicated that the change of chlorophyll content in leaves of the four plants under different Al^{3+} treatments was similar, i.e., Chl a, Chl b and total Chl contents increased gradually as the Al concentration increased from 0 to 400 mg/L (Table 2). The Chl content increased most significantly in *A. indica* leaves, and the Chl a, Chl b, and total Chl contents increased by 9.46%, 27.71%, and 17.56%, respectively, under 400 mg/L Al^{3+} treatment compared with 0 mg/L Al^{3+} treatment. For 2 000 mg/L Al^{3+} treatment, the Chl content reduced sharply, and the Chl a and total Chl contents fell to the lowest level among all treatments ($P < 0.05$). Compared with control, the Chl content in *C. occidentlis* decreased most, and the Chl a, Chl b, and total Chl contents reduced by 17.56%, 29.68%, and 21.63%, respectively. However, the Chl a (6.22%) and total Chl contents (3.58%) in *A. indica* decreased least. The Chl b in *A. indica* decreased least. The Chl b content in *P. nil* decreased least, i.e., only by 0.232%. The above results suggested that Al, at middle or low concentrations (80 and 400 mg/L), promoted the Chl content in plant leaves, whereas Al at high concentration caused remarkable decrease of the Chl content. The four plants showed different responses to Al at aspect of Chl content in leaves. Chl content in *A. indica* leaves increased most under middle or low Al concentration (80 and 400 mg/L) and decreased least under high concentration (2 000 mg/L). However, *C. occidentlis* responded oppositely to *A. indica*.

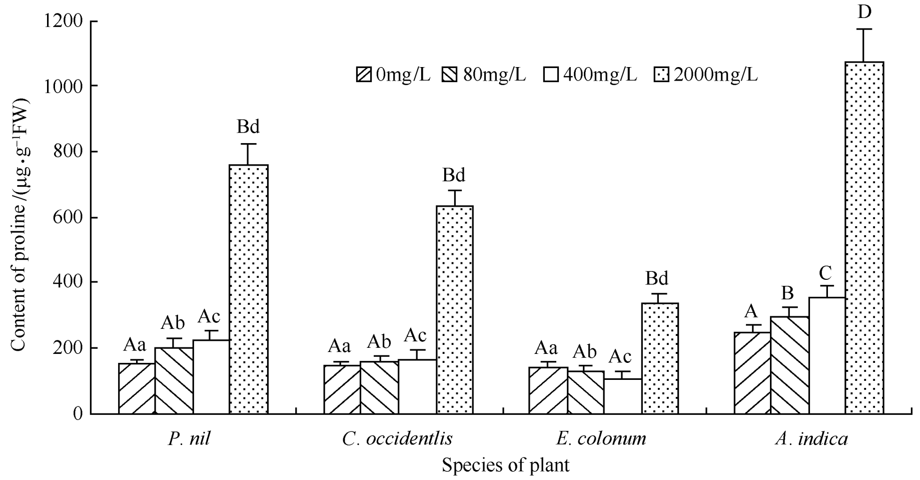
3.3 Effect of Al on the contents of proline of the four herbaceous plants in leaves

Results indicated that the proline content in the four plant leaves increased evidently under 2 000 mg/L Al^{3+} treatment (the difference between this treatment and others was significant, $P < 0.01$) (Fig. 1). Compared with control, the proline content in leaves of *A. indica, P. nil*, *C. occidentlis,* and *E. colonum* increased by 435.83%, 409.05%, 347.1%, and 139.62%, respectively. This indicated that Al at high concentration could induce generation of large amount of proline in plant leaves, which could stabilize interior environment of plant system. Changes under other treatments were less than those under high concentration. The proline content in leaves of *A. indica, P. nil*, *C. occidentlis* increased gradually as the Al^{3+} concentration increased from 0 to 400 mg/L. Proline content (37.02% and 49.94%) in *P. nil* leaves increased more than that in control under 80 mg/L and 400 mg/L Al^{3+} treatments, respectively. However, the proline content (11.51% and 23.97%) in *E. colonum* leaves decreased less than that in control under 80 mg/L and 400 mg/L Al^{3+} treatments, respectively.

Table 2 Effect of Al on the chlorophyll of the four herbaceous plants in leaves (mg/g FW) (means ± SD)

Al treatment /(mg·L^{-1})	Contents of chlorophyll	*Pharbitis nil*	*Cassia occidentlis*	*Echinochloa colonum*	*Aeschynomene indica*
0	a	1.840±0.02a*	2.597±0.03a	2.549±0.04a	2.315±0.03a
	b	0.862±0.02a	1.314±0.01a	1.428±0.02a	1.404±0.01a
	a +b	2.802±0.04a	3.911±0.03a	3.967±0.05a	3.719±0.04a
80	a	1.938±0.02a	2.661±0.02a	2.675±0.03a	2.437±0.02a
	b	0.894±0.01a	1.347±0.02a	1.772±0.02b	1.426±0.02a
	a+b	2.832±0.03a	4.008±0.05a	4.247±0.06b	3.863±0.02a
400	a	1.951±0.03a	2.724±0.02a	2.660±0.04b	2.534±0.03b
	b	1.086±0.04a	1.218±0.01a	1.787±0.03b	1.793±0.02a
	a+b	3.037±0.05a	3.942±0.04b	4.470±0.03b	4.372±0.05a
2 000	a	1.639±0.03b	2.141±0.03b	2.240±0.04b	1.971±0.03b
	b	0.860±0.02a	0.924±0.02b	1.360±0.03a	1.415±0.04a
	a+b	2.499±0.06b	3.065±0.05b	3.600±0.06b	3.386±0.07b

* Significant difference ($P < 0.05$) between the treatments in the same index (of same species) with letters.



Note: The differences between the treatments (of same species) without the same letters were very significant ($P < 0.01$, capital letters) or significant ($P < 0.05$, small letter), the same as follow

Fig. 1 Effect of Al on the contents of proline of the four herbaceous plants in leaves

3.4 Effect of Al on the contents of MDA of the four herbaceous plants in leaves

The four herbaceous plants showed a remarkable increase under 2000 mg/L treatment ($P < 0.05$) (Fig. 2). The MDA contents in leaves of *A. indica, P. nil*, *C. occidentlis* and *E. colonum* increased by 64.44%, 41.85%, 228.38%, and 212.21%, respectively, which indicated that Al at this concentration caused stress to plants. Responses of the four herbaceous plants to Al treatment could be divided into three classes. As the concentration of Al^{3+} increased from 0 mg/L to 400 mg/L, the MDA content in *C. occidentlis* increased gradually to 54.73% (more than control). The MDA content (9.62% and 21.41%) in *A. indica* and *P. nil* decreased more than control, however in *E. colonum* changed differently (7.63% declined under 80 mg/L treatment and 55.73% enhanced compared with control under 400 mg/L Al treatment). These results showed that Al at middle or low concentration was helpful to some plants, such as *A. indica* and *P. nil*, whereas adverse to some other plants, such as *C. occidentlis,* in resisting peroxidation.

3.5 Effect of Al on the MP of the four herbaceous plants in root

MP of *C. occidentlis* increased gradually with increasing Al^{3+} concentration from 0 to 400 mg/L, whereas it is increased dramatically under 2000 mg/L Al treatment ($P < 0.05$) (Fig. 3). MPs of *A. indica* and *P. nil* declined to a minimal value, but rose obviously under 2000 mg/L Al^{3+} treatment. MP of *E. colonum* decreased when the concentration rose from 0 to 80 mg/L Al^{3+}, and increased when the concentration rose from 80 to 400 mg/L $Al^{3+}$and increased distinctly under 2 000 mg/L Al^{3+} treatment. The MP in plant roots changed consistently with the MDA content in leaves.

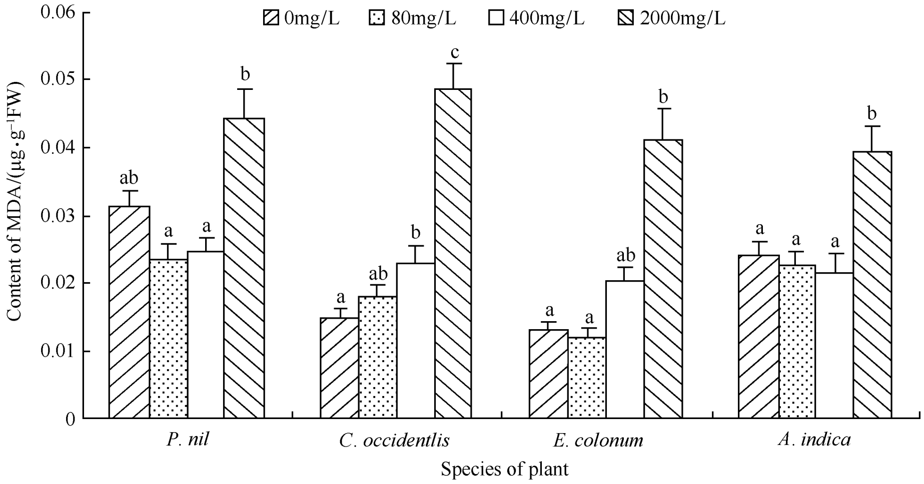


Fig. 2 Effect of Al on the contents of MDA of the four herbaceous plants in leaves

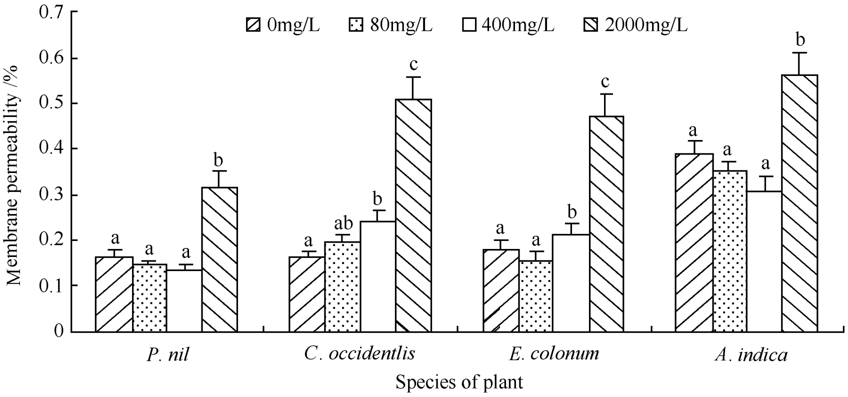


Fig. 3 Effect of Al on the MP of the four herbaceous plants in root

3.6 Effect of Al on the POD and CAT activities of the four herbaceous plants in leaves

The POD and CAT activities in *C. occidentlis* decreased gradually with increasing Al (Fig. 4). Under 2 000 mg/L Al^{3+} treatment, the POD and CAT activities in *C. occidentlis* decreased to 84.81% and 76.24% respectively (very significantly different from those under other treatments, $P < 0.01$). The POD and CAT activities in *A. indica* and *P. nil* leaves increased as Al^{3+} concentration rose from 0 to 400 mg/L, and significantly increased in *P. nil* ($P < 0.05$) compared with control. under 2 000 mg/L Al^{3+} treatment, the POD and CAT activities in both plants decreased significantly ($P < 0.01$, 47.73 % and 52.24%, and 13.4% and 42.22% for *A. indica* and *P. nil* respectively). The POD and CAT activities in *E. colonum* leaves rose slightly under 80 mg/L Al^{3+} treatment, and decreased dramatically under 400 mg/L Al^{3+} and 2 000mg/L Al^{3+} treatments (74.04% for POD and 55.87% for CAT). The decreasing of POD and CAT activities of *C. occidentlis* was the highest, *E. colonum* the second, *A. indica* the third, and *P. nil* the lowest.

3.7 Effect of Al on the soluble sugar of the four herbaceous plants in leaves

Figure 5 shows that SS content in *C. occidentlis* increased with increasing Al^{3+} concentration ($P < 0.05$). It was suggested that Al stress affected the synthesis of carbohydrate, and resulted in decreasing of SS content; at the same time it inhibited the transportation of carbohydrate away from leaves to other parts of the plant. Hence, higher SS content in leaves was observed. The SS content in *A. indica* and *P. nil* first decreased , and then increased. Al^{3+} concentration increased from 0 to 400 mg/L, and the SS content in leaves declined slightly. There was no significant difference ($P > 0.05$) of SS in *A. indica* and *P. nil* leaves between 400 mg/L and control, 400 mg/L $Al^{3+}$and 80 mg/L Al^{3+}. It was deduced that this Al^{3+}concentration was still not enough to inhibit carbohydrate transportation. However, it increased when Al concentration increased from 400 to 2 000 mg/L due to inhibition of carbohydrate transportation. Difference in SS content between 80 mg/L treatment and control was not obvious, and that under concentration of 400 mg/L and 2 000 mg/L increased (differences were not significant, $P > 0.05$).

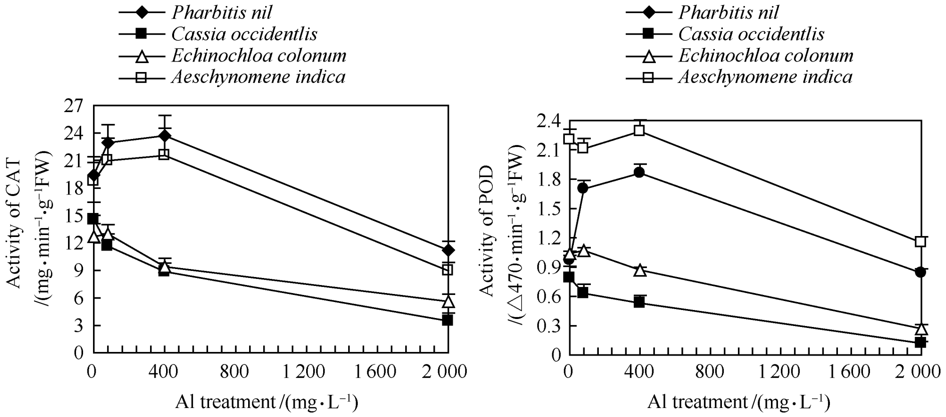


Fig. 4 Effect of Al on the POD and CAT activities of the four herbaceous plants in leaves

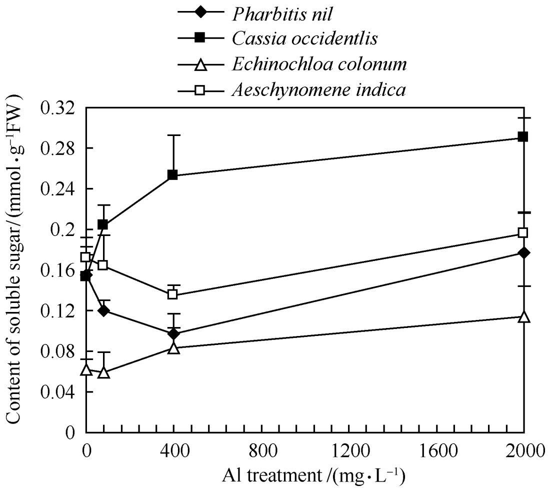


Fig. 5 Effect of Al on the soluble sugar of the four herbaceous plants in leaves

4 Discussion

Plants generate large amount of ROS and ions such as O_2^-, $H_2O_2^-$, OH^-, etc. under stress. ROS can initiate lipid peroxidation, damage cell membrane, increase exosmosis of electrolyte in plant cells and subsequently raise the conductance of all plant parts (Kochian and Jones, 1997). POD and CAT are antioxidant enzymes that are important in plant protective system. These antioxidant enzymes can scavenge reactive free radicals mentioned above effectively, avoid lipid peroxidation, balance the generation and elimination of reactive free radicals, and protect plants against damage under stresses (Kochian and Jones, 1999; Liu and Yang, 2000). At the same time, plants can accumulate a great deal of proline to decrease cell osmotic potential, keep pressure potential, retain and stabilize macromolecules, participate in chlorophyll synthesis, and maintain normal functions of cellular membrane (Liu and Yang, 2000). Besides, the SS content in plant organs can reflect carbohydrate synthesis and transportation in plants under stresses. From our results, the content of MDA and MP, and activities of POD and CAT in the four herbaceous plants changed differently under different Al treatments. This difference has a close correlation with plant tolerance to Al. All tested indices suggested that *P. nil* was the most tolerant plant among the four herbaceous plants. Its MDA and MP contents decreased distinctly, activities of POD and CAT ascend remarkably under 80 mg/L or 400 mg/L Al^{3+}. While under 2 000 mg/L Al^{3+} it exhibited the least increasing of MDA content, lipid peroxidation, decline of POD and CAT activity. *C. occidentlis* is the lest tolerant plant among the 4 herbaceous plants, it shows increasing content of MDA and MP, decreasing activities of POD and CAT under 80 mg/L or 400 mg/L Al^{3+}, and more significant variations other plants under 2 000 mg/L Al^{3+}. The tolerance to Al toxicity of *P. nil* is the highest, *A. indica* the second, *E. colonum* the third, *Cassia occidentlis* the lowest. Their physiological responses are consistent with the morphological responses and growth we observed (results to be published). On the other hand, though the tested 4 plants can grow well and distribute widely on acid red soil, reduced germination, increased MDA content and lipid peroxidation, declined chlorophyll content, activity of POD and CAT are all observed under high Al concentrations (2 000 mg/L Al^{3+} for example). Obviously, these changes go against plant growth and normal physiological activity. All species can not germinate when the Al concentration reachs 10 000 mg/L, which indicates that this Al^{3+} concentration has exceeded plant tolerance.

Many studies (Qin and Chen, 1999; Kidd and Proctor, 2000; Liu et al., 2003; Yan et al., 2003; Liu et al., 2004; Yang and Liu, 2005) indicate that minim of Al can accelerate plant growth, though Al is nonessential element to plants. For instance, in this study, the effects of 80 mg/L Al^{3+} on all physiological index of *A. indica* and *E. colonum* were propitious to their growth. Mechanisms involved have not been well-understood, while it is considered that Al at low concentration can probably maintain the stability of cellular membrane and reduce exosmosis of cellular electrolyte, thus avail plant growth (Liu et al., 2003, 2004). Al is toxic to plants only when the concentration exceeds a certain value, that is, influence of Al toxicity to plants has a critical value. Critical value varies with plants, such as 12 mg/L for *Saccharun sinensi*s (hydroponic cultured) (Chen et al., 2001), 40~90 mg/L for *Cassia Linnaeus* (hydroponic cultured) (Fang et al., 2003), 10 mg/L for *Cucurbita moschata* (hydroponic cultured) (Yu et al., 1994), 1 mg/L for *Pisum sativum* (hydroponic cultured) (Yan et al., 2003), 0.185 mmol/L for *Dimocarpus longan* (hydroponic cultured) (Xiao et al., 2002), 4.0 cmol/kg for *Triticum aestivum* and *Brassila campestris* var. *oleifera* (soil cultured) (Qin and Chin, 1999), 4.4 cmol/kg for *Arachis hypogaea* (soil cultured) (Qin and Chin, 1999), 4.8 cmol/kg for *Zea mays* (Qin and Chin, 1999). It has also been found that this critical value varies with growth phases (Li et al., 2000) and crop genotypes (Pan et al., 1998). Few studies have been done on toxic effects on the tested 4 plants by Al, and no report on the critical value was found. In our sand culture study, critical values for *P. nil* and *A. indica* are higher than that for other plants when Al is above 400 mg/L Al^{3+}. Critical value for *E. colonum* is between 80 and 400 mg/L Al^{3+}, while critical value for *C. occidentlis* is lower (below 80 mg/L Al^{3+}).

The 4 plants exhibite different physiological responses and tolerances to Al, but they show similar physiological accommodation to Al at low or middle concentration (80 mg/L and 400 mg/L Al^{3+}). Compared with control, responses of each physiological index are more beneficial to plant development, which indicates that keeping higher activity of POD and CAT, content of proline and chlorophyll and lower content of MP and MDA is an important physiological basis of plant adaptation to Al stress. Taking the least tolerant plant *C. occidentlis* for example, under 80 mg/L and 400 mg/L Al^{3+}, content of proline and chlorophyll increase, and seed germination reduces to an extent which is not very large. Although content of MP and MDA increase and activity of POD and CAT decrease under 80 mg/L and 400 mg/L Al^{3+} compared with control, MDA content under 80 mg/L, 400 mg/L and 2000 mg/L Al^{3+} are 21.62%, 54.73% and 228.38% above control respectively, for MP 19.75%, 50.62% and 215.4% above control respectively, for POD 20.25%, 32.91% and 84.81% below control, for POD 20.06%, 39.08% and 76.24% below control. The changes under low or middle concentration Al^{3+} are much smaller than that under 2000 mg/L Al^{3+}. At present, two major mechanisms on plant tolerance to Al are proposed (Kong et al., 2000; Barceló and Poschenrieder, 2002; Ermolayev et al., 2003; Dehorah and Tesfaye, 2003). One is exterior mechanism (namely excluding Al by plants), supposing that plant endure Al toxicity mainly by preventing Al ions from entering plant system or arriving at sensitive metabolic parts of plant cell. The other is interior mechanism (namely plant interior tolerance), considering plants obtaining resistance to Al through detoxifcation or physiological reaction after Al ions entering plant cell. Plant tolerance to Al is a dominant polygene trait, that is, it is controlled by one or more major genes and several polygenes. Hence, both exterior and interior mechanisms probably involved in tolerance of most plants (Rout et al., 2001; Ermolayev et al., 2003). Antioxidant enzymes and other antioxidant substances are generated by cellular membrane and cell played an important role in either exterior mechanism or interior mechanism (Oteiza, 1994; Kochian and Jones, 1997; Devi et al., 2003). Acclimation of plant to Al may occur in both physiological level and molecule level, and physiological response is the basis of acclimation in molecule level. The physiological acclimation of 4 herbaceous plants to Al at low or middle concentration (such as keeping higher activity of POD and CAT, content of proline and chlorophyll and lower content of MP and MDA) provides foundations for their tolerance to Al. Their physiological responses also help to reveal the mechanisms of plant adaptation and tolerance to Al stress.

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