Effects of cobalt and DFMA on polyamine content and membrane-lipid peroxidation in wheat seedling under osmotic stresses

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Abstract: The objective of this study was to elucidate whether spermidine and ethylene suffered substrate competition and how polyamines and ethylene influenced lipid peroxidation in wheat seedling leaves under the root osmotic stresses. The osmotic stresses simulated with -1.0 MPa polyethylene glucose (PEG) solution was applied to wheat seedling roots for 6 h, 12 h, 18 h and 24 h respectively. The results showed that the putrescine and spermidine contents and the ethylene evolution in wheat seedlings were increased significantly when the osmotic stresses lasted 6 h. As the osmotic stresses prolonged, however, the putrescine and spermidine contents were declined and the ethylene evolution increased gradually. When DL-α-Difluoromethylarginine (DFMA) was added to the PEG solution with its concentration reaching 0.5 mmol/L, the putrescine and spermidine contents of the leaves under the stresses decreased significantly, but the ethylene evolution of the leaves was not affected markedly. The above results showed that there was probably no evident substrate competition between spermidine and ethylene when wheat seedlings were under root osmotic stress simulated with -1.0 MPa PEG solution. The results also showed that the ethylene evolution got inhibited and the polyamines content got improved relatively, when $CoCl_2$ was added to the PEG solution with its concentration at 2 mmol/L. The addition of $CoCl_2$ also improved the activities of anti-oxidative enzymes, and reduced the reactive oxygen levels and MDA contents significantly when the stresses got aggravated, so $CoCl_2$ protected the cell membrane in some way. The above results indicatd that lipid peroxidation probably had a close relation with the variation in polyamines content, and $CoCl_2$ could prevent the seedling membrane damage under the osmotic stresses.

Keywords: cobalt; ethylene; membrane-lipid peroxidation; osmotic stress; polyamines; wheat seedling

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Drought is the most important environmental factor that depresses global agriculture, and more than half of the land is in the arid and semi-arid zones in China. In these zones the crops suffer from drought every year. Even in the non-arid zones, the crops may suffer from periodical or accidental drought. Therefore, researches on plant stress physiology have been carried out worldwide in these years. In order to reduce damages from drought stress, agricultural production has acclimate or harden crop seedlings by applying some chemical substances, such as ABA and rare-earth elements to the seedlings. Among these substances, Co^{2+} has rarely been used although it is capable of inhibiting ethylene evolution[1]. As a by-product in lipid peroxidation, ethylene promotes senescence and maturing in some ways, and thus Co^{2+} may play a role in lipid peroxidation under osmotic stress.

Leeuwenhook observed a kind of crystalline substance in human semen in the early 20th century, the substance was proved to be a kind of salt from spermine in 1924. Nowadays, putrescine, spermidine and spermine have been detected in more and more living organisms. Since 1960s, the effects of polyamines on plant growth and development have attracted much attention[2,3] and is speculated to be similar to that of cAMP, so that the function of polyamines may have a close connection with nucleic acid thereby influencing nucleic acid metabolism and proteins synthesis[4,5]. Other researches have proved that polyamines inhibit proteinase activity and biological effects of ethylene, and stabilize biological membrane[6]. Therefore, polyamines are regarded as a group of important bio-active substances.

Polyamines have a close relation with ethylene metabolism under osmotic stress[7,8]. According to Icekson, ethylene retarded polyamines synthesis and reduced polyamines content in pea seedlings[9], but improved polyamines synthesis in rice seedlings[10]. Under some

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other circumstances polyamines were capable of inhibiting ethylene biosynthesis[7,8,11]. So it was suggested that the correlation between polyamines and ethylene metabolism should vary greatly with plant species and status, However, the mechanism remains unclear, thus more researches need to be carried out to probe the metabolism, and in particular whether there exists a substrate competition between polyamines and ethylene. As Co^{2+} inhibits ethylene evolution[1] and DFMA inhibits arginine decarboxylase activity thus reducing putrescine synthesis[12], this study employed Co^{2+} and DFMA to inhibit ethylene evolution and polyamines synthesis respectively. In addition, because polyamines and ethylene both have a close relation with membrane system, the study aimed to investigate the relationship among polyamines content, ethylene evolution and lipid peroxidation in wheat seedling leaves while the roots suffered different osmotic stresses.

1 Materials and methods

1.1 Plant materials

Fengchan 3, a drought-resistant wheat variety (*Triticum aestivum* L. cv.), was chosen as its material. The seedlings were osmotic stressed treatments according to Wang's method[13]. The seeds were washed with tap water and then soaked in water for 24 h at room temperature. Then the seeds were took out from water and placed in a growth chamber to germinate for 24 h at 25 ± 2℃, and then the seeds were planted in vermiculite contained in pans, which were placed in growth chamber, the temperature, photoperiod and light intensity were set at 25 ± 1.5℃, 14-hours illumination and 100 μmol/(m^2·s). The seedlings were supplemented with water every day until they grew two genuine leaves. Then the seedlings were taken out from the pans, their seed capsules were removed and their roots were washed clean with tap water. and then the seedlings suffering no injuries were chosen and placed under the treatments described below.

1.2 Treatments

There were four treatments in this study: ① Distilled water as control, ② −1.0 MPa PEG 4000, ③ −1.0 MPa PEG 4000 solution plus 0.5 mmol/L DFMA, ④ −1.0 MPa PEG 4000 solution plus 2 mmol/L $CoCl_2$. 30 mL of each above solutions were added into different 50 mL beakers. The bases of the seedlings were wrapped with sponge pieces whose sizes were 25 cm long, 2 cm wide and 0.5 cm thick. The water potential of the solutions was measured with a freezing point osmometer (model FM − 4). The beakers were wrapped with black paper, then the seedlings were placed in growth chamber in which 100 μmol/(m^2·s) light was kept all day long and the temperature was 25 ± 1.5℃.

After 6 h, 12 h, 18 h and 24 h of the stresses described above, the first genuine leaves of the seedlings were used for all of the measurements described below.

1.3 Measurements

1.3.1 Water potential The leaf water potentials were measured with a pressure chamber (Plant Water Condition Equipment(ZLZ − 4, Lanzhou University, China)).

1.3.2 Polyamines content The extraction and HPLC analysis of polyamines were conducted according to the method of Flores and Galston[14]. Cold 5% $HClO_4$(E. Merck, Darmstadt, Germany) was added to the leaves of the seedlings in a chilled mortar at the ratio of 100 mg fresh weight/mL $HClO_4$, and then the leaves were ground with a pestle. The obtained homogenate was kept in an ice bath for 60 min, oscillated and centrifuged at 27 700-g and 4℃ for 20 min. And then the precipitate was dissolved in $HClO_4$, kept in ice bath for 5 min, oscillated and centrifuged. The first and second supernatants in the first and second centrifugings were collected and stored at −20℃ for free polyamine determination[14]. The stored supernatants and authentic standards of putrescine and spermidine(Sigma Co., St. Louis) were benzoylated following the procedure described by Flores and Galston[14]. The polyamines concentrations were measured by the programmable liquid chromatography (Model 322, Altex-Beckman Inc., Japan). The solvent consisted of methanol and water (65% methanol) and its flow rate was 1 mL/min. The benzoylated extracts were eluted through a reverse-phase column (Zorbax-ODS, 4.6 mm × 150 mm, 5 um particle size) at 254 nm with a UV detector at room temperature. The temperature of the column was 25℃ and the results were quantified with C − R 25 integrator.

1.3.3 Ethylene evolution The ethylene evolution was analyzed according to the method of Narayana et al[15]. The gas-chromatography (Model GC-9A, Altex-Beckman Inc., Japan) was adopted with a column (Paropark) at a column temperature of 90℃. The flow-gas was N_2. The

leaf samples were 1.5 cm - long. The leaf pieces cut from the first leaves of the seedlings were placed into penicillin bottles with rubber caps and kept in them for 12 hours, and then the airs in the bottles were extracted for ethylene concentration measurement. The results were quantified with C - R 25 integrator.

1.3.4 **SOD activity** The activities of superoxide dismutase (SOD) were measured according Rabinowitch et al' method[16].

1.3.5 **MDA content** MDA contents were measured according the method developed by Shimazaki et al[17].

1.3.6 **Relative cell membrane permeability** The relative cell membrane permeability were defined as the quotient: The conductivity of the solution(purified water immerged the tissue for 30 min) divided by the conductivity of the above solution after 15 min boiling and 30 min cooling[18].

1.4 Data analysis

There were three replicates and each replicate was repeated at least three times. The data were presented in the form of means "+" or "-" standard error (S.E.). The data were statistically analysed by the one-way ANOVA of SPSS for windows 10, taking $P < 0.05$ as significant.

2 Results and analysis

2.1 Influences of Co^{2+} and DFMA on the water potentials in wheat seedling under the osmotic stresses

When the wheat seedlings suffered the root osmotic stresses simulated with -1.0 MPa polyethylene glucose (PEG) solution, their leaves' water potentials decreased gradually as the osmotic stresses prolonged. Where DL-α-Difluoromethylarginine (DFMA), an irreversible enzyme inhibitor, was added to the PEG solution, with its final concentration reaching 0.5 mmol/L, the leaves' water potentials of wheat seedlings did not vary much. Where $CoCl_2$ was added to the PEG solution with its final concentration reaching 2 mmol/L, the leaves' water potentials became a little higher(lower in absolute value) than that under the osmotic stress simulated with -1.0 MPa PEG solution(Fig.1). These results showed that both 0.5 mmol/L of DFMA and 2 mmol/L of $CoCl_2$ did not have much influences on the leaves' water potentials under the osmotic stress.

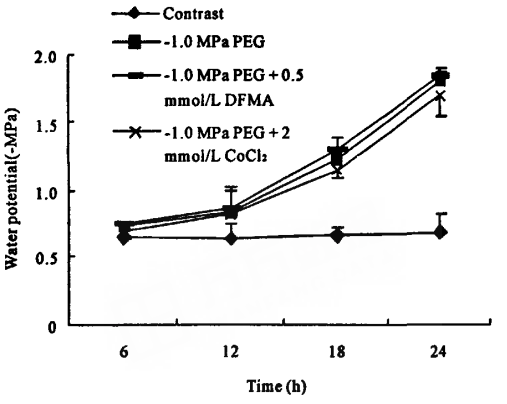

Fig.1 Influence of $CoCl_2$ and DFMA on water potential in wheat seedlings' during -1.0 MPa PEG root osmotic stress

2.2 Influences of Co^{2+} and DFMA on putrescine and spermidine contents and ethylene evolution in wheat seedling under the osmotic stresses

When the osmotic stresses simulated with -1.0 MPa PEG solution lasted 6 h, the putrescine(Put) and spermidine(Spd) content increased considerably in the wheat seedling. As the osmotic stress prolonged, the contents of Put and Spd reduced gradually and finally became lower than that in the control. When DFMA was added to the PEG solution with its concentration finally reaching 0.5 mmol/L, the leaves' putrescine and spermidine contents became lower than those with the PEG solution. When $CoCl_2$ was added into the PEG solution with its concentration finally reaching 2 mmol/L, the leaves' putrescine and spermidine contents obviously increased under the osmotic stresses(Fig.2 A - B). These results showed that as the root osmotic stress prolonged, DFMA reduced the leaves' putrescine and spermidine contents and $CoCl_2$ increased them.

Under the root osmotic stress simulated with -1.0 MPa PEG solution, ethylene evolution in the wheat seedlings was increased steadily, especially after the stress prolonged. When DFMA was added to the -1.0 MPa PEG solution with its final concentration reaching 0.5 mmol/L, the leaves' ethylene evolution was not much affected. When $CoCl_2$ was added to the -1.0 MPa PEG solution, the leaves' ethylene evolution did not get enhanced during the whole period of the osmotic stress(Fig. 2 C).

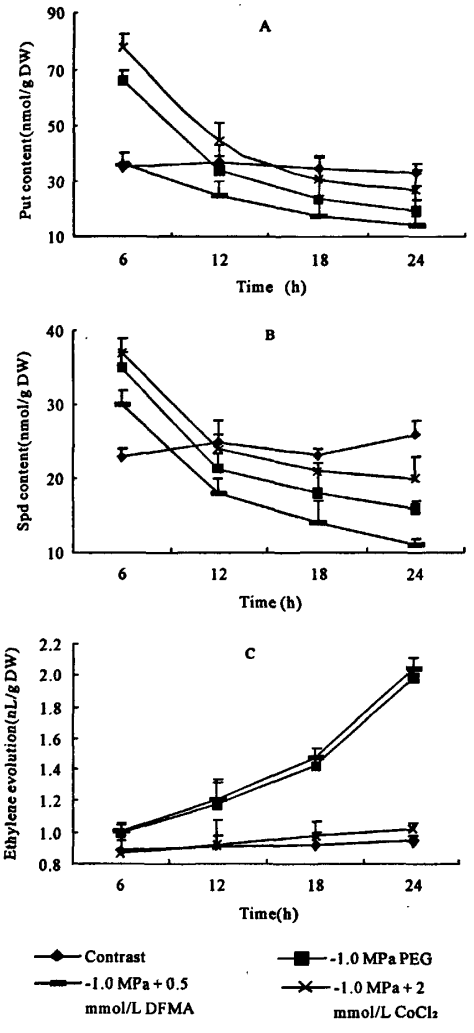

Fig.2 The influence of $CoCl_2$ and DFMA on the content of purscine and spermidine and the evolution of ethylene in wheat seedlings during root osmotic stress of −1.0 MPa PEG solution

2.3 Influences of Co^{2+} and DFMA on the activities of the anti-oxidative enzymes in wheat seedling under the osmotic stresses

Under the root osmotic stress simulated with −1.0 MPa PEG solution, the activity of SOD and CAT in wheat seedling were varied significantly. When the osmotic stress lasted 6 h, the activities of SOD and CAT were much higher than those in the control. As the osmotic stress prolonged, the activities of the two anti-oxidative enzymes decreased gradually and at last became lower than those in the control. When DFMA was added to the −1.0 MPa PEG solution, the SOD and CAT activities decreased markedly. When $CoCl_2$ was added, the SOD and CAT activities relatively got enhanced under the whole osmotic stress period(Fig.3 A,B).

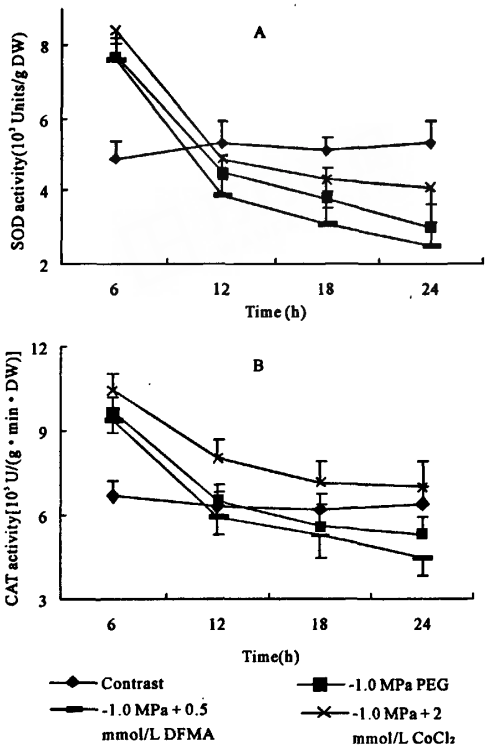

Fig.3 The influence of $CoCl_2$ and DFMA on the activity of anti-oxidative enzymes in wheat seedlings during root osmotic stress of −1.0 MPa PEG solution

2.4 Influences of Co^{2+} and DFMA on the the production rate of H_2O_2 and O_2^- in wheat seedling under the osmotic stress

The production rate of H_2O_2 and O_2^- did not vary much when the osmotic stress lasted 6 h and 12 h, but then increased significantly as the stress prolonged. The additions of DFMA and $CoCl_2$ didn't have much influence on the production rates of H_2O_2 and O_2^- when the stress lasted 6 h and 12 h, but when the stress lasted 24 h, DFMA improved and $CoCl_2$ reduced the prodution rate of H_2O_2 and O_2^- significantly(Fig.4 A,B).

2.5 Influences of Co^{2+} and DFMA on MDA contents and relative cell membrane permeability in wheat seedling under osmotic stress

MDA is a substance produced in lipid peroxidation and metabolism in plant cells. In the early period of the root osmotic stress(6 h and 12 h), the MDA content of the leaves was not much higher than that of the control,

and the addition of DFMA and $CoCl_2$ had not much influence on the content. However, the MDA content of the leaves increased significantly when the stress lasted 24 h. Meanwhile, the MDA contents of the leaves got increased by the addition of DFMA and decreased by the addition of $CoCl_2$ obviously(Fig.5 A).

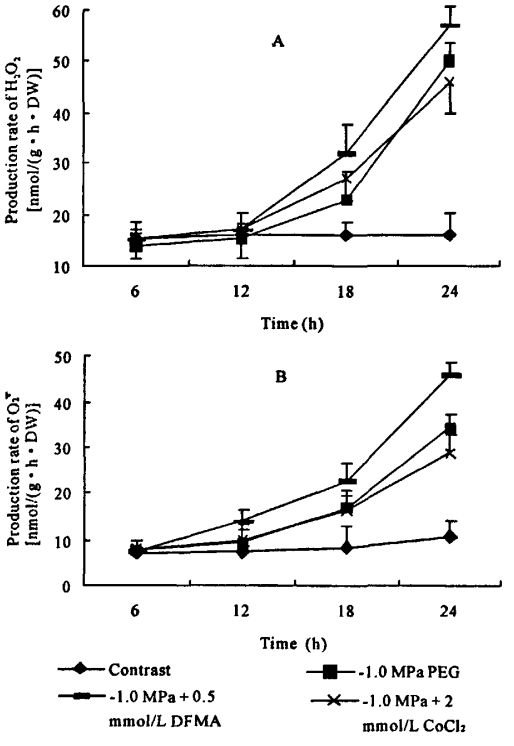

Fig.4 The influence of $CoCl_2$ and DFMA on the production rate of H_2O_2 and O_2^- in wheat seedlings during root osmotic stress of -1.0 MPa PEG solution

The relative cell membrane permeability (CMP) of wheat leaves did not increase much during the first 12 h of root osmotic stress simulated with -1.0 MPa PEG solution and then increased significantly. The CMP increased markedly when DFMA was added into the -1.0 MPa PEG solution, and reduced significantly when $CoCl_2$ was added into the -1.0 MPa PEG solution. These results probably showed that the cell membrane got damaged by DFMA and protected by $CoCl_2$ especially when the osmotic stress lasted 24 h(Fig.5 B).

3 Discussion

The contents in plant of polyamines varied depending on different stresses and plant species. It was reported that the putrescine and spermidine contents of oat leaf segments were highest when the segments were placed to float in sorbitol solution for 4 h and then decreased gradually[19]. Our results showed that under the root osmotic stress simulated with -1.0 MPa PEG solution, the putrescine and spermidine contents of wheat leaves varied greatly. The putrescine and spermidine contents increased significantly when the osmotic stress lasted 6 h, then decreased gradually and even became lower than that of the control leaves as the osmotic stress prolonged (Fig.2 A, B). Under this situation, the ethylene evolution increased gradually (Fig.2 C). The results showed that polyamines and ethylene were not remarkably correlated under the osmotic stress. When DFMA was added to the PEG solution, the putrescine and spermidine contents decreased evidently (Fig.2 A, B), and the, ethylene evolution did not vary much (Fig.2 C). It was concluded from the two results that the substrate competition between spermidine and ethylene synthesis was not the main factor that affected their synthesis under root osmotic stress, although both spermidine and ethylene used the same substrate S-adenosylmethionine[20].

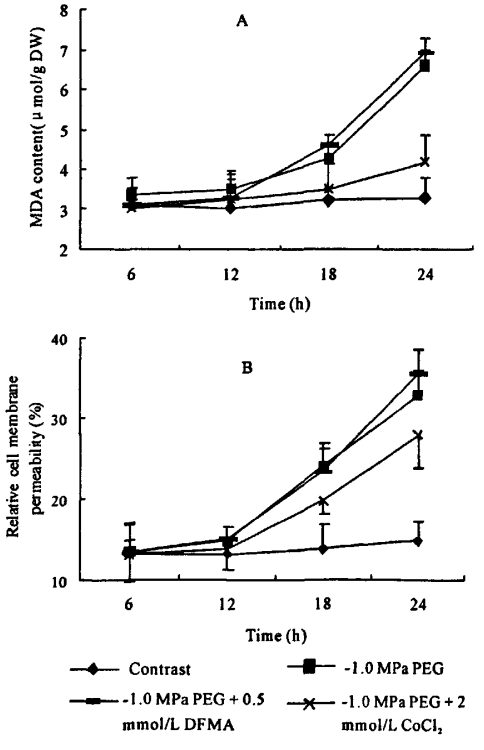

Fig.5 Influence of Co^{2+} and DFMA content and relative cell membrane permeability in wheat seedling during root osmotic stress of -1.0 MPa PEG solution

While being stressed under a severely adverse environment, the plant reduces its capablity for eliminating free radicals, thus finally results in membrane damage[7,16]. Our results also indicated that as the osmotic stresses aggravated, the leaf lipid peroxidation increased gradually (Fig.3 A, B) and the results were in accordance with the variation in SOD and CAT activity under the stress(Fig.4 A, B). When $CoCl_2$ was added into the PEG solution, the reactive oxygen species(Fig.4 A, B), MDA contents(Fig.5 A) were evidently reduced when the stress got aggravated after 24 h stress(Fig.1), and the CMP improvement was alleviated markedly(Fig.5 B). When DFMA was added into the PEG solution, the results were quite opposite (Fig.4 A, B, Fig.5 A, B). These results were in accordance with the variation in leaves' putrescine and spermidine contents(Fig.2 A, B). These results indicated that the polyamines contents were closely correlated with lipid peroxidation under the osmotic stress, and Co^{2+} could alleviate lipid peroxidation and consequently protected the cell membrane. Based on the results mentioned above, the final conclusions are as follows:

1) Under the root osmotic stress simulated with -1.0 MPa PEG solution, the spermidine and ethylene synthesis of wheat seedling showed no obvious substrate competition, or the substrate competition was not the main factor that inhibited their synthesis.

2) Under the root osmotic stress simulated with -1.0 MPa PEG solution, Co^{2+} was capable of inhibiting the ethylene evolution of wheat leaves, increasing polyamines contents and relatively inhibiting lipid peroxidation. Therefore, Co^{2+} could probably be used in dryland crop farming, although its side-effects and physiological roles on other plants needs further research.

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Effect of different water and potassium levels on root and stem hydraulic conductivity of tobacco (*Nicotiana tabacum* L.)

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Abstract: Under different water (50 mL/2d and 20 mL/2d) and potassium levels (2.4 mmol/L,5.4 mmol/L,9.9 mmol/L), Yun 89 tobacco (*Nicotiana tabacum* L.) was selected as an experimental material. The experiment was carried out in greenhouse to evaluate the total absorption area, active absorption area, active area and dry weight of tobacco root system, plant height, stem diameter, hydraulic conductivity of root and stem of tobacco. The results showed that the role of water was more important than potassium for tobacco plant height, stem diameter, root active absorption area and hydraulic conductivity at later growth stages. Under normal water supply, potassium fertilizer can enhance root and stem hydraulic conductivity of tobacco. But there were not remarkable differences on dry weight and total absorption area of tobacco root system between these ways.

Keywords: tobacco (*Nicotiana tabacum* L.); water stress; potassium level; hydraulic conductivity

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渗透胁迫下钴和 DFMA 对小麦幼苗多胺含量及膜脂过氧化的影响

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摘要: 探讨了渗透胁迫下小麦幼苗乙烯与多胺之间是否存在底物竞争以及 $CoCl_2$ 和 DFMA 对膜脂过氧化的影响。研究结果表明,-1.0 MPa 聚乙二醇(PEG)溶液对小麦幼苗根系渗透胁迫 6 h 时,叶片腐胺、亚精胺含量及乙烯释放量均显著提高,之后随胁迫时间延长,腐胺、亚精胺含量逐渐下降,乙烯释放量逐渐增加;当 -1.0 MPa PEG 溶液中加入 DFMA 0.5 mmol/L,在渗透胁迫过程中,相比于未加 DFMA 的处理,叶片腐胺和亚精胺含量均显著下降,而乙烯释放量没有显著变化;说明在 -1.0 MPa PEG 溶液根系渗透胁迫过程中,叶片内乙烯与亚精胺之间并不存在显著的底物竞争关系。当 -1.0 MPa PEG 溶液中加入 $CoCl_2$ 2 mmol/L,乙烯释放量的增加被抑制,且腐胺、亚精胺含量显著提高;在 PEG 溶液中加入 $CoCl_2$ 还提高了叶片抗氧化酶的活力,并在胁迫至 24 h 时,显著降低了活性氧水平以及 MDA 含量,进而对细胞膜表现出保护作用。然而,在 PEG 溶液中加入 DFMA,上述指标表现为相反的变化趋势。说明当渗透胁迫加深时,$CoCl_2$ 提高多胺含量及抑制乙烯产生可以相对降低脂质过氧化程度,且能够减轻细胞膜在深度渗透胁迫下所受伤害。

关键词: 钴;渗透胁迫;小麦幼苗;多胺;乙烯;脂质过氧化