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Induction of tolerance by chlorocholine chloride in *Sequoia sempervirens* seedlings under natural cooling and drought

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Abstract: Two-years-old *Sequoia sempervirens* seedlings were foliar sprayed once and twice with chlorocholine chloride (CCC) at 0, 100, 500, 1 000, 1 500 and 2 000 mg·l^{-1}. The purpose was to investigate the effect of CCC on the growth and photosynthetic activity of *S. sempervirens* seedlings under natural cooling and drought in autumn and winter. The findings showed that the increments of plant height and crown diameter were significantly decreased with the increase of chlorocholine chloride concentration, and the increment of root collar diameter, net photosynthetic rate, actual photochemical quantum yield and photosynthetic electron transport rate showed the trend of increasing first and then decreasing, and reached the maximum at concentrations of 1 000~2 000 mg·l^{-1}. There was not a significant difference between two applications and single application. It suggests that 1 000~2 000 mg·l^{-1} chlorocholine chloride can protect the photosynthetic activity of *S. sempervirens* seedlings and alleviate the stress induced by low temperatures and drought in autumn and winter.

Keywords: plant growth regulators; coast redwood; growth indicators; physiological condition; environment stress

Chlorocholine chloride (2-chloroethyltrimethylammonium chloride, CCC), as a plant growth inhibitor, is widely researched and used in plant production (Wang et al. 2010; Wu et al. 2014; Karimi et al. 2014). Earlier studies have shown that CCC application can dwarf plant growth and inhibit branch extension, but it increases photosynthetic capacity and yield of plant (Wang et al. 2009; Xu et al. 2011; Li et al. 2015). Some previous studies have suggested that CCC can increase plant resistance to salt damage (Liu et al. 2013), UV-B radiation (Kreslavskii et al. 2011), lodging (Zhang et al. 2015a) and leaf spot disease (Kundu et al. 2014). In the practice of agriculture and forestry, a suitable application method of CCC is usually selected based on the criteria of minimum restriction of plant growth, minimum physiological and metabolic damage and significant improvement of plant resistance (Liu et al. 2013; Zhang et al. 2015a).

Coast redwood (*Sequoia sempervirens* Endl.) belongs to relic plants, Taxodiaceae (Zuo et al. 2000; Ma et al. 2005; Zhang et al. 2015b), as one of the world's five major landscaping tree species and large calibre fast-growing timber species (Olson et al. 1990; Zuo et al. 2000, 2003; Ju et al. 2007; Cown et al. 2013); its successful introduction can beau-

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tify the environment, enrich biodiversity, improve the local forestry structure, and bring good ecological, social and economic benefits. Now, it has been introduced and cultivated in more than 30 countries, and it has also been successively introduced to many provinces in southern China after 1972 (Zuo et al. 2000, 2003; Liu et al. 2006). Coast redwood was introduced to Xuzhou in 2003 (Zuo et al. 2000; Ju et al. 2009). During the Tertiary Period various genera of coast redwoods occurred throughout the northern hemisphere. Coast redwood was eliminated from its former area of distribution by the increasingly drier and cooler climates of the mid and late Tertiary Period. Temperature and precipitation are the main factors affecting the survival and distribution of coast redwood (Simmons, Thomas 1975; Ma et al. 2005; Zhang et al. 2015b). On average, the mean annual temperature (MAT) for the *Sequoia* region varies from 13.8 °C to 11.3 °C, the temperature rarely drops below –9 °C or rises above 38 °C and the mean minimum temperature of the coldest month is about 6 °C. Annual precipitation varies between 640 and 3 100 mm and mostly winter rains occur in the *Sequoia* forest region. It is suggested that the coast redwood was living in a warm and humid subtropical climate (Ma et al. 2000; Zhang et al. 2015b). Xuzhou is located in central and eastern China, it belongs to the sub-humid warm temperate continental monsoon climate, four distinct seasons, with hot and rainy summer, low temperature and drought in winter. According to the above analysis, the low temperature and drought in autumn and winter are the main stress factors for successful introduction of coast redwood to Xuzhou. For years, studies on adaptability of coast redwood in Xuzhou have shown that low temperature and drought in autumn and winter could make the twigs of coast redwood become withered (Ju et al. 2009), which has limited the cultivation and promotion of coast redwood in central and eastern China. So, improving the resistance of coast redwood has become a practical problem that needs to be solved urgently for further application and dissemination.

We could consider the application of a plant growth inhibitor to coast redwoods to limit the second growth peak in autumn, increase lignification of branches, and improve the resistance to low temperature and drought, so that they could safely survive in winter in Xuzhou. In the present study, the purpose was to test the possibility that CCC application would protect coast redwood seedlings from damaging effects of natural cooling and drought in autumn and winter.

MATERIAL AND METHODS

Site description. The experimental field is located at a nursery base, Xuzhou Institute of Technology, in the eastern suburb of Xuzhou, Jiangsu province (34°15'N, 117°11'W), China, belonging to the warm temperate semi-humid monsoon climate, with strong spring winds, warm humid summer and dry cold winter. The sunshine duration is 2 284 to 2 495 hours, while the sunshine rate is 52 to 57%, the annual temperature is 14.58 °C, the average lowest temperature is –10.52 °C, the average extreme minimum temperature is –37.43 °C, the annual accumulated temperature is 5 143.5 °C, the average annual frost-free period is about 210 days, the average annual rainfall is 853.1 mm. The highest average temperature in November is 14 °C and the lowest average temperature is 4 °C (Figure 1). The maximum temperature for the test day is 12 °C and the minimum temperature is 4 °C.

Plant culture and CCC treatments. The experiments were carried out during September to November 2014. Uniform 2-years-old seedlings of coast redwood were used as experimental material. The experiment consisted of 12 treatments: (1) Single application of CCC (0, 100, 500, 1 000, 1 500, 2 000 mg·l^{-1}) on September 01, 2014 (2014-9-01); (2) Two applications of CCC (0, 100, 500, 1 000, 1 500, 2 000 mg·l^{-1}) on September 01 and September 08, 2014 (2014-9-01; 2014-9-08). Six CCC solutions were prepared by dissolving the appropriate quantities of 50% CCC water solution in tap water. Spraying with pure water served as a control. Different concentrations of CCC solutions were sprayed onto plants until drops began to fall from the foliage. The experiment was arranged in a complete randomized design with five replicates for each treatment and each treatment had five seedlings.

Measurements of growth indices. Growth indices, including plant height, crown diameter and root collar diameter, were measured before CCC application and after the CCC treatment for 70 days, computational Equations (1–3):

Increment of plant height:

$$IPH \text{ (cm)} = H_2 - H_1 \tag{1}$$

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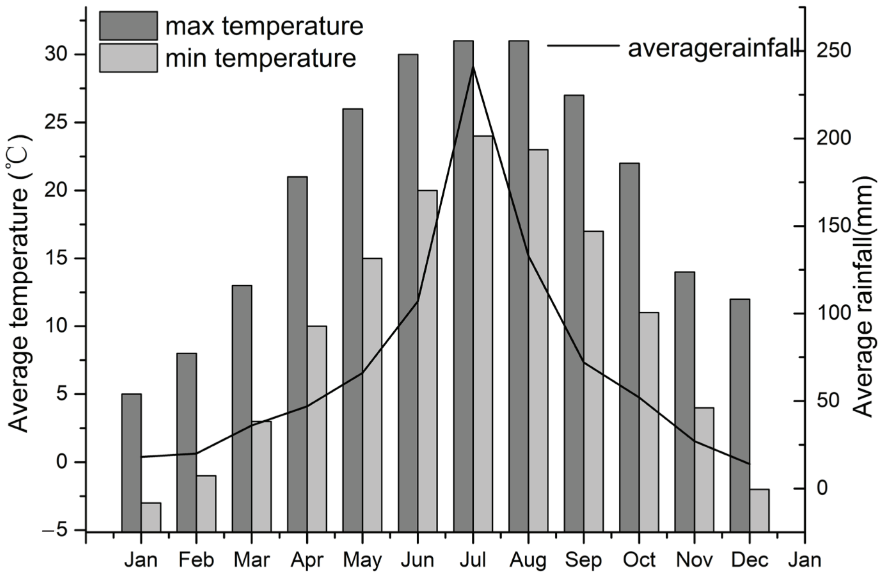

Figure 1. Agricultural meteorological indicators: average maximum and minimum temperature (°C), average rainfall (mm) of the month in Xuzhou area, China (2010 to 2018 years)

Increment of crown diameter:

$$ICD\ (\text{cm}) = C_2 - C_1 \quad (2)$$

Increment of root collar diameter:

$$IRCD\ (\text{mm}) = D_2 - D_1 \quad (3)$$

H_1, C_1 and D_1 represent the plant height, crown diameter and root collar diameter of coast redwood seedlings determined on September 01, 2014, respectively. H_2, C_2 and D_2 represent the plant height, crown diameter and root collar diameter of the corresponding plants determined on November 09, 2014, respectively.

The crown diameter (the mean of the minimum and maximum canopy diameters) and plant height (the distance between the base of the stem and the top of the canopy) were measured with a measuring tape. The root collar diameter (the diameter of the base of the plant measured in cm at 5 cm above the ground) was measured with a calliper to the nearest 1 mm.

Measurements of photosynthetic parameters. The measurement of the net photosynthetic rate (P_n) was performed between 14:00 p.m. and 15:00 p.m. on November 09, 2014, using a portable photosynthetic system (LI-6400, LI-Cor 6400, USA). Measurements were done on the third fully expanded leaf counting from the top of each plant at 20 ± 2 °C, 380 ± 15 μmol·mol^{-1} atmospheric CO_2 concentration and 600 μmol·m^{-2}·s^{-1} saturating light at photosynthetically active photon flux density (PPFD) (Januskaitiene 2011; Zhao et al. 2015). Measurements for each leaf were taken three times and averaged, one leaf per seedling and five seedlings randomly selected per treatment.

Measurements of chlorophyll fluorescence parameters. The third fully expanded leaf counted from the top of each seedling was selected to test the chlorophyll fluorescence parameters, the actual photochemical quantum yield (*Yield*) (Genty et al. 1989) and photosynthetic electron transport rate (*ETR*) (Genty et al. 1989; Schreiber 2004) using a chlorophyll spectrometer (MINI-PAM, Walz, Germany), from 14:00 p.m. to 15:00 p.m. on November 09, 2014. During the measurements, the photosynthetically active radiation and temperature in a leaf chamber were set to 1 000 μmol·m^{-2}·s^{-1} and 10 °C, respectively. Three measurements per leaf were recorded and averaged, one leaf per seedling and five randomly selected seedlings per treatment.

Statistical analysis. The means ± standard deviation were calculated using SPSS 19 software (IBM, Armonk, New York, USA). The least significant difference (LSD) between the different treatments was analyzed by the one-way analysis of variance (ANOVA) and the interactions between spraying times and concentrations of CCC were analyzed by the two-way ANOVA using SPSS 19 software. Correlations between the measured indicators were analyzed using Origin 8.0 software (OriginLab, Northampton, USA). Student's t-test was applied to determine the significance of the differences between the individual treatments (P < 0.05 or 0.01).

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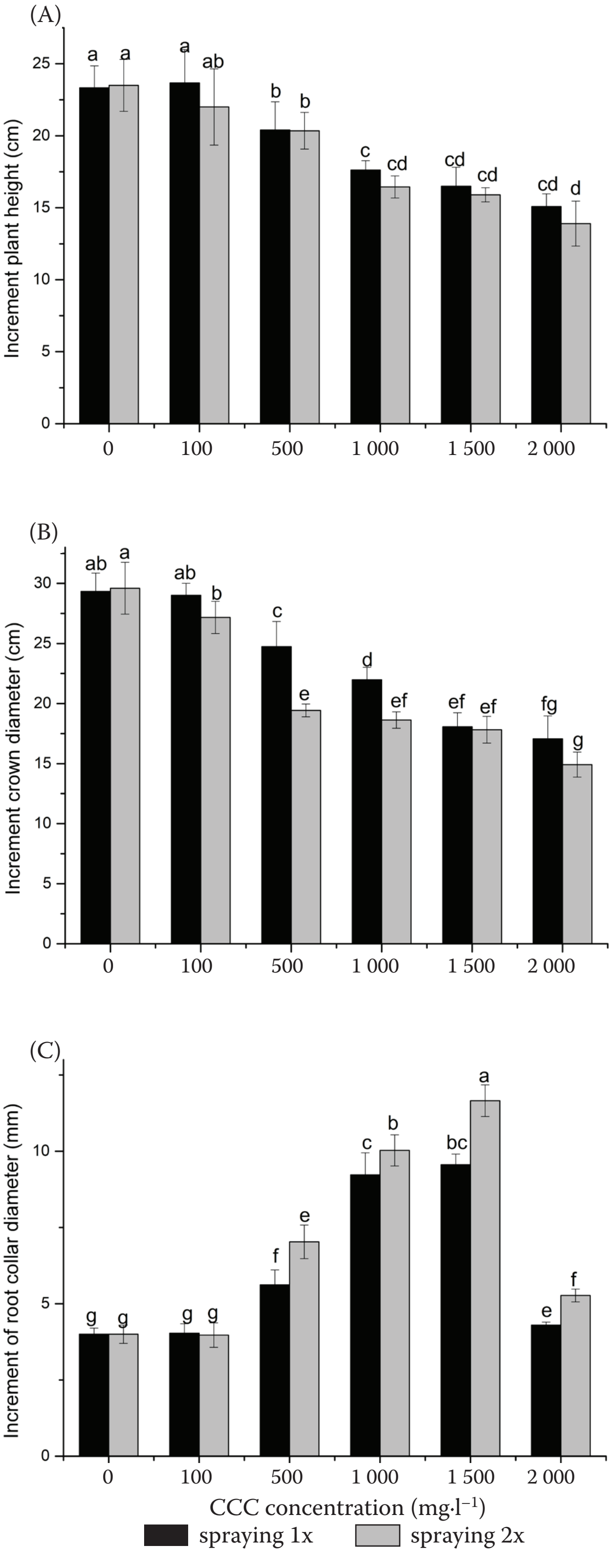

Figure 2. Effects of chlorocholine chloride (CCC) on the increment of plant height (A), increment of crown diameter (B), increment of root collar diameter (C) in *S. sempervirens* seedlings under natural cooling and drought; significant differences at $P < 0.05$ are shown by different letters; $n = 5$

RESULTS

Effects of CCC on the growth of coast redwood seedlings in autumn and winter

Figure 2 shows the CCC concentrations increased from 500 to 2 000 mg·l^{-1}, when increments of plant height and crown diameter were significantly lower than those of the control, decreasing gradually with the increase of the concentration, but the reduction was not significant in the range of 1 500 to 2 000 mg·l^{-1}. However, the increment of root collar diameter increased obviously compared to the control, with a trend of increasing first and then decreasing. The dates of application significantly affected the root collar diameter, followed by the crown diameter, and had no marked effect on the plant height. Two applications significantly increased the root collar diameter compared to single application in a range of 500 to 2 000 mg·l^{-1}, and the maximum was reached at the concentration of 1 500 mg·l^{-1} with two applications. The results of two-way ANOVA revealed an obvious interaction between the concentration and dates of CCC application that affected the increments of plant height, crown diameter and root collar diameter (F:31.733, $P < 0.01$; F:57.419, $P < 0.01$; F:57.311, $P < 0.01$, respectively). The increments of plant height and crown diameter negatively correlated with the increment of root collar diameter ($p < 0.05$) while the increment of plant height positively correlated with the increment of crown diameter ($p < 0.01$) (Table 1).

Effects of CCC on P_n of coast redwood seedlings in autumn and winter

Figure 3 shows that the application of CCC could help the coast redwood seedlings keep higher P_n than that of the control, with a trend of increasing first and then decreasing with the increase of CCC concentration, then the maximum was reached at 1 000–2 000 mg·l^{-1} CCC. Two applications were better than single application of 100 mg·l^{-1} CCC, but two applications significantly decreased P_n compared with that of single application of 2 000 mg·l^{-1} CCC. In coast redwood seedlings treated with CCC in a range of 500–1 500 mg·l^{-1}, differences in P_n in leaves sprayed once or twice were not significant under the same concentration conditions. The two-way ANOVA results showed an evident interaction between CCC concentrations and application dates that affected the P_n of

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Table 1. Correlation coefficients between indicators determined in this experiment

	IPH (cm)	*ICD* (cm)	*IRCD* (mm)	P_n (μmol CO_2 $m^{-2}{\cdot}s^{-1}$)	*Yield*
ICD (cm)	0.903**				
IRCD (mm)	–0.439*	–0.435*			
P_n (μmol CO_2 $m^{-2}{\cdot}s^{-1}$)	–0.844**	–0.784**	0.746**		
Yield	–0.618**	–0.644**	0.446*	0.652**	
ETR	–0.214	–0.374*	0.624**	0.492**	0.579**

IPH – increment of plant height; *ICD* – increment of crown diameter; *IRCD* – increment of root collar diameter; P_n – net photosynthetic rate; *Yield* – actual photochemical quantum yield; *ETR* – photosynthetic electron transport rate; *indicates significance at 0.05 level, ** indicates significance at 0.01 level

coast redwood seedlings under natural cooling and drought (F:167.648, $p < 0.01$). The correlation analysis indicated that the increment of root collar diameter positively correlated with P_n ($P < 0.01$), and the increments of plant height and crown diameter negatively correlated with P_n ($P < 0.01$) (Table 1).

Effects of CCC on fluorescence parameters of coast redwood seedlings in autumn and winter

Data (Figure 4) document that the application of CCC could maintain higher *Yield* and *ETR* in the leaves of coast redwood in autumn and winter. With the increasing concentrations of CCC, *Yield* and *ETR* showed a trend of increasing first and then decreasing. For *Yield*, the effect difference between different concentrations of CCC (500–2 000 mg·l^{-1}) was not obvious, and under the same concentration, the effect difference between two applications and single application was not distinct either. *ETR* also had a similar effect on *Yield*. *Yield* reached the maximum at concentrations of 500–2 000 mg·l^{-1} CCC with single application while it reached the maximum at concentrations of 100–2 000 mg·l^{-1} CCC with two applications. *ETR* reached the maximum at concentrations of 1 000–2 000 mg·l^{-1} CCC with single application and reached the maximum at concentrations of 500–1 500 mg·l^{-1} CCC with two applications. Two-way ANOVA results indicated an interaction between the CCC concentrations and application dates that affected *Yield* and *ETR* in the leaves of coast redwood seedlings under natural cooling and drought. The correlation analysis indicated that *Yield* and *ETR* were positively correlated with P_n ($P < 0.01$).

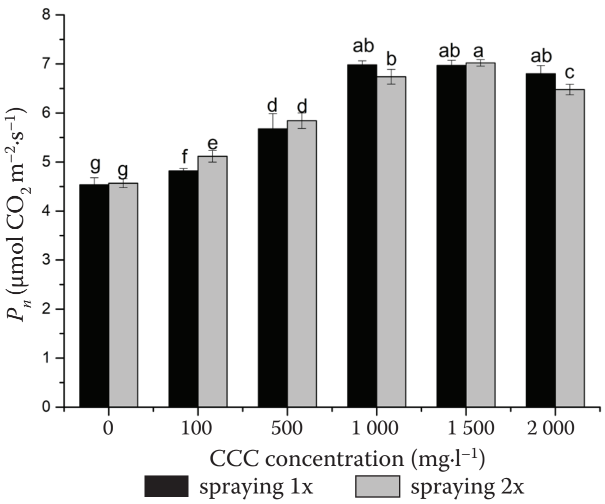

Figure 3. Effect of chlorocholine chloride (CCC) on the net photosynthetic rate (P_n) in *S. sempervirens* seedlings under natural cooling and drought; significant differences at $P < 0.05$ are shown by different letters; $n = 5$

DISCUSSION

CCC is a plant growth inhibitor which can change vegetative growth of plants, reduce plant height and increase stem diameter (Wu et al. 2012, 2014), regulate physiological activity in plants, especially under environmental stress (Kreslavskii et al. 2011; Karimi et al. 2014). Our findings showed a similar conclusion that the application of CCC significantly decreased the increment of plant height and crown diameter of coast redwood seedlings, and increased the root collar diameter. This study also showed under the conditions of low temperature and drought in autumn and winter in Xuzhou that the high photosynthesis and fluorescence activity were maintained by the application of CCC, which indicated that CCC could improve the resistance of coast redwood seedlings. The effect of CCC treatment depended on the concentration and application dates (Wu et al. 2012; Karimi et al. 2014; Li et

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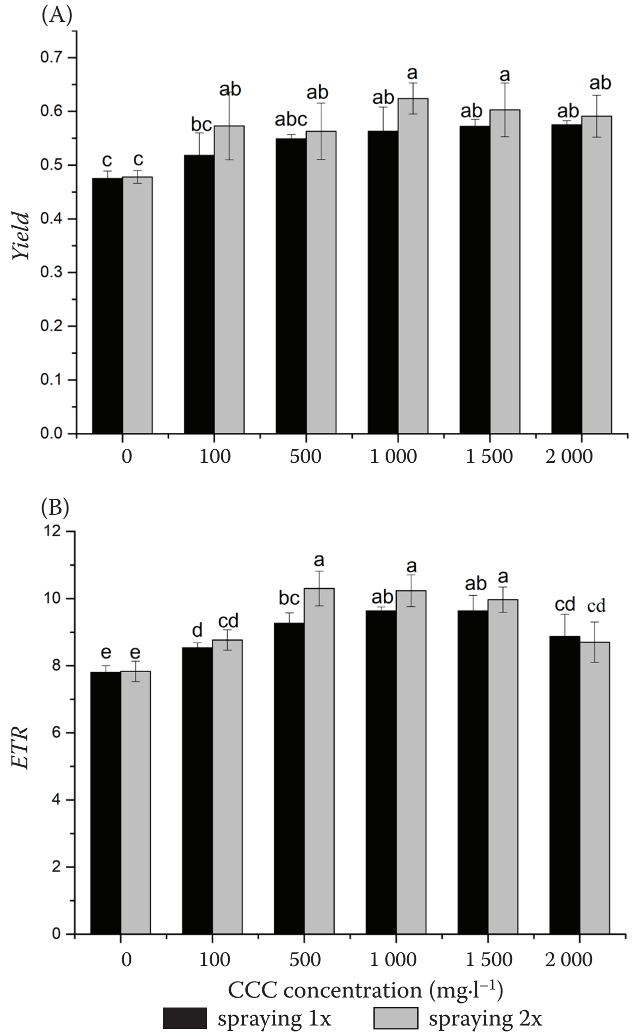

Figure 4. Effects of chlorocholine chloride (CCC) on the actual photochemical quantum yield of PSII photochemistry (*Yield*) (A), photosynthetic electron transport rate (*ETR*) (B) in *S. sempervirens* seedlings under natural cooling and drought; significant differences at $P < 0.05$ are shown by different letters; $n = 5$

al. 2015). In this study, the highest photosynthetic activity was the main index, and the relatively high growth index (root collar diameter, plant height and crown diameter) was used a reference to determine the appropriate treatment mode of CCC. So, the application effect of 1 000–1 500 mg·l^{-1} CCC was the best.

Photosynthesis converts the light energy into chemical energy which is the basis of plant survival (Bernacchi et al. 2013). Some findings suggested that photosynthetic capacity decreased under the environmental stress. The photosynthetic rate (P_n) is the most important parameter to evaluate photosynthetic capacity of plants. So, P_n is also an important indicator to evaluate plant resistance (Hu et al. 2016a, b; Polishchuk et al. 2016; Sun et al. 2016). Higher P_n indicates the more organic matter is synthesized in plants and the more energy for consumption, the stronger the ability to resist environmental stress. In this study, the correlation analysis showed that P_n was significantly positively correlated with the root collar diameter, *Yield* and *ETR* ($P < 0.01$) were significantly negatively correlated with the plant height and plant width ($P < 0.01$) (Table 1). So P_n could be an important index to evaluate the effect of CCC on alleviating the impact of the low temperature and drought stress. Our results also show that the application of CCC could increase P_n compared to the control (Figure 3), which indicated that CCC application could improve the resistance of coast redwood, relieve the stress of low temperature and drought in autumn and winter. The results concur with the findings of Kreslavskii et al. (2011), who also reported that the application of CCC increased the UV-radiation resistance of common bean according to photosynthetic characteristics improved. Xu et al. (2011) and Dong et al. (2012) also reported that spraying with CCC increased P_n in the leaves of *Ginkgo biloba* and *Pistacia chinensis*.

The absorption and the conversion of light energy can impact photosynthetic efficiency in plants. *Yield* and *ETR*, as the important fluorescence parameters, reflect the actual light energy conversion efficiency and actual photosynthetic electron transport rate of a plant (Genty et al. 1989; Schreiber 2004). *ETR* and *Yield* are widely used to evaluate the effect of environmental stress on plants, including low temperature and drought (Zhang et al. 2015b). Studies have shown that drought and low temperature significantly reduced *Yield* and *ETR*. Plant growth inhibitors can improve plant resistance to low temperature and drought, maintain high *Yield* and *ETR* (Li et al. 2015; Zhang et al. 2015a; Hu et al. 2016a, b). Our findings showed that *Yield* and *ETR* increased significantly in the leaves of coast redwood seedlings treated with CCC (Figure 4), which indicated that the application of CCC increased the resistance of coast redwood seedlings.

CONCLUSION

CCC application onto coast redwood seedlings inhibited the elongation of their shoots, improved their P_n, *Yield* and *ETR*, enhanced their resistance

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and alleviated the stress caused by low temperatures and drought in the autumn and winter. The best protection was obtained in the plants treated with CCC at 1 000–2 000 mg·l^{-1}. Therefore, the application of CCC in early September could be a suitable strategy for coast redwood cultivated and promoted in the Xuzhou region, China. However, the experiment was carried out from September to November, and the damage by severe low temperature and drought from December to February to the coast redwood and the mitigative effect of CCC should be further studied.

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