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INFLUENCE OF VARIOUS GROWTH MODULATORS ON THE ROOTING, ENZYMATIC ACTIVITY, AND NUTRIENT CONTENT OF *CATALPA BIGNONIOIDES* (BIGNONIACEAE)

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Abstract

Background: Ecosystem restoration is a major effort to promote sustainable human development. As a green tree species, the role of the American wood bean tree in promoting the industrialization of seedlings and the strength of scientific and technological innovation cannot be ignored, but the introduction of the American wood bean tree propagation and cultivation system is still immature. The goals of this investigation were to improve the survival rate and rooting rate (RR) of *Catalpa bignonioides* cuttings; to screen out the optimal formula and processing method; and to offer a theoretical basis and technical direction for further improving the prompt reproduction and widespread administration of *C. bignonioides*. Using fresh softwood of a 3-year-old parent *C. bignonioides* as material, three-factor orthogonal tests involving three growth regulator types (indole-3-acetic acid (IAA), indole-3-butyric acid (IBA) and rhizogenic powder-1 (ABT-1)), growth regulator concentrations (500, 1000 and 1 500 mg·L^{-1}), and growth regulator action times (10 min, 30 min, and 60 min) were performed to analyze the influence of these three factors on the rooting index during the rooting of cuttings and to determine the MDA content, related enzymatic activity, and changes in soluble sugar (SS) and soluble protein (SP) levels of cutting phloem. The order of influence of the 3 kinds of growth regulators on *C. bignonioides* was IBA>ABT-1>IAA>contral (CK). Different growth regulator concentrations had significant effects on the RR of *C. bignonioides* cuttings. Cutting with a processing time of 60 min had the highest RR, callus production rate, and average root number. Among the 3 main factors, growth regulator had the greatest influence on rooting, with each index reaching a significant level. Overall, the malondialdehyde (MDA) levels of cutting treatments were drastically reduced, compared to the CK; the peroxidase (POD), polyphenol oxidase (PPO) and superoxide dismutase (SOD) activity was markedly elevated, relative to CK, and the SS and SP levels were also elevated, compared to the CK overall. Among the three growth regulators, IBA exposure had the most significant impact on the cutting effect, and the rooting effect of 1000mg • L^{-1} treatment was the best of 60 min was the best for the indicators of the rooting of cuttings. T5 (IBA+1000 mg·L^{-1}+60 min) was the optimal treatment combination, carrying a RR of 84%. Treatments with different growth regulators can reduce the MDA content and increase the related enzymatic activity and nutrient content in cuttings, thus promoting the rooting of cuttings.

Key words: *C. bignonioides*; Growth regulator; Rooting of cutting; Enzymatic activity; Nutrient.

Introduction

C. bignonioides, otherwise called crape myrtle catalpa, American catalpa and Indian bean tree, is a deciduous tree from the Bignoniaceae family, found within North America, particularly, in certain regions of Canada, as well as central and southern United States. More recently, *C. bignonioides* was also planted within Inner Mongolia, Liaoning and other provinces in China (Flora of China Committee, Chinese Academy of Sciences, 1990). *C. bignonioides* is primarily employed for street and garden greening in North America. Its beauty can be viewed in three seasons, including spring leaves, summer flowers, and autumn fruits. With a broad canopy, it is often used as a windscreen tree in open areas (Zhu *et al*., 2010). When studying 260 types of garden plants, *C. bignonides*, a large flower, was rated as a precious first-class garden plant with excellent landscape greening effects (Wei *et al*., 2008). Sheng *et al.*, (2005) briefly introduced the seedling technology of western *catalpa*. The SOD activity was assessed via the nitroblue tetrazolium (NBT) photoreduction technique with U/(g·min) as the unit (Li, 2000). The POD activity was measured by guaiacol staining, with U/(g·min) as the unit. PPO function was measured by the catechol method, with U/(g·min) as the unit. Soluble sugar (SS) levels were measured using the anthrone technique, with % as the unit. The soluble protein (SP) content was evaluated via the Coomassie brilliant blue G-250 staining, with mg/g as the unit. Each sample was assayed in triplicate. There are relatively more studies on propagation techniques for species in this genus, but relatively little research has been conducted on the reproductive techniques of *C. bignonioides*.

To promote the introduction and cultivation of *C. bignonioides* in China, it is necessary to quickly produce seedlings in large quantities. During the course of this study, *C. bignonioides* was found to have difficulties with seed reproduction due to seed dormancy and slow rooting and germination, which are serious constraint to rapid reproduction (Wei *et al.*, 2008). At present, limited seed resources restrict its large-scale production and application in China. Cutting propagation is the most cost-effective means of reproduction at present and has the advantages of maintaining the excellent traits of the female parent, early flowering and fruiting, and accelerating the propagation and promotion of seedlings (Li, 1987). Therefore, *C. bignonioides* cutting propagation technology is conducive towards development, promoting / administering seedling industrialization. Currently, systematic research on *C. bignonioides* softwood cutting technology has not been carried out in China or other countries. In the early stages of studying this species, it was noted that its cuttings had

difficulty in rooting (Wang *et al.*, 2020; Bi *et al.*, 2020), and this reduced cutting rooting rate (RR) is a challenge for forestry development in China.

Based on prior research, the RR of exogenous growth regulators-treated cuttings was reported to be markedly elevated, compared to untreated cuttings (Ren *et al.*, 2019; Yan *et al.*, 2017; Bai *et al.*, 2016). Related experiments have proved that the concentrations of phytohormones, longistin and CK, vary significantly along the stem segments of the stock. Within shoots, peak significant, physiologically active auxin, IAA, is made within growing foliage / shoots, transported to the root in stems via polar auxin transport (PAT) within xylem parenchyma / cambium cells, or in phloem in conjunction with transport of assimilated material (Kramer & Bennett, 2006; Petrasek & Friml, 2009; Leyser, 2011; Barbier *et al.*, 2015). Moreover, exposure to growth modulators with very elevated or reduced concentration is not favorable to cutting rootings (Quan *et al.*, 2017), as it can impair the delicate balance of endogenous hormones within cuttings, thereby preventing promote adventitious root (AR) formation (Wang *et al.*, 2011). Wang Qing *et al*., examined *Chukrasia tabularis* shoots grown in MS-supplemented medium and reported that IBA and 500 mg·L^{-1} ABT-1 promotes rooting after 10 days. Moreover, IBA processing is superior to ABT-1 processing, carrying a RR over 85% (Wang *et al.*, 2020).

By using 3 differing growth modulators (naphthaleneacetic acid (NAA), IBA and IAA) with differing doses / exposure durations, Zhai Yafang and colleagues performed a cutting-propagation examination involving *Lonicera tartarii* cuttings. Based on their analysis, the RR under 500 mg·L^{-1} IBA produced the optimal results at 86% (Zhai *et al.*, 2021). Wang Xiaoling *et al*., submerged tetraploid *Robinia pseudoacacia* softwood in varying dosing gradients (500 mg/L, 1000 mg/L, 1500 mg/L) of several hormones (IBA, NAA and IAA) over six hours. The optimal results were observed with 1000 mg/L IBA, carrying a RR of 80.4% (Wang *et al.*, 2011). Zhang Enliang exposed *Catalpa* softwood to 2000 mg/L IBA concentration, carrying a RR of 85.6% (Zhang *et al.*, 2018). A related study established the cutting rooting capability of five catalpa softwood species. Following submersion in 3000 mg/L IBA for 1 min, the RR of *Catalpa* was up to 94.5% (Ma *et al.*, 2014). Zheng *et al*. employed varying ABT-1, NAA, and IAA concentrations for treatment of 1-year-old *Brassica chinensis* cuttings and got best RR from 500 mg/L ABT-1 exposure, then IAA treatment (Zheng *et al.*, 2020). Liang *et al*., (2021) employed varying exogenous hormones IAA and IBA concentrations for Huangguohougui softwood treatment and reported that the 250 mg/L IAA treatment produced the optimal results at 66.7% RR.

Li Huimin *et al*. examined the varying plant growth modulators (IBA, IAA and NAA) concentrations influence on rooting survival rate of original perfume rose variation cuttings. The best survival was achieved from 500 mg/L IAA-treated cuttings (Yan *et al.*, 2020). Wu Kaiyun *et al*. employed several plant growth modulators (IBA, ABT-1, NAA, GGR6 and IAA) concentrations to submerge hardwood cuttings from the persimmon rootstock Yalin 6, prior to inserting them into a sterile matrix. The largest RR was achieved with 500 mg/L IAA treatment, then ABT-1 treatment (Wu *et al.*, 2021). The superior growth modulators commonly employed for the rapid enhancement of cutting RR are IBA, ABT-1, and IAA at concentrations between 500-2000 mg/L.

There are also many studies on the effect of treatment time on the spike. Liu *et al*., (2022) used young stiff branches, Hu *et al*., (2019) used stiff branches, and Zhai *et al*., (2021) used young branches for propagation of cuttings, and the results all showed that the best rooting rate was achieved when the cuttings were treated in IBA solution for 1h. Some studies also concluded that the best rooting results were obtained when the cuttings were treated for 30 min. For example, gunnera cuttings were placed in IBA solution for 30 min (Lin *et al.*, 2020), ABT-1 millennial tree semi-woody spring tips were treated with ABT-1 for 30 min (Zhou *et al.*, 2020), and Ebei bald cedar cuttings were soaked in ABT1 at a mass concentration of 500 mg-L-1 for 30 min (Liu *et al.*, 2021), the rooting effect of the cuttings under these treatments reached the highest level. In addition, the maximum cuttings were obtained with the best hormone IBA and the best treatment time was 10 min (Xiong *et al.*, 2021; Zheng *et al.*, 2020).

The above study showed that the hormone type, concentration and treatment time could promote the rooting of the spike. Therefore, three kinds of growth regulators (IAA, IAB and ABT-1 at three different mass concentrations of each (500 mg/L, 1000 mg/L, and 1500 mg/L) under the cutting bases were investigated using fresh softwood cuttings of *C. bignonioides* as the material. This study for the first time screened out the optimal growth modulator for the RR and survival of *C. bignonioides* softwood of cutting, and offered a theoretical foundation for future work. Herein, the rooting mechanism was elucidated from a physiological and biochemical perspective, which can be utilized in establishing a rapid *C. bignonioides* seedling cutting propagation system for extensive seedlings production with outstanding genetic features. In addition, background and typical protocols for industrial propagation of *C. bignonioides* were presented.

Methodology

Testing resources, processing and sampling: Softwood cutting of *C. bignonioides* was harvested in mid-June at the experimental station of Henan Agricultural University. The parent tree was uniform in height, and with robust cuttings at 0.6-0.8 cm in diameter, fresh branches of uniform length were pruned into cuttings of 12-15 cm in length. Individual cuttings were made flat on the top, and bevelled at 45° on the bottom.

The three studied factors were growth regulator, growth regulator concentration, and processing time. Each factor was set to 3 levels, and interactions were not considered. In addition, the orthogonal experimental design of L9 (3^4) was adopted. The scheme design is shown in (Table 1). Specifically, A is the growth regulator species (IAA, IBA and ABT-1), B is the growth regulator concentration (500, 1000, 1500mg L^{-1}), and C is the treatment time (10min, 30min, 60min). In all, this investigation had 9 treatments, with three replicates per treatment. Each group consisted of 50 cuttings as a

bundle. A cutting base submerged in water for 1 hour was employed as the CK. The tables / figures below describe experimental outcomes, as follows: T1: IAA 500 mg/L 10 min; T2: IAA 1000 mg/L30min; T3: IAA 1500 mg/L 60min; T4: IBA 500 mg/L 30 min; T5: IBA 1000 mg/L 60min; T6: IBA 1500 mg/L 10min; T7: ABT-1 500 mg/L 60min; T8: ABT-1 1000 mg/L 10 min; T9: ABT-1 1500 mg/L 30min; CK: Control.

Table 1. Orthogonal experimental design with varying growth modulator ratios.

Treatment number	Factor		
	Growth regulators A	Concentration B (mg·L^{-1})	Treatment time C (min)
T1	1（IAA）	1(500)	1(10)
T2	1	2(1000)	2(30)
T3	1	3(1500)	3(60)
T4	2（IBA）	1	2
T5	2	2	3
T6	2	3	1
T7	3(ABT-1)	1	3
T8	3	2	1
T9	3	3	2
CK	Water		

Different treatments were applied on 0, 7, 15, 25 and 35 days post cutting. Six cuttings were arbitrarily chosen per treatment to observe and record the changes in morphological indicators. After washing and drying the moisture, the cortex approximately 2 cm from the cutting base was peeled off as soon as possible, sliced into pieces, covered in tin foil and placed in liquid nitrogen. These cuttings were then brought back to the laboratory in a -80°C freezer for subsequent measurement of the MDA content, oxidase activity and nutrient content.

Cutting and post management: The softwood cutting experiment was carried out in June 10, 2018, under the outdoor shade net of the seedling breeding center of Henan Agricultural University, with all-light spray softwood cutting seedling breeding technology. A cutting pond of 5 m in length, 4 m in width and 0.5 m in depth was encircled with bricks. The seedbed matrix was pure fine river sand, vermiculite and perlite with a ratio of 3:1:1. The automatic spraying system was placed 1.5 m above the cutting pool, and a shade net was arranged above it. One week before cutting, 50% carbendazol wettable powder resuspended in water (800 times dilution) was uniformly sprayed around the seedbed and substrate. Before cutting, the seedbed substrate was watered. The depth was 7-8 cm, and the density was 40 m^{-2}. After cutting, water control was performed every 30 min from 8:00 to 18:00 every day. It should be noted that the moisture timer controller made by Beijing Academy of Forestry was employed for monitoring the water spray interval and duration. To maintain leaf moisture, the timer was sprayed every 30 min. To prevent the leaves from shrinking or falling off due to lack of water during high summer temperatures, the shade net was used to shade the cuttings on sunny days from 11:00 to 16:00. The air humidity was kept at approximately 70%, and the cutting substrate humidity was maintained at approximately 50%, that is, a loose state.

Determination of physiological and biochemical indicators: The physiological indicators of *C. bignonioides* cutting phloem were determined as follows: The content of MDA was measured by the thiobarbituric acid technique (Gao, 2006), with mmol/g as the unit. The SOD activity was assessed via the NBT photoreduction technique (Li, 2000), with U/(g·min) as the unit. The POD activity was measured by guaiacol staining, with U/(g·min) as the unit. The PPO activity was measured by the catechol method, with U/(g·min) as the unit. The SS levels were evaluated using the anthrone technique, with % as the unit. The SP content was assessed via Coomassie brilliant blue G-250 staining, with mg/g as the unit. Each sample was assayed in triplicate.

Results and Analysis

Morphological observation and division of the *C. bignonioides* cutting base during rooting: The following morphological changes were observed in the *C. bignonioides* cuttings. Starting on 7 days post cutting, several cutting bases generated little bits of milky calli (Fig. 1B), which increased gradually by 15 days post cutting (Fig. 1C), and continued to grow by 20 days post cutting (Fig. 1D). On 30 days post cutting, a few ARs had generated from the cutting barks (Fig. 1E). Some ARs persisted in extending from inside the calli (Fig. 1F), and some originated from the calli interior and cortex (Fig. 1G) and grew longer. Moreover, new roots formed on the newly formed ARs. Ultimately, a complicated intertwined rooting system was generated (Fig. 1H). Based on the morphological alterations in the *C. bignonioides* cutting base, there were 5 stages, namely, the initiation stage (day 1 after cutting), callus stage (days 2-15), root primordium stage (days 16-25), AR generation stage (days 26-30), and AR elongation stage (days 31-50). Figure 1 illustrates that the mixed rooting type of *C. bignonioides* cuttings (Figs. 1E, F and G).

Impact of growth regulators, growth modulator concentrations, and processing times on *C. bignonioides* cuttings rooting

Influence of different types of growth regulators on *C. bignonioides* cutting morphology: The RR, callus production rate, mean root quantity, as well as mean maximum root length and diameter treated with different growth modulators were markedly elevated, compared to those treated with clean water (Table 2). The effect of the 3 kinds of growth regulators on C. bignonioides was IBA>ABT1>IAA. The RR, callus RR, and average rooting number under IBA treatment were significantly higher than those in ABT1 and IAA treatment groups. Table 3 shows the ANOVA results of *C. bignonioides* cuttings. According to the results, the effects of the different categories of growth modulators on the RR (RR between treatments F=31.632, and significance level P=0.000), callus production rate (callus production rate between treatments F=34.914, and significance level P=0.000), and average root number (RR between treatments F=11.033, and significance level P=0.001) of the cuttings all reached a very significant level. Furthermore, there was no significant effect on mean maximum root length and diameter.

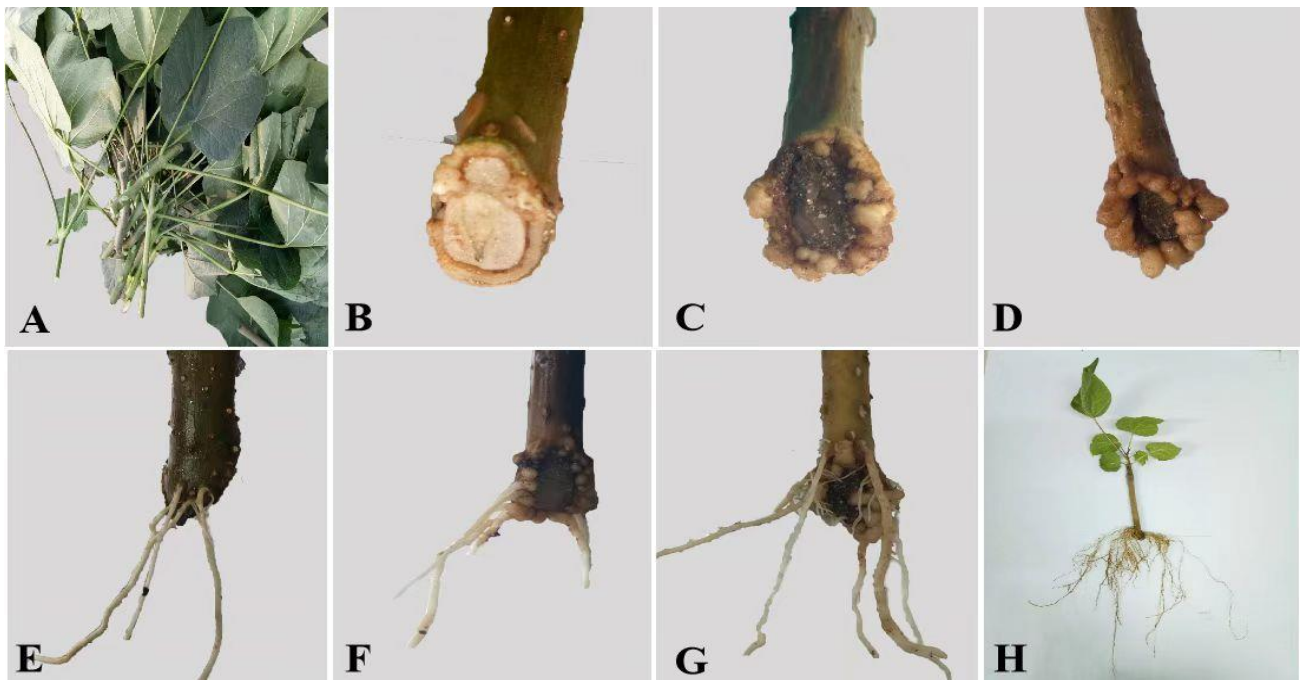

Fig. 1. Rooting of the *C. bignonioides* cutting base. A: *C. bignonioides* cuttings; B: Some callus generation; C: Massive calli production; D: Callus increase; E: Adventitious roots (AR) formation from the bark; F: ARs protruding from the calli; G: Calli and bark of the cutting with ARs; H: Calli and bark of the cutting with elongated ARs.

Table 2. Multiple comparisons of *C. bignonioides* cutting morphology under different exposures. Data presented as mean ± standard error.

Source of variation	Level	Rooting rate (%)	Callus production rate (%)	Average root number(n)	Average maximum root length(cm)	Average maximum root diameter (mm)
Growth regulator	IAA	35.44 ± 2.46Cc	16.22 ± 1.39Bb	8.33 ± 0.97Bb	16.34 ± 2.71Aa	1.47 ± 0.21Aa
	IBA	62.89 ± 5.88Aa	36.67 ± 1.89Aa	16.56 ± 2.08Aa	18.31 ± 2.45Aa	1.70 ± 0.27Aa
	ABT-1	48.22 ± 2.88Bb	22.44 ± 1.76Bc	10.11 ± 1.78Bb	20.51 ± 1.43Aa	1.27 ± 0.11Aa
Concentration(mg·L^{-1})	500	43.67 ± 4.44Bb	24.67 ± 2.29Aa	10.89 ± 1.34Aab	18.03 ± 2.15Aa	1.40 ± 0.21Aa
	1000	58.00 ± 6.55Aa	26.22 ± 3.95Aa	14.11 ± 2.39Aa	16.23 ± 1.15Aa	1.54 ± 0.27Aa
	1500	44.89 ± 4.19Bb	24.44 ± 3.87Aa	8.44 ± 1.67Ab	20.90 ± 2.43Aa	1.49 ± 0.16Aa
Treatment time(min)	5	44.78 ± 4.79Bb	24.00 ± 3.61Aa	13.22 ± 1.53Aa	21.91 ± 1.97Aa	1.71 ± 0.19Aa
	30	43.11 ± 1.01Bb	24.67 ± 1.83Aa	7.67 ± 1.12Bb	17.07 ± 2.70Aa	1.29 ± 0.13Aa
	60	58.67 ± 7.34Aa	26.67 ± 4.38Aa	14.11 ± 2.55Aa	16.18 ± 1.72Aa	1.44 ± 0.28Aa
CK		8.00 ± 2.00	2.00 ± 2.00	9.33 ± 5.03	10.40 ± 1.13	0.70 ± 0.10

Distinct lowercase alphabets (a, b, c and d) within the same column denote significant differences (p<0.05), and distinct uppercase alhabets (A, B, C and D) within the same column represent very high significant differences (p<0.01)

Table 3. ANOVA of the *C. bignonioides* cutting rooting index under different conditions.

Character indices	Source of variation	Quadratic sum	Mean square	*F*-value	*P*-value
Rooting rate (%)	A	3394.741	1697.37	31.632	0.000**
	B	1136.519	568.259	10.590	0.000**
	C	1312.963	656.481	12.234	0.000**
Callus production rate (%)	A	1976.889	988.444	34.914	0.000**
	B	16.889	8.444	0.298	0.745
	C	34.667	17.333	0.612	0.552
Average root number (n)	A	336.889	168.444	11.033	0.001*
	B	84.222	42.111	2.758	0.088
	C	219.556	109.778	7.191	0.004*
Average maximum root length (cm)	A	78.207	39.103	0.933	0.41
	B	99.707	49.853	1.190	0.325
	C	171.127	85.563	2.042	0.156
Average maximum root diameter (mm)	A	0.851	0.426	0.987	0.390
	B	0.092	0.046	0.106	0.900
	C	0.809	0.405	0.938	0.408

A represents categories of growth regulator, B represents growth regulator concentration, and C represents processing time. A significance level of P<0.05 denoted significant difference (SD), and p<0.01 denoted considerable SD

Table 4. Range analysis of the average rooting rate of the *C. bignonioides* cuttings exposed to different exposures.

Treatment number	Factor			Rooting rate (%)
	Growth regulator A	Concentration B (mg·L^{-1})	Treatment time C (min)	
T1	1 (IAA）	1 (500)	1 (10)	28.33
T2	1	2 (1000)	2 (30)	44.67
T3	1	3 (1500)	3 (60)	33.33
T4	2 (IBA)	1	2	44.00
T5	2	2	3	84.00
T6	2	3	1	60.67
T7	3 (ABT-1)	1	3	58.67
T8	3	2	1	45.33
T9	3	3	2	40.67
K1	106.33	131.0	134.33	
K2	188.67	174.0	129.34	
K3	144.67	134.67	176.0	
k_1	35.44	43.67	44.78	
k_2	62.89	58.00	43.11	
k_3	48.22	44.89	58.67	
R	27.45	14.33	15.56	
Primary and secondary factors: A＞C＞B				
Optimal portfolio: T5				

Ki: Level effect, that is, the sum of test results corresponding to the levels sign of i in any colum; *ki*. Average effect, level and divided by number of levels; R: Range, difference between the maximum and minimum k value in any column

Impact of varying growth modulator concentrations on *C. bignonioides* cutting morphology: The impact of different growth regulator concentrations on the *C. bignonioides* cuttings rooting index is shown in Table 2. The impact of varying concentration treatments on the *C. bignonioides* cutting morphology was relatively small (Table 2). Of the treatments, the 1000 mg/L produced the highest RR (58.00%), which was markedly elevated, compared to the 500 mg/L and 1500 mg/L treatments. In addition, of the treatments, the 1000 mg·L^{-1} exposure had the optimal effect on callus production rate, average root number, and average maximum root diameter (26.22%, 14.11, and 1.54 mm, respectively); however, these values were not significantly different from the other two treatment groups. In terms of mean maximum root length, 1500 mg·L^{-1} treated cuttings had the best effect (20.90 cm), without a significant difference from that of the 500 mg·L^{-1} (18.03 cm) and 1000 mg/L treated cuttings (16.23 cm). According to the variance results (Table 3), different growth regulator concentrations had a significant influence on the RR of the *C. bignonioides* cuttings (RR between treatments F=10.590, significance level P=0.000) but not on callus production rate, average root number, mean maximum root length or diameter.

Influence of different processing times on *C. bignonioides* cutting morphology: Table 2 shows the effects of different treatment times on the rooting indices of mullein cuttings samples. The maximum values of rooting rate (58.67%), healing tissue production rate (26.67%) and average number of roots (14.11 roots/plant) of the cuttings were achieved at a treatment time of 60 min; moreover, the RR of the cuttings at 60 min treatment was significantly different from the other two treatment timings. No significant differences were observed between treatment groups with different treatment times; the plugs with treatment time of 10 min had the maximum mean longest root length and diameter (21.91 cm and 1.71 mm, respectively), which were not significantly different from the other two treatment groups. The analysis of variance in Table 3 showed that the effect of different treatment times on the RR of the plugs (RR between treatments F=12.234, and significance level P=0.000) reached a highly significant level, on the mean root number (verage root number between treatments F=7.191, and significance level P=0.004) reached a significant level, and on the callus production rate, mean maximum root length and diameter was not significant.

Range analysis of RR of *C. bignonioides* cuttings exposed to different treatments: To further analyze the influence of different factors on the RR of *C. bignonioides* cuttings, a range analysis of the relevant data was performed, as shown in Table 4. The R value of growth regulator type (27.45) was greater than the R value of processing time (15.56), and the R value of processing time was greater than the R value of growth regulator concentration (14.33); that is, A>C>B. Therefore, the categories of growth regulators had the greatest impact on the RR of the *C. bignonioides* cuttings. Based on the results in (Table 4), the best combination was T5 (IBA + 1000 mg·L^{-1}+60 min).

Alterations in the enzymatic activity of *C. bignonioides* cutting phloem under different treatments

Alterations in the MDA levels of the *C. bignonioides* phloem cuttings: According to (Fig. 2), the MDA levels of

the *C. bignonioides* cutting phloem exposed to individual treatments revealed a trend of increasing, then decreasing over time. (Treatments 5, 7, and 8 show an "up-down-up" trend.) On day 15, the CK and treatments 2, 5, 6, 7, 8, and 9 peaked at 56.31 mmol/g, 50.67 mmol/g, 32.45 mmol/g, 37.88 mmol/g, and 45.37 mmol/g from the initial values of 11.31 mmol/g mmol/g, 45.21 mmol/g, and 46.839 mmol/g, respectively. On day 30, treatments 1, 3, and 4 peaked at 50.34 mmol/g, 44.45 mmol/g, and 42.34 mmol/g, respectively. Among them, CK had the maximum increase, with an increase of 79.91%, and treatment 5 had the least increase, with an increase of 65.15%. During the whole rooting process, the MDA levels of individual treatments were reduced, compared to CK. In addition, the MDA content of treatment 5 was generally lower than that of the other treatments.

By analyzing the rooting morphology and cutting period, the MDA levels of the *C. bignonioides* cuttings increased in the callus stage and decreased in the root primordium stage, as well as the AR generation and elongation stages. Additionally, there was partially processed MDA content that was increased during the AR elongation stage. Using cutting rooting analysis following exposure to various growth modulators, concentrations and processing durations, a reduced MDA content meant enhanced rooting yield.

Changes in the SOD activity in the phloem the *C. bignonioides* cuttings: According to (Fig. 3), SOD activity of the *C. bignonioides* cutting phloem in individual treatments revealed a trend of increase, then decrease (increasing on 0-15 days and decreasing on 15-50 days post cutting). Overall, treatment 5 resulted in the biggest rise, from the starting value of 70.87 U/ (g min) to the peak value of 343.93 U/(g min), an increase of 79.39%. During the whole rooting process, the SOD activity of the CK showed a gentle upward and downward trend, with a small change range.

By analyzing the rooting morphology and cutting period, the SOD activity of the *C. bignonioides* cuttings was increased in the callus stage and decreased in the root primordium stage, as well as the AR generation and elongation stages. Using cutting rooting analysis following exposure to various growth modulators, concentrations and processing durations, the higher the SOD activity was, the better the rooting yield.

Changes in the POD activity of the *C. bignonioides* cutting phloem: According to (Fig. 4), the POD activity of *C. bignonioides* cutting phloem in each treatment revealed a pattern of "up-down-up" over time (increasing on 0-15 days, decreasing on 15-30 days, and rising on 30-50 days). Overall, treatment 5 had the biggest rise, from the starting value of 400 U/(g min) to the peak value of 2466.67 U/(g min), with an increase of 83.78%. The POD activity of CK was consistently reduced, compared to other treatments on days 0-30. At day 15, the activity of CK was 920 U/(g·min), while the activity of treatment 5 was 2.68 times that of CK.

By analyzing the rooting morphology and cutting period, the POD activity of the *C. bignonioides* cuttings was increased in the callus stage, decreased in the root primordium and AR generation stages, and then gradually increased in the AR elongation stage. This indicates that plant growth regulator treatment can significantly change the POD activity at the base of the spike and promote root formation, and the higher the POD activity, the better the rooting rate.

Alterations in the PPO activity of the *C. bignonioides* cutting phloem: According to (Fig. 5), the PPO activity of the *C. bignonioides* cutting phloem in individual treatments revealed a pattern of "up-down-up" over time (increasing on 0-7 days, decreasing on 7-30 days, and rising on 30-50 days post cutting). The PPO activity of treatments 7, 8, and 9 and CK rose on 0-15 days, decreased on 15-30 days, and increased on 30-50 days after cutting. In the first rising stage, treatment 5 had the most prominent rise, from the starting value of 0.39 U / (g min) to the peak value of 10.90 U / (g min), with an increase of 88.17%. On days 0-30, the PPO activity of treatment 5 was essentially the highest.

The PPO activity of the *C. bignonioides* cuttings was increased in the callus stage, as determined by analyzing the rooting morphology and cutting period. Most of the PPO activity peaked early in callus formation and then gradually decreased. The PPO activity dropped to a minimum at the AR elongation stage and then increased again at the AR generation stage. This can be explained by the fact that PPO acts at the early stage of adventitious root germination and that the rooting rate of the spike increases with the increase of PPO activity. From these results, it can be concluded that exogenous hormones enhance the rooting ability of *Catalpa bignonioides* by dynamically regulating the PPO content in the spikes.

Alterations in the nutrient levels of *C. bignonioides* cutting phloem in different treatments

Alterations in SS levels of the *C. bignonioides* cuttings phloem: According to (Fig. 6), SS content of the *C. bignonioides* cutting phloem in individual treatments revealed a pattern of decrease, then increase over time (decreased on 0-15 days and increased on 15-50 days after cutting). Among them, treatment 5 had the least decrease, from the starting value of 5.94% to 3.16% on the 15th day, with a decrease of 46.80%. The CK had the maximum decrease from the starting value of 5.94% to 1.04%, with a decrease of 82.49%. The SS levels of individual treatments were elevated, compared to CK, and the SS levels of treatment 5 were always at the highest state.

Through the analysis of the rooting form and cutting period, the SS levels of the C. *bignonioides* cuttings was decreased sharply in the callus stage and rose in the AR generation and elongation stages. The cuttings rooting effect analysis revealed significant differences in the SS levels among treatments. Treatment 5 showed the maximum increase SS levels and RR. Treatment 1 and the CK showed the least decline in SS content, with relatively lower RRs. Comprehensive analysis revealed an intricate link between the SS levels and cutting rootings. The higher the SS levels was, the better the rooting impact.

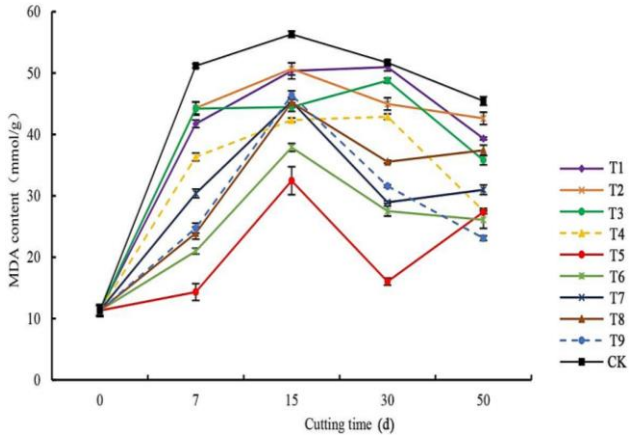

Fig. 2. Alterations in the MDA levels of the *C. bignonioides* cuttings phloem during rooting.

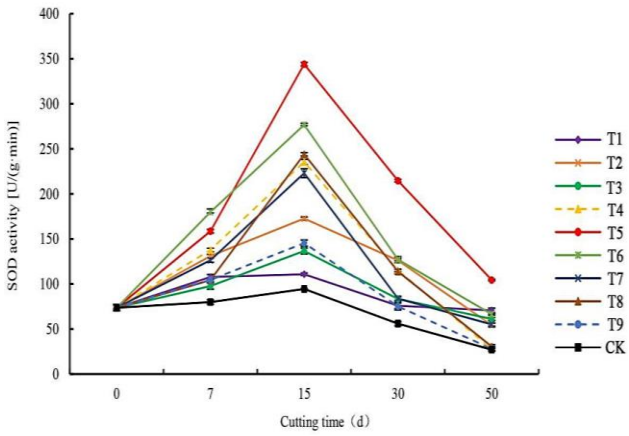

Fig. 3. Alterations in the *C. bignonioides* cutting phloem SOD activity during rooting.

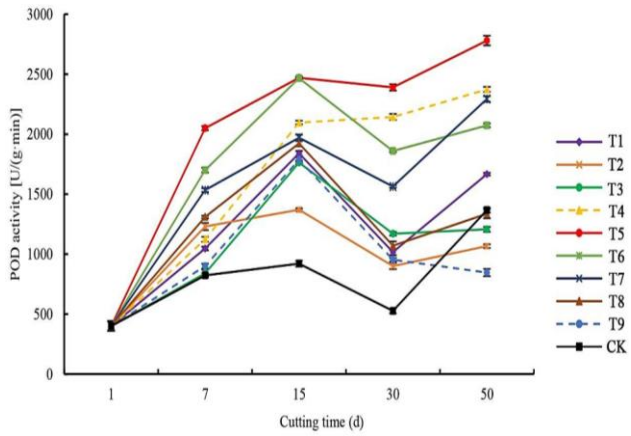

Fig. 4. Alterations in the POD activity of the *C. bignonioides* cutting phloem during rooting.

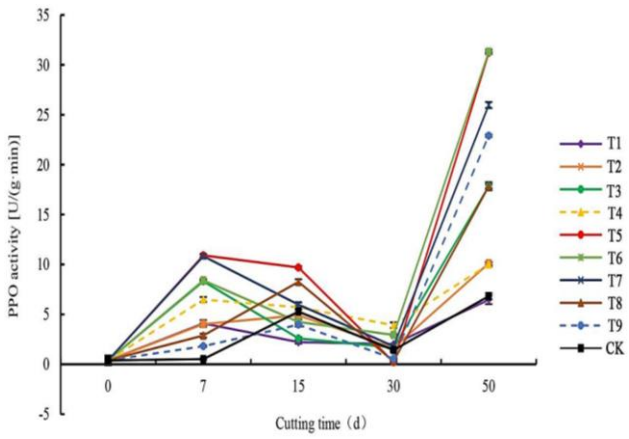

Fig. 5. Alterations in the PPO activity of the *C. bignonioides* cutting phloem during rooting.

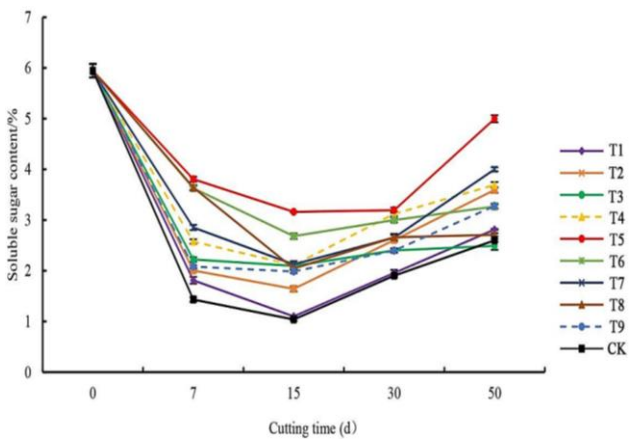

Fig. 6. Changes in the soluble sugar levels of the *C. bignonioides* cuttings phloem during rooting.

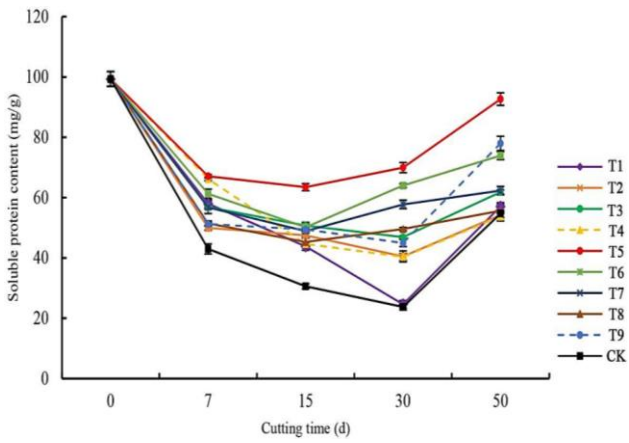

Fig. 7. Changes in the soluble protein levels of the *C. bignonioides* cuttings phloem during rooting.

Alterations in the SP levels of the *C. bignonioides* cuttings phloem: According to (Fig. 7), SP content of the *C. bignonioides* cutting phloem in individual treatments revealed a pattern of decrease, then increase over time. Treatments 5, 6, 7, and 8 decreased on days 0-15 and increased on days 15-50. Treatments 1, 2, 3, 4, 9, and the CK decreased on 0-30 days and increased on 30-50 days post cutting. Treatment 5 had the least decrease, from the starting value of 99.30 mg/g to 63.46 mg·L^{-1} on day 15, with a decrease of 36.09%. The SP levels in CK decreased the most, from a starting value of 99.30 mg/g to 23.74 mg·L^{-1}, with a decrease of 76.09%. The SP levels of individual treatments were elevated, compared to CK, and the SP levels of treatment 5 were always at the highest state.

By analyzing the rooting morphology and cutting period, the SP levels of the *C. bignonioides* cuttings was decreased sharply in the callus stage and increased in the AR generation and elongation stages. The cutting rooting

effect analysis demonstrated significant differences in the SP levels among treatments. Treatment 5 showed the largest increase in SP levels and RR. The CK always produced the lowest SP levels and worst rooting effect. The SP content with a high RR increased early in the root primordium stage. Comprehensive analysis showed that an elevated SP level represented better rooting yield.

Discussion

Influence of growth modulators on various indicators of *C. bignonioides* cutting rootings: The mixed rooting type of *C. bignonioides* softwood cutting rootings was employed in this study. Most studies (Liu *et al.*, 2017; Wang *et al.*, 2015) revealed that IBA treatment markedly enhanced the cutting RR. Nevertheless, there are also reports (Wang *et al.*, 2014) stating that the rooting effect of cuttings treated with ABT1 is best. Owing to the ubiquitous IAA endogenous growth regulator in plants, root development is typically influenced by alterations in IAA levels. Emerging evidences revealed that IAA promoted the rooting of *Dalbergia serrata* cuttings (Xu *et al.*, 2021), *Cinnomum coninna* (Liang *et al.*, 2021) and carnation (Garrido *et al.*, 2002). Herein, three distinct growth modulators promoted AR production in *C. bignonioides* softwood cuttings. In brief, following IBA exposure, callus formed considerably early in rootings, and the RR augmented by 76.00% relative to control. Moreover, the rooting number, length and index were markedly elevated, compared to CK. Hence, it could be concluded that the IBA treatment produced the best rooting yield, which corroborates with earlier publications (Sun *et al.*, 2017; Zeev *et al.*, 1995; Copes *et al.*, 2000).

Rooting correlates with changes in MDA content and enzymatic activity: MDA content can be used to evaluate the antioxidant capacity of cells and reflect the degree of damage plants experience from adverse conditions. Normally growing plants have little MDA content, which increases under stressful conditions. In the present experiment, ex vivo cuttings were injured by adverse conditions during the early cutting stage and callus generation, which caused the MDA content to rise to a peak. In the AR generation stage, the physiological function of the cuttings gradually recovered, and the growth tended to be stable. At this point, the MDA content remained low; however, in the AR elongation stage, the partially processed MDA content rose slightly. This result may have been due to the strong transpiration of the leaves generated in the upper part of the cutting, resulting in enhanced cutting stress resistance (Xie *et al.*, 2009). Thus, the MDA content showed regular changes with the rooting process. Compared with the CK group, the growth regulator treatment group reduced the MDA content, which was beneficial to the rooting of the cuttings. These findings corroborate with the study of Hua *et al.*, (2008).

Enzyme activity is essential for plant growth and it has a close relationship with the occurrence and development of plant ARs. POD is an oxidase closely related to rooting that can regulate the level of IAA *In vivo* and affect the formation of root primordia and ARs. SOD is a key enzyme in the plant antioxidant system that reduces the toxic effects of free radicals on plants by catalyzing the conversion of O_2^- into H_2O_2 *In vivo* (Ma *et al.*, 2020). PPO can catalyze the formation of an "IAA-phenolic acid complex" between phenolic substances and IAA, thereby promoting the activity of forming ARs (Nina *et al.*, 2015), catalyzing the metabolism of growth regulators, and accelerating the occurrence and development of ARs (Zhou *et al.*, 2016). Based on analysis, the change in the POD activity of the *C. bignonioides* cuttings revealed a pattern of "rising-slightly falling-rising", which is consistent with the change in the POD activity of plant cuttings that have difficulty in rooting (Liu *et al.*, 2007). The SOD activity of the *C. bignonioides* cuttings changed drastically with different cutting adversity states. For example, the SOD activity of the cutting increased rapidly in the early cutting stage due to the adversity conditions of the parent plant and then decreased with the generation of ARs and the relaxation of the growth adversity state, which corroborates with the Zhang Jinchun *et al*., (2015) study. The PPO activity of the *C. bignonioides* cuttings revealed a pattern of "up-down-up", and the elevated PPO activity at the early cutting stage may have led to an increase in the rooting-promotion factor "IAA-phenolic acid complex", which is advantageous to root groups development and ARs induction (Jiang *et al.*, 2014). With ARs formation and the decomposition of phenolic substances, the demand for PPO in the cuttings decreased, and thus PPO activity decreased. In the AR elongation stage, the PPO activity of the cuttings was increased because the formation of ARs was conducive to the cuttings absorbing exogenous nutrients to form the "IAA-phenolic acid complex". The rooting of the *C. bignonioides* cuttings was closely related to the activities of POD, SOD and PPO, indicating a certain regularity in the different cutting period. It has been shown that one of the effective ways to break through the difficulties in propagation of plugs is to effectively regulate enzyme activities and MDA content (Hua *et al.*, 2008). Li *et al*., (2022) found that plant growth regulator treatment of plug spikes increased SOD, POD and CAT activities, increased soluble protein content and decreased MDA content, thus promoting root development, which is consistent with the results of this study. Therefore, their roles in the rooting process are both independent and interconnected. Furthermore, they may affect rooting by interacting.

Changes in nutrient content: Plant rooting is a process that consumes number of nutrients and energy (Wang *et al.*, 2009; Wang *et al.*, 2015). SS is not only an indispensable nutrient for rooting and growth but also the main energy source for cuttings that are rooting to maintain survival. The rooting process of plants usually includes nutrient consumption before the cuttings root and energy accumulation generated by photosynthesis after they root (Ao *et al.*, 2002; Ma *et al.*, 2013; Li *et al.*, 2012). The dynamic changes in SS content before and after the *C. bignonioides* cutting rootings were consistent with the process of nutrient consumption and accumulation. Due to the relatively long rooting period of the *C. bignonioides* cuttings, rooting was hindered by the continuous consumption of SSs and nutrients. At the AR generation

stage, the appropriate addition of nutrients can improve the survival rate of cuttings, and the rebound of SS at the AR elongation stage and this may be due to photosynthesis by the cuttings to synthesize SS, which supplements the drastically reduced SS content. As the main component of plant cells and the main substance used during plant metabolism and cell division, SPs regulate cell growth and differentiation (Guo *et al.*, 1997). According to previous studies, the SP content of plant cuttings usually shows a pattern of increase, decrease; that is, SPs are accumulated in the cutting before rooting, and they are transformed and consumed after rooting (Liu *et al.*, 2003; Xu *et al.*, 2008). In this study, the change in the SP content of the C. *bignonioides* cuttings was not obvious and only slightly decreased in the early cutting stage. In addition, SPs were clearly accumulated during the rooting of the cuttings, which tended to balance the rooting of the cuttings. This process may be related to the conversion of nutrients into SP after plant rooting or participation in cell growth regulation and differentiation. Compared with the CK, the *C. bignonioides* cutting treatments resulted in the nutrient content increasing with the impact of varying concentrations of growth modulators.

Conclusion

It was concluded from 3 types of growth regulators that when the mass concentration of IBA was 1 000 mg/L, the rooting characteristics of the cuttings, such as RR (84.0%), root number (22.0) and root diameter (2.19 mm), were the best, while those of the CK performed the worst. The enzymatic activity and nutrient content of the cuttings were changed, which in turn affected the rooting process of cuttings. During the AR initiation stage, elevated contents of POD, PPO, SSs, and SPs favored the induction of root primordium in the *C. bignonioides* softwood cutting, while a decrease in MDA favored the rooting of the cuttings. Therefore, POD, PPO, SOD, SSs and SPs mainly promoted *C. bignonioides* softwood cutting rootings, while MDA inhibited rooting. In addition, there were complex mechanisms and various physiological and biochemical factors affecting the rooting of the cuttings. Therefore, in-depth research on the rooting mechanism of cutting propagation still requires additional studies as well as further exploration based on molecular techniques.

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