# Effects of Selenium (Se) on the Content and Balance of Endogenous Hormones and the Function of Antioxidant System during Seed Development of Red Sandalwood (*Pterocarpus santalinus*)

**Chengxiang XU[1,2*], Sitong LI[2], Shuyi LIU[2], Yufeng WEN[2], Yupeng LIN[2]**

1. Guangdong University of Business and Technology, Zhaoqing 526020, China; 2. College of Life Sciences, Zhaoqing University, Zhaoqing 526061, China

**Abstract** [**Objectives**] This study was conducted to investigate the regulatory effects of selenium (Se) on the content and balance of endogenous hormones and the function of antioxidant system during seed development in Red sandalwood (*Pterocarpus santalinus*). [**Methods**] Two basic treatments, seven single-fertilization treatments, and four combined fertilization treatments were designed. Sampling was conducted at 2, 5, 8, and 18 weeks after flower withering to measure the embryo abortion percentage (EAP), the contents of three endogenous hormones (IAA, $GA_3$, ABA), and the activities of four antioxidant enzymes (CAT, APX, SOD, GR). [**Results**] Se application significantly inhibited embryo abortion in Red sandalwood, with $Na_2SeO_3$[Se (IV)] showing superior effects to $Na_2SeO_3$(Se (VI)) and far exceeding the efficacy of individual applications of KCl, $H_3BO_3$, $CO(NH_2)_2$, $Ca(H_2PO_4)_2$, NPK compound fertilizer, or EFOF. The combined treatment of Se with NPK compound fertilizer and EFOF [EFOF + NPK compound fertilizer + Se (IV)] was the most effective, reducing the abortion percentage by 77.8% compared with UMC at 18 weeks after flower withering. Se application significantly increased the levels of three endogenous hormones and the (IAA + $GA_3$)/ABA ratio in Red sandalwood seeds (including the embryonic stage). In the optimal treatment, the (IAA + $GA_3$) content was 240.7%, 256.4%, 353.7%, and 502.9% higher than that of UMC at 2, 5, 8, and 18 weeks after flower withering, respectively. Se application also concurrently enhanced antioxidant enzyme activities, with all four antioxidant enzymes in seeds of Se-treated plants showing significant increases. Notably, the selenoenzyme GR maintained considerably high activity even at 18 weeks after flower withering. The EAP was highly significantly negatively correlated with IAA content and GR activity, identifying IAA and (IAA + $GA_3$) content as key hormonal indicators and GR as the core antioxidant enzyme, together constituting the central regulatory factors. The results indicate that Se suppresses embryo abortion in Red sandalwood through a dual regulatory pathway: by elevating IAA and $GA_3$ levels along with the (IAA + $GA_3$)/ABA ratio to optimize hormonal signaling networks, and by enhancing the activities of antioxidant enzymes such as GR to alleviate oxidative stress induced by cool-season low temperatures. [**Conclusions**] This study provides a theoretical basis and technical strategy for precision fertilization and stress resistance management in the cultivation of Red sandalwood.

**Key words** *Pterocarpus santalinus*; Embryo abortion; Selenium nutrition regulation; Endogenous hormones; Antioxidant enzyme activity

**DOI**:10.19759/j.cnki.2164-4993.2025.05.006

The content, balance and composition of endogenous hormones are closely related to the morphogenesis, growth and development, physiological functions and quality status of plant organs[1]. Recent studies have also shown that hormones and mineral nutrients coordinately regulate plant growth and development[2], while hormones and microRNAs synergistically control seed size and development[3]. Reactive oxygen species (ROS) often act as key signaling molecules in plant responses to biotic and abiotic stresses. Although they play important roles in triggering cellular signaling and maintaining redox homeostasis, excessive ROS can significantly damage biomacromolecules such as growth factors, transcription factors, proteins, nucleic acids, carbohydrates, and lipids[4]. Antioxidant enzymes play a crucial role in mitigating damage to plant life activities by preventing the excessive accumulation of ROS and scavenging surplus ROS[5]. It is evident that the disruption of endogenous hormone balance and oxidative stress serve as important physiological bases for seed embryo abortion in plants under adverse conditions.

Selenium (Se) is an essential mineral element for humans and animals. Within appropriate thresholds, Se participates in the synthesis of human selenoproteins and is involved in enzyme systems such as glutathione peroxidase (GPX), thioredoxin reductases (TrxR), iodothyronine deiodinases, and a series of proteins designated as selenoproteins. It plays roles in disease resistance, cancer prevention, inhibition of the development of the human immunodeficiency virus (HIV), and related immune system functions[6]. Selenoprotein R interacts with various proteins, including actin, transient receptor potential channels, and beta-amyloid proteins. It has important functions in the central nervous system and is closely associated with the development and progression of neurodegenerative diseases[7].

Se is not essential for the growth of higher plants. However, in regions with Se-deficient soils, such as Finland and New Zealand, Se-containing fertilizers are applied to farmland not to promote plant growth, but to increase the Se content in plants to meet the nutritional needs of local animals and humans[8]. It demonstrates

Received: July 27, 2025 Accepted: September 29, 2025

Supported by National Natural Science Foundation of China (31270674); Science and Technology Planning Project of Zhaoqing City, Guangdong Province (2019N012); National Undergraduate Innovation and Entrepreneurship Training Program (202210580007).

Chengxiang XU (1963-), male, P. R. China, Professor, Ph. D, devoted to research on plant stress physiology.

* Corresponding author.

the importance of Se. Numerous studies have shown that Se application can enhance the antioxidant levels and stress resistance of plants. Research on the physiological and biochemical effects of Se on plants has been conducted in various species, indicating that Se promotes the growth of aging seedlings. Studies on soybean (*Glycine max*), lettuce (*Lactuca sativa*), and broad bean (*Vicia faba*) have shown that Se inhibits oxidative damage in higher plants through GPX and some non-enzymatic systems, thereby delaying plant senescence. Se alleviates the toxic effects of cadmium (Cd) and enhances the activity of antioxidant enzymes in radicles[9-10]. However, there have been no reports on the improvement of Se nutritional status and its effects on plant seed development quality.

Red sandalwood (*Pterocarpus santalinus*) is one of the most precious rosewood species[11]. Currently, in China, only a small number of mature trees are cultivated in the central and western regions of Hainan Province. However, the rate of seed embryo abortion and the resulting percentages of empty pods and shriveled seeds are extremely high. It is primarily because its flowering period begins in early December, peaks in mid-December, and ends in late December, with the samaras maturing by the end of April or early May of the following year. Nearly half of the fruit development period is susceptible to relatively low-temperature stress[12]. In recent years, we have focused on studying soil nutrient management in Red sandalwood forests to enhance cold resistance during fruit growth and development. The results indicate that Se application significantly improves seed quality, increases seed yield, and promotes germination, seedling emergence, and seedling growth of the produced seeds. This paper reported the effects of Se application on the content and balance of endogenous hormones, as well as the function of the antioxidant system, during seed development in Red sandalwood.

## Materials and Methods

### Site conditions

The local annual average temperature is 23.3 ℃, and the annual rainfall is 1 850 mm. The soil is lateritic, developed from marine sedimentary parent material. The chemical properties of the 0 – 30 cm soil layer were as follows: pH 4.8, organic matter 11.5 g/kg, alkali-hydrolyzable nitrogen 7.9 g/kg, available phosphorus 1.52 mg/kg, available potassium 60.4 mg/kg, exchangeable calcium 693.5 mg/kg, exchangeable magnesium 80 mg/kg, available zinc 1.8 mg/kg, available boron 0.278 mg/kg, and Se content 0.365 mg/kg. The tested Red sandalwood fruiting trees had an average diameter at breast height of 28.5 cm, an average height of 13.6 m, an average height under the branch of 6.6 m, and an average crown width of 6.8 m.

### Experimental design

One basic treatment and 13 different treatments in three categories were designed. For all fertilizers and chemical substances, 60% of the total application amount was applied as the basal fertilizer in mid-May, and the remaining 40% was applied as the basal fertilizer in mid October of the same year. Local adult Red sandalwood trees begin flowering in mid December, and reach full bloom in late December, and the fruits mature in early May of the following year. The period from full bloom to fruit maturity takes approximately 20 weeks. The forest land is managed year-round. Apart from the differences in fertilization treatments, all other management measures were consistent across the different treatments.

**Basic treatments** Unmanaged control (UMC): No agricultural operations were implemented, including fertilization, irrigation, and weeding. That is, no human management was conducted.

Understory vegetation mulching (UVM): Weeds within the canopy range were cut and used as mulch covering the tree disc, once per month.

**UVM-derived single fertilization treatments**

EFOF: UVM + enzyme-microbe fermented organic fertilizer (10 kg per plant).

N: UVM + urea (400 g per plant, equivalent to 180 g of N).

P: UVM + calcium superphosphate (1 000 g per plant, equivalent to 180 g of $P_2O_5$, 150.0 g of Ca, 100.0 g of S).

K: UVM + potassium chloride (300 g per plant, equivalent to 180 g of KCl).

NPK: UVM + NPK compound fertilizer (equivalent to 180 g of N, 180 g of $P_2O_5$, 180 g of KCl per plant) + $Na_2SeO_3$ (8.5 g per plant, equivalent to 3.6 g of Se).

B: UVM + Boric acid (10 g per plant, equivalent to 1.7 g of B).

Se (VI): UVM + $Na_2SeO_3$ (8.5 g per plant, equivalent to 3.6 g of Se).

Se (IV): UVM + $Na_2SeO_3$ (8.5 g per plant, equivalent to 3.6 g of Se).

**UVM-derived compound fertilization treatments**

EFOF + NPK: UVM + EFOF + NPK compound fertilizer (equivalent to 180 g of N, 180 g of $P_2O_5$, 180 g of KCl per plant) + $Na_2SeO_3$ (8.5 g per plant, equivalent to 3.6 g of Se).

NPK + Se (IV): UVM + NPK compound fertilizer (equivalent to 180 g of N, 180 g of $P_2O_5$, 180 g of KCl per plant) + $Na_2SeO_3$ (8.5 g per plant, equivalent to 3.6 g of Se).

EFOF + NPK + Se (IV): UVM + EFOF + NPK compound fertilizer (equivalent to 180 g of N, 180 g of $P_2O_5$, 180 g of KCl per plant) + $Na_2SeO_3$ (8.5 g per plant, equivalent to 3.6 g of Se).

### Sampling methods and observation of embryo abortion percentage

Sampling was conducted four times: 2 weeks after flower withering (initial stage of embryogenesis), 5 weeks after flower withering (embryo morphogenesis stage), 8 weeks after flower withering (material accumulation stage), and 18 weeks after flower withering (early maturation and dehydration stage). Fruit clusters were randomly collected from the middle outer part of the tree crown using an averruncator. Two sets of samples were collected. One set was used for observing and recording seed embryo abortion, and the other was used for testing antioxidant system enzyme activity and endogenous hormone levels. The embryo abortion

percentage (EAP) was calculated based on the total number of seeds observed, with 60 fruits examined per treatment per sampling period. The actual number of observed seeds was used for statistical analysis. The criteria for determining embryo abortion were as follows: complete absence of the ovule or embryo within the samara locule, severe browning, blackening, necrotic shriveling, or tissue softening with obvious shrinkage and wrinkling.

**Determination of endogenous hormone levels**

Hormone extraction was performed following the method of Zeng *et al.* [13]. A 100 μl aliquot of 30% methanol-water was used to redissolve the sample, which was vortexed to ensure complete dissolution of target substances, and then centrifuged at 12 000 g for 15 min. The supernatant was collected into injection vials. The contents of indole-3-acetic acid (IAA), gibberellins (GAs) and abscisic acid (ABA) (in ng/g FW) were determined using liquid chromatography-tandem mass spectrometry (LC-MS/MS). Chromatographic separation conditions: A Shim-pack CLOODS 150 mm ×6.0 mm stainless steel column was used. The mobile phase for determining IAA and ABA was acetonitrile : water = 25 : 75 (*v*/*v*), while the mobile phase for determining gibberellic acid ($GA_3$) was acetonitrile : water = 15 : 85 (*v*/*v*). The LC separation was performed with a flow rate at 0.8 ml/min for both mobile phases and a column temperature at 30 ℃. The detection wavelength was 210 nm. The injection volume was 10 μl. Experimental data were acquired using an N2000 chromatography workstation.

**Antioxidant enzyme extraction and activity assay**

The procedure followed the method of Jiang and Zhang[14]. A 0.2 g sample of Red sandalwood seeds stored at ultra-low temperature (−80 ℃) was taken and ground into powder in liquid nitrogen. The powder was then homogenized in 6 ml of extraction buffer [50 mmol/L phosphate buffer (pH 7.0), 1 mmol/L EDTA, 1% insoluble polyvinylpyrrolidone (w/v), and 1.0 mmol/L ascorbic acid (AsA)]. The homogenate was centrifuged at 15 000 ×g for 20 min at 4 ℃, and the supernatant was collected for enzyme activity assays. Catalase (CAT) activity was determined according to the method of Aebi[15]. Superoxide dismutase (SOD) activity was measured following the method of Donahue *et al.* [16]. Glutathione reductase (GR) activity was assayed using the method described by Halliwell and Foyer[17].

**Protein content determination**

Protein content was determined according to the method of Bradford (1976)[18], using bovine serum albumin as the standard.

**Data statistics and analysis**

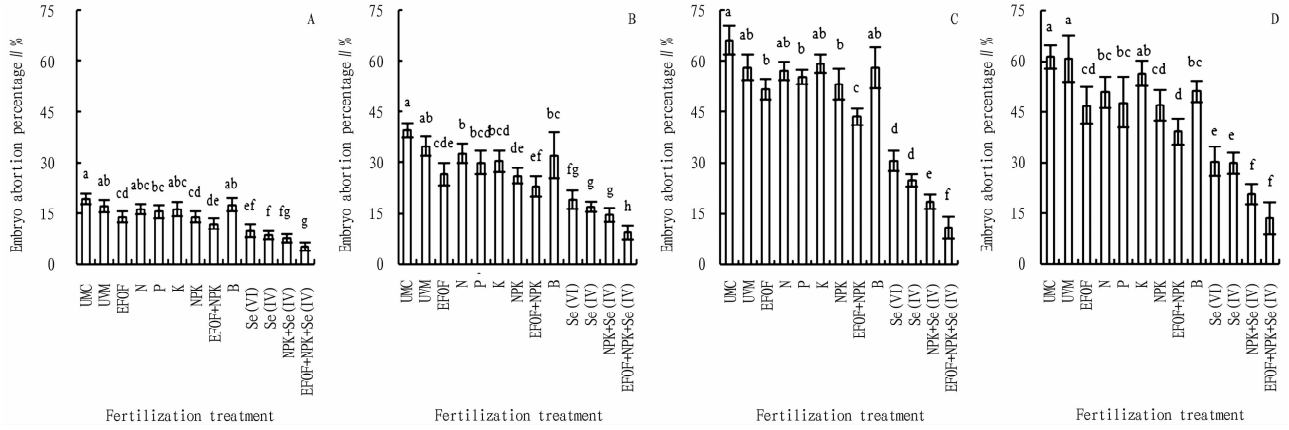
Means and standard deviations were calculated and graphs were generated using Microsoft Office Excel 2013. Significant differences were assessed using Duncan's new multiple range test. Correlation and regression analyses were performed using SPSS 20.0.

## Results and Analysis

**Effects of Se on the EAP in Red sandalwood**

As shown in Fig. 1-A, at 2 weeks after flower withering, the EAP of the UMC treatment was 19.3%. The EAP values for UVM and the single application treatments of N, K, and B fertilizers based on UVM were 17.2%, 16.4%, 16.4%, and 17.6%, respectively, showing no significant differences compared with UMC. In contrast, the EAP for the single P fertilizer treatment was significantly lower than that of UMC, with a reduction of 19.5%. The single application treatments of enzyme-microbe fermented organic fertilizer (EFOF) or NPK compound fertilizer on the UVM basis resulted in an EAP value of 14.0%, a 27.6% reduction compared with UMC, but showed no significant difference from the single P fertilizer treatment. The (EFOF + NPK) treatment yielded an EAP of 11.9%, which was significantly lower than the (EFOF + P) treatment[1]. The single application treatments of Se (IV) and Se (VI) led to EAP reductions of 49.7% and 56.5%, respectively, compared with UMC, and Se (IV) showed a slightly higher EAP than Se (VI). Furthermore, their EAP values were significantly lower than that of the (EFOF + NPK) treatment. The EAP of the [EFOF + NPK + Se (IV)] treatment was lower than that of the (EFOF + Se (IV)) treatment. Both values were significantly lower than those of the single P fertilizer or (EFOF + NPK) treatments, and also lower than that of the single application treatment of Se (VI) or Se (IV), all falling below 10.0%. The [EFOF + NPK + Se (IV)] treatment exhibited the lowest EAP, representing a 73.3% reduction compared with UMC.

At 5 weeks after flower withering, the differences in EAP among the aforementioned treatments further increased (Fig. 1-B). By 8 weeks after flower withering (when EAP tended to stabilize and no longer decreased significantly), these differences reached their maximums. As shown in Fig. 1-C, at 8 weeks after flower withering, the EAP values for UVM and the application treatments of N fertilizer, K fertilizer, or Se (VI) on the UVM basis were comparable, all showing no significant difference from UMC (65.9%). The EAP values for the application treatments of P fertilizer, EFOF, or NPK compound fertilizer were similar and significantly lower than that of UMC. The (EFOF + NPK) treatment demonstrated a significantly stronger effect in suppressing embryo abortion compared with all the aforementioned treatments, with an EAP reduction of 27.2% relative to UMC. However, it remained substantially higher than the four Se application treatments. Among them, the two treatments with Se application alone [Se (VI) and Se (IV)] reduced the EAP by 46.9% and 54.8%, respectively, compared with UMC. At 18 weeks after flower withering, the EAP values of the Se treatments were significantly lower than those of the other treatments. The EFOF + NPK + Se (IV) treatment showed the lowest EAP, with a 77.8% reduction compared with UMC, and the effect of Se (IV) was superior to that of Se (VI) (Fig. 1-D). These results further demonstrated that Se was the most effective and significant in suppressing embryo abortion in Red sandalwood, far exceeding the effects of the single application treatments of B, N, K, P fertilizers, EFOF, and NPK compound fertilizer.




A: 2 weeks after the flower withering; B: 5 weeks after the flower withering; C: 8 weeks after flower withering; D: 18 weeks after flower withering. The error bars represent the standard deviation (SD). The bars labeled with the same letter indicate no significant difference therebetween ($P > 0.05$). The meanings of the treatment abbreviations on the horizontal axis are as follows: UMC: unmanaged control; UVM: understory vegetation mulching; EFOF: enzyme-microbe fermented organic fertilizer; N: UVM + Urea; P: UVM + calcium superphosphate; K: UVM + potassium chloride; NPK: UVM + NPK-compound fertilizer (CF); EFOF + NPK: UVM + EFOF + NPK-CF; B: UVM + boric acid; Se (VI): UVM + $Na_2SeO_3$; Se (IV): UVM + $Na_2SeO_3$; NPK + Se (IV): UVM + NPK-CF + $Na_2SeO_3$; EFOF + NPK + Se (IV): UVM + EFOF + NPK-CF + $Na_2SeO_3$. The same applies to Fig. 2-Fig. 10.

**Fig. 1 Effects of chemical components of fertilizers on EAP of Red sandalwood**

## Effects of Se on endogenous hormone content and balance in Red sandalwood Seeds

Endogenous hormones play a central role in signal regulation and metabolic coordination during plant embryonic development. The test results revealed the overall characteristics of hormonal changes during the seed development in Red sandalwood. In specific, the IAA content was relatively higher at 2 weeks after flower withering (56.3 ng/g FW), slightly increased by 5 weeks (60.7 ng/g FW), followed by a sharp decline. The $GA_3$ content was higher than IAA at all stages, and remained stable until the mid-phase (approximately 80 ng/g FW). The ABA content was the highest among the hormones, and exhibited a continuous accumulation trend, with minimal differences among treatments. The (IAA + $GA_3$)/ABA ratio continuously decreased in UMC, while a smaller decline was observed in the Se treatment groups.

**(IAA + $GA_3$) content** During the development of Red sandalwood seeds, the (IAA + $GA_3$) content exhibited a significant dynamic pattern of "increasing first and then decreasing". Compared with the level at 2 weeks after flower withering, the average content increased by 8.9% at 5 weeks, decreased by 21.4% at 8 weeks, and further decreased by 47.5% at 18 weeks. This trend reflected the need for higher levels of growth-promoting hormones in the early stages of seed development to support embryo morphogenesis, while the development at the later stages gradually transitioned towards maturation and dehydration preparation. The Se treatments [Se (VI), Se (IV), NPK + Se (IV), EFOF + NPK + Se (IV)] significantly increased the (IAA + $GA_3$) content in the seeds. At all measured stages, the (IAA + $GA_3$) content was significantly higher than in the Se treatments than in other treatments. Specifically, the values of the Se treatments were 127.9% – 187.9% higher on average than UMC, and 46.9% – 64.1% higher than the best-performing non-Se treatment (EFOF + NPK). Moreover, the (IAA + $GA_3$) content in the Se treatment groups exhibited characteristics of "large increase, small decrease, and strong stability". In terms of temporal dynamics, compared with the 2-week level within the same treatment, the (IAA + $GA_3$) content increased by 12.7% – 16.3% at 5 weeks after flower withering, remained 5.4% – 6.9% higher at 8 weeks, and decreased by only 9.3% – 11.9% by 18 weeks. In contrast, the UMC treatment showed a 47.5% reduction at 18 weeks compared with its 2-week level. Inter-treatment comparison revealed that EFOF + NPK + Se (IV) was the most effective, and Se (IV) overall outperformed Se (VI) (Fig. 2).

**IAA content** Among the four sampling periods, the IAA content was relatively higher at 2 weeks after flower withering, with UMC reaching 56.3 ng/g FW. At 5 weeks after flower withering, the IAA content increased slightly, with UMC reaching 60.7 ng/g FW, showing an increase of 7.8% compared with the 2-week level. Subsequently, it decreased sharply. As shown in Fig. 2-C and Fig. 2-D, at 8 and 18 weeks after flower withering, the IAA content of UMC was 42.7 and 26.2 ng/g FW, respectively, representing reductions of 24.2% and 53.5% compared with the 2-week level, and 29.7% and 56.8% compared with the 5-week level. Compared with UMC, other 12 forest management and fertilization treatments all increased the IAA content in Red sandalwood seeds. However, the extent of increase or decrease in seed IAA content varied significantly among different treatments. The combination of EFOF + NPK compound fertilizer with Se (IV) resulted in the greatest increase and the smallest decrease throughout the seed development process. As shown in Fig. 2, throughout the four sampling periods, the IAA content in the four Se application treatments was significantly higher than those in other nine treatments. On average, the values were 115.7%, 131.2%, 166.4%, and 188.4% higher than that of UMC, respectively. During the period of highest IAA content (5 weeks after flower withering) and the period of lowest IAA content (18 weeks after flower withering), the IAA levels in the four Se application treatments were, in sequence, 82.4%, 90.4%, 127.6%, and 142.0% higher than

that of UMC at 5 weeks, and 208.3%, 237.6%, 301.3%, and 317.8% higher than that of UMC at 18 weeks (Fig. 3).

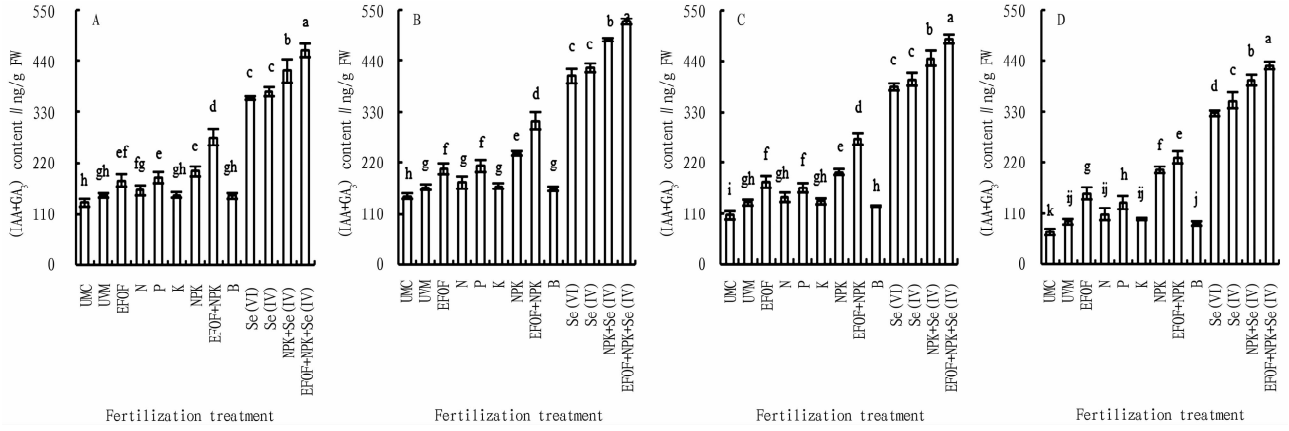



**Fig. 2 Effects of Se on the ($IAA + GA_3$) content in Red sandalwood seeds**

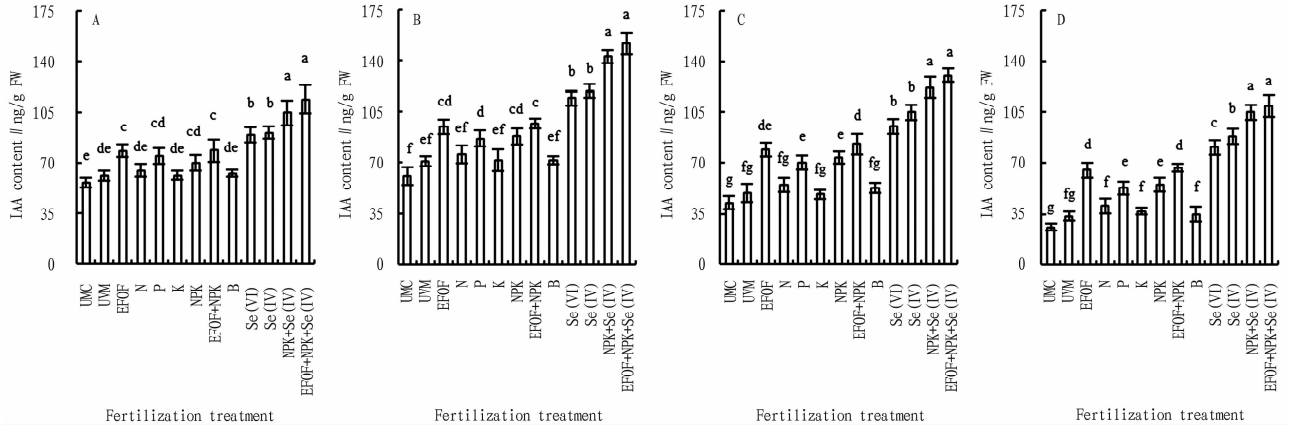



**Fig. 3 Effects of Se on IAA content in Red sandalwood seeds**

**$GA_3$ content** In the four measured periods, the $GA_3$ content in Red sandalwood seeds was consistently significantly higher than the IAA content. Meanwhile, its changing pattern throughout seed development distinctly differed from that of IAA. In the UMC group, it remained relatively stable until the mid-stage, with levels at 2, 5, and 8 weeks after flower withering essentially maintained around 80 ng/g FW. Se application in cultivation management significantly increased the $GA_3$ content in Red sandalwood seeds. As shown in Fig. 4, in the four periods, the $GA_3$ content in seeds from the four Se application treatments was substantially higher than in other nine treatments. On average, the values were 325.1%, 345.6%, 392.9%, and 444.6% higher than that of UMC, respectively. During the period of highest $GA_3$ content (5 weeks after flower withering), the values were 352.4%, 303.3%, 258.3%, and 244.6% higher than the control, respectively. In the period of lowest $GA_3$ content (18 weeks after flower withering), the increases were 611.2%, 551.9%, 491.5%, and 448.1%, respectively. Among the treatments without Se application, the best-performing one (EFOF + NPK compound fertilizer) showed $GA_3$ content in seeds 147.9%, 150.6%, 203.8%, and 307.4% higher than UMC in the four measured periods, respectively. In contrast, the treatment with Se (IV) added on the basis of EFOF + NPK compound fertilizer) resulted in $GA_3$ content 77.2%, 80.5%, 89.6%, and 95.9% higher than the same treatment without Se (IV), respectively, and the magnitude of increase was significantly greater than that of IAA in the same treatment during corresponding periods.

**ABA content** The ABA content in Red sandalwood seeds was significantly higher than both the IAA and $GA_3$ contents. Compared with UMC, at 2, 5, 8, and 18 weeks after flower withering, the ABA content was 79.9%, 27.7%, 98.4% and 46.0% higher than IAA, respectively, and 377.6%, 248.9%, 940.1% and 504.8% higher than $GA_3$, respectively, and the average was 166.5 ng/g FW. However, unlike the dynamic changes observed in IAA and $GA_3$ levels, the ABA content exhibited a relatively mild and continuous accumulation process throughout seed development. Moreover, the differences of ABA among different treatments were the smallest among the three endogenous hormones measured. As shown in Fig. 5, compared with UMC, all 12 treatments increased the ABA content in Red sandalwood seeds to some extent. However, whether the fertilizer formula contained Se had a significant impact. Similar to the responses of IAA and $GA_3$ content, the nine treatments without Se application resulted in significantly lower seed ABA content, while the four Se application treatments showed significantly higher ABA levels. By 18 weeks after flower withering, these four treatments had increased ABA content by 51.8%,

58.9%, 71.5%, and 92.8%, respectively, compared with UMC at the same period. Among the treatments without Se, the highest ABA content was observed in EFOF and its combination with NPK compound fertilizer, but it was only comparable to the single application of Se (VI).

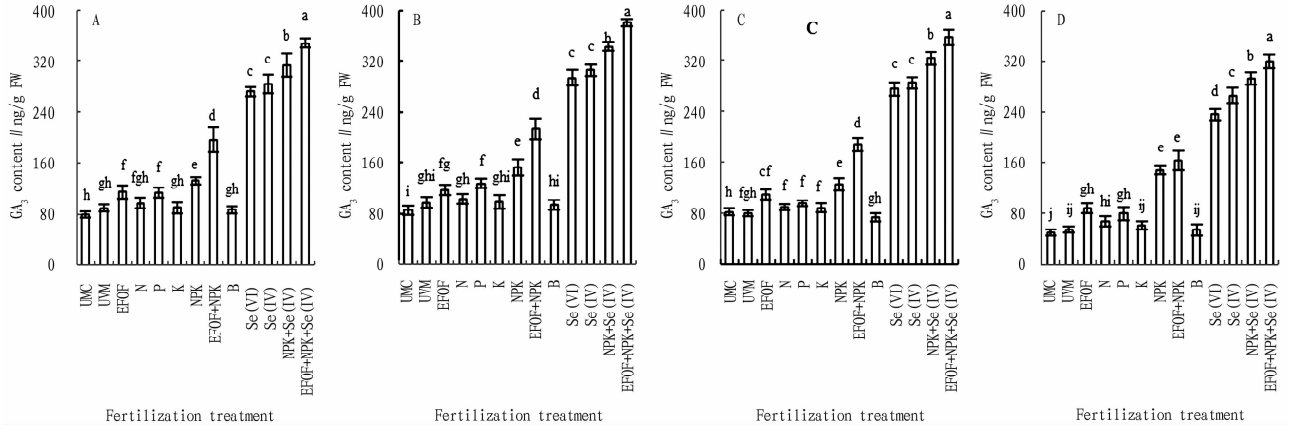



**Fig. 4 Effects of Se on $GA_3$ content in Red sandalwood seeds**

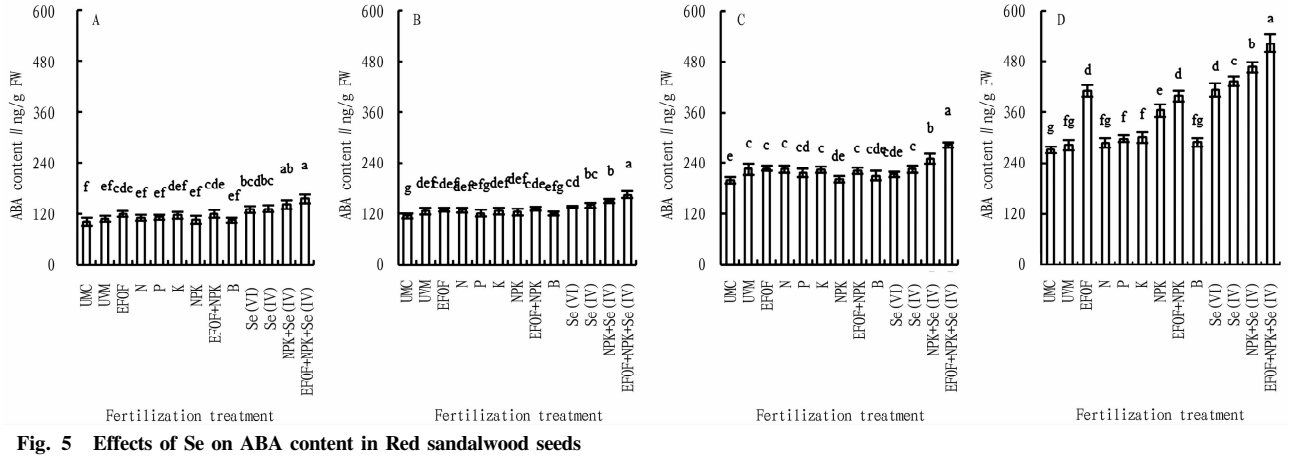



**Fig. 5 Effects of Se on ABA content in Red sandalwood seeds**

**$(IAA + GA_3)/ABA$** Under UMC, the $(IAA + GA_3)$/ABA ratio continuously decreased during Red sandalwood seed development, and the differences among treatments showed a clear trend of reduction. As shown in Fig. 6, compared with the ratio at 2 weeks after flower withering, the $(IAA + GA_3)$/ABA ratio for UMC decreased by 11.2%, 61.9%, and 79.8% at 5, 10, and 18 weeks after flower withering, respectively, dropping from the value initially greater than 1.3 to less than 0.3. The $(IAA + GA_3)$/ABA ratio under the 12 treatments showed responses similar to those of IAA, $GA_3$, and ABA contents. It increased slightly at 5 weeks after flower withering, but then decreased significantly thereafter, consistent with the control. However, the four Se application treatments resulted in seeds with a larger increase and a smaller decrease in the $(IAA + GA_3)$/ABA ratio. In the four measured periods, these four treatments were on average 80.9%, 99.3%, 132.9%, and 106.8% higher than other nine treatments, respectively, and 80.9%, 99.3%, 83.4%, and 106.8% higher than the best-performing non-Se treatment (EFOF + NPK compound fertilizer), respectively. Nevertheless, the differences among the four Se treatments were very small (Fig. 6).

**Effects of Se on antioxidant enzyme activities in Red sandalwood seeds**

**CAT activity** The CAT activity in Red sandalwood seeds was relatively lower at 2 and 5 weeks after flower withering, but increased significantly by 8 weeks after flower withering, and continued to rise gradually thereafter. All 12 fertilization treatments significantly enhanced seed CAT activity compared with UMC, but the four Se application treatments exhibited even stronger CAT activity, particularly the [EFOF + NPK compound fertilizer + Se (IV)] treatment. As shown in Fig. 7, the CAT activity of UMC at 2, 5, 8, and 18 weeks after flower withering was 0.211, 0.482, 0.952, and 1.486 μmol $H_2O_2$/(min · mg protein), respectively. Compared with UMC, the four Se application treatments increased CAT activity by 122.3%, 127.1%, 158.6%, and 209.5% at 2 weeks after flower withering, respectively, by 77.1%, 83.3%, 97.9%, and 129.2% at 5 weeks after flower withering, respectively, by 59.7%, 66.6%, 68.5%, and 86.0% at 8 weeks after flower withering, respectively, and by 41.6%, 48.3%, 56.9%, and 74.2% at 18 weeks after flower withering, respectively. Compared with the best-performing non-Se treatment (EFOF + NPK

compound fertilizer), the CAT activity of the Se treatments was on average 13.3%, 14.6%, 15.3%, and 18.3% higher at the four time points, respectively.

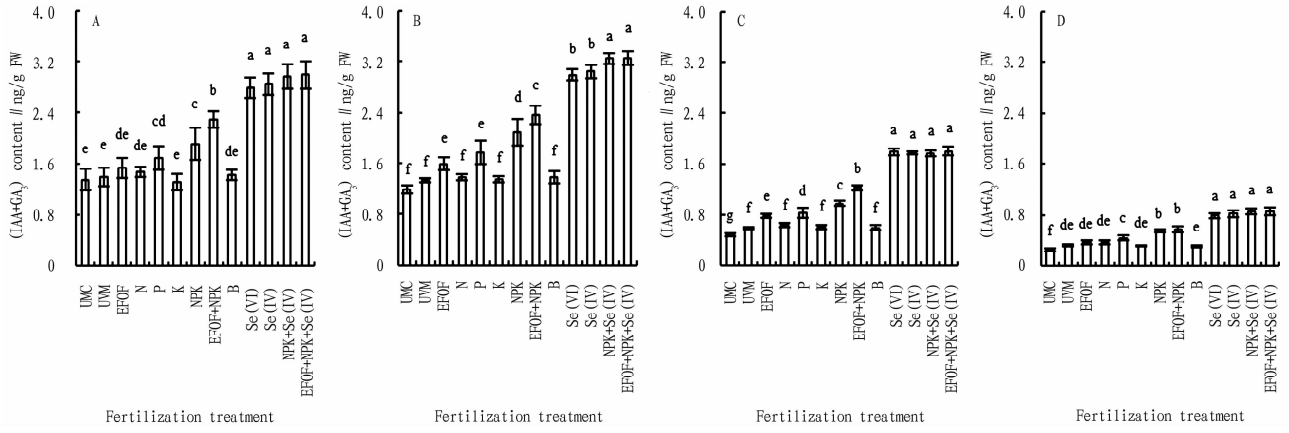



**Fig. 6 Effects of Se on (IAA + $GA_3$)/ABA in Red sandalwood seeds**

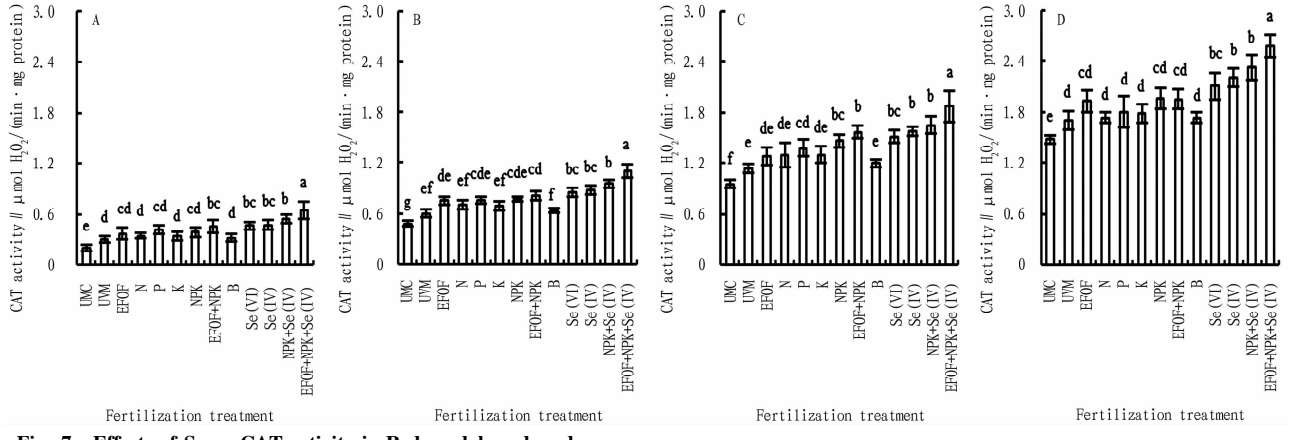



**Fig. 7 Effects of Se on CAT activity in Red sandalwood seeds**

**APX activity** The APX activity in Red sandalwood seeds continuously decreased during development, with the most significant reduction occurring at 8 weeks after flower withering. All fertilization treatments significantly enhanced seed APX activity compared with UMC, but the four Se application treatments exhibited markedly stronger activity and showed a smaller decline throughout seed development. As shown in Fig. 8, the APX activity of the control (UMC) at 2, 5, 8, and 18 weeks after flower withering was 2.31, 1.75, 0.83, and 0.42 μmol/min/mg protein, respectively. Compared with the level at 2 weeks after flower withering, the APX activity at 5, 8, and 18 weeks decreased by 24.2%, 64.1%, and 81.8%, respectively. For the four Se application treatments, compared with their respective UMC, the APX activity increased by 178.3%, 177.8%, 192.5%, and 226.8% at 2 weeks after flower withering, respectively, by 204.6%, 208.7%, 226.5%, and 267.4% at 5 weeks after flower withering, respectively, by 327.1%, 338.8%, 372.5%, and 461.5% at 8 weeks after flower withering, respectively, and by 378.3%, 412.5%, 469.2%, and 568.3% at 18 weeks after flower withering, respectively. Compared with other nine treatments, the average increases were 33.7%, 46.5%, 76.7%, and 109.4%, respectively. When compared with the best-performing non-Se treatment (EFOF + NPK compound fertilizer), the average increases were 17.5%, 15.0%, 26.6%, and 35.3%, respectively.

**SOD activity** During the development of Red sandalwood seeds, SOD activity also showed a continuous decreasing trend, but the degree of reduction was significantly smaller than that of APX activity. All 12 fertilization treatments significantly enhanced seed SOD activity compared with UMC, with the four Se application treatments still exhibiting the strongest activity. As shown in Fig. 9, the SOD activity in the Red sandalwood tree seeds in UMC was 15.7, 12.0, 9.2, and 7.3 U/mg protein at 2, 5, 8, and 18 weeks after flower withering, respectively. Compared with the level at 2 weeks after flower withering, the SOD activity at 5, 8, and 18 weeks decreased by 23.6%, 41.4%, and 53.5%, respectively. For the four Se application treatments, at 2, 5, 8, and 18 weeks after flower withering, the SOD activity was on average 31.0%, 38.9%, 54.2%, and 62.6% higher than other nine treatments, respectively. When compared with the corresponding UMC, the SOD activity increased by 157.2%, 162.8%, 180.4%, and 214.0% at 2 weeks after flower withering, respectively, by 183.3%, 195.8%, 216.7%, and 253.6% at 5 weeks after flower withering, respectively, by 207.1%, 224.0%, 253.2%, and 295.1% at 8 weeks after flower withering, respectively, and by

230.9%, 255.5%, 277.8%, and 321.5% at 18 weeks after flower withering, respectively. Compared with the best-performing treatment without Se application (EFOF + NPK compound fertilizer), the average increases were 9.7%, 12.4%, 14.9%, and 9.8%, respectively. The optimal treatment (EFOF + NPK compound fertilizer + Se (IV)) showed increases of 114.0%, 153.6%, 196.7%, and 221.5% compared with UMC, respectively.

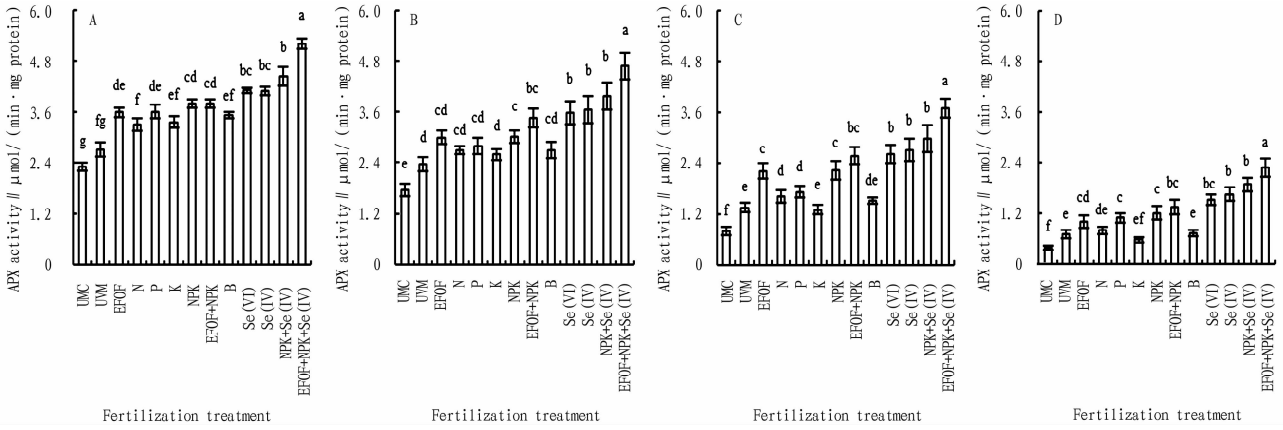



**Fig. 8 Effects of Se on APX activity in Red sandalwood seeds**

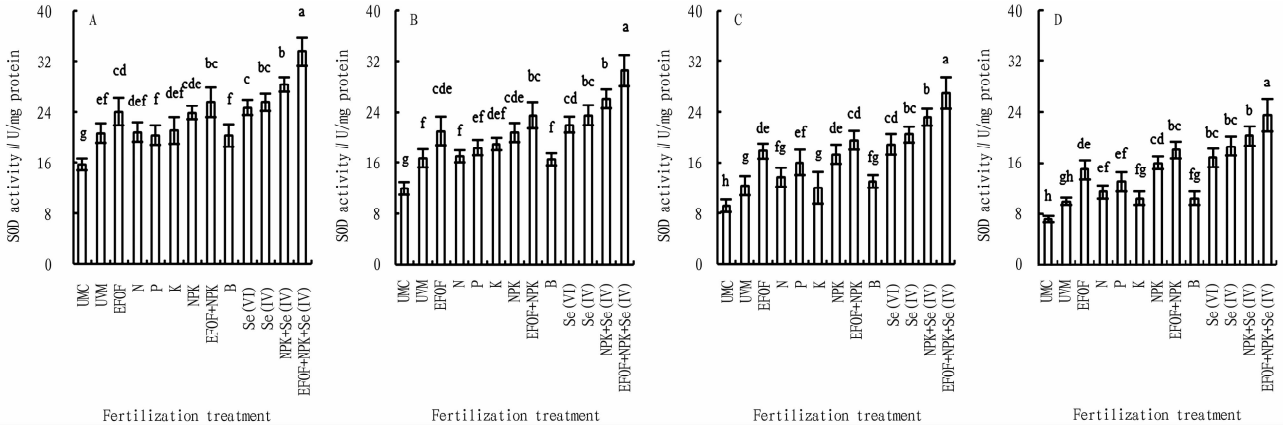



**Fig. 9 Effects of Se on SOD activity in Red sandalwood seeds**

**GR activity** The overall characteristics of enzyme activity changes during the growth and development of Red sandalwood seeds were analyzed. CAT: The CAT activity increased significantly at 8 weeks after flower withering and continued to rise gradually thereafter. APX: The CAT activity decreased continuously, with the most significant reduction at 8 weeks. SOD: The SOD activity decreased continuously, but the degree of reduction was smaller than that of APX. GR: The GR activity decreased continuously, with the smallest decline, and the Se treatments maintained the highest activity. As shown in Fig. 10, the GR activity of UMC at 2, 5, 8, and 18 weeks after flower withering was 70.8, 62.4, 45.1, and 30.6 μmol NADPH/(min · mg protein), respectively. At 5, 8, and 18 weeks, the GR activity decreased by 10.9%, 36.3%, and 56.8%, respectively, compared with the level at 2 weeks. During this period, the GR activity of the four Se application treatments was on average 17.9%, 28.4%, 40.0%, and 67.6% higher, respectively, than that of other nine treatments. Compared with the best-performing treatment without Se application (EFOF + NPK compound fertilizer), the GR activity of seeds from the four Se application treatments was on average 9.3%, 11.4%, 14.1%, and 20.7% higher for the four periods, respectively. The optimal treatment (EFOF + NPK compound fertilizer + Se (IV)) showed GR activity increases of 51.0%, 72.7%, 106.8%, and 219.9% compared with UMC during the four periods, respectively.

**Correlation of endogenous hormone levels and antioxidant enzyme activities with EAP in Red sandalwood**

In the UMC treatment at various stages, the EAP of Red sandalwood showed a highly significant negative correlation with seed IAA content ($r = -0.782$). The correlations with $GA_3$ and (IAA + $GA_3$) content were not significant. In contrast, it exhibited a highly significant positive correlation with ABA content and the (IAA + $GA_3$)/ABA ratio, with correlation coefficients of 0.848 and 0.863, respectively. Additionally, the abortion percentage was highly significantly positively correlated with CAT, SOD, and GR activities, but highly significantly negatively correlated with APX activity (Table 1). After implementing forest management, particularly scientific fertilization, these relationships changed significantly. Specifically, the EAP showed a highly significant negative correlation with seed IAA content, $GA_3$ content, (IAA + $GA_3$) content, ABA content, (IAA + $GA_3$)/ABA ratio, CAT

activity, APX activity, SOD activity, and GR activity, with the absolute values of the correlation coefficients all exceeding 0.950. Among these, the hormonal indicator most strongly correlated with the abortion percentage was IAA content ($r = -0.989$). Among the four antioxidant enzyme activities, the enzyme indicator most strongly correlated with the abortion percentage was GR activity ($r = -0.975$) (Table 1). Table 2 presents regression models analyzing the relationships between the aforementioned nine influencing factors and the EAP in Red sandalwood. The optimal regression models were all polynomial equations, with $R^2$ values all greater than 0.900 0, indicating highly significant differences. Path analysis results indicated that the contributions of the nine factors to the EAP in Red sandalwood varied significantly. Among them, the factor with the greatest direct effect was ($IAA + GA_3$) content, followed by IAA content, which contributed far more than $GA_3$ content. The path coefficients were −384.411, −309.624, and −75.478, respectively. For indirect effects, the most influential factors were also ($IAA + GA_3$), IAA, and $GA_3$ contents, with path coefficients of 383.424, −310.603, and −76.464, respectively. The total path coefficients were −0.987, −620.227, and −151.942, respectively, indicating that IAA had the greatest comprehensive effect on the target variable, EAP (Table 3).

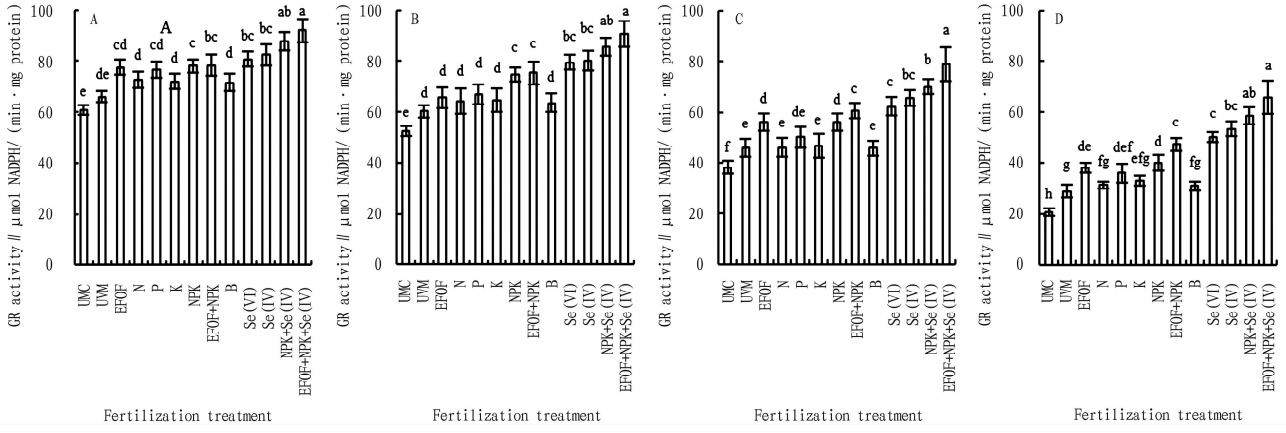



**Fig. 10 Effects of Se on GR activity in Red sandalwood seeds**

**Table 1 Correlation of endogenous hormone contents and antioxidant enzyme activities with EAP during seed development of Red sandalwood seeds**

| Physiological indicator | Correlation coefficient | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | EAP | IAA content | $GA_3$ content | ($IAA + GA_3$) content | ABA content | ($IAA + GA_3$) /ABA | CAT activity | APX activity | SOD activity | GR activity |
| EAP | 1.000 | −0.802** | −0.286 | −0.487 | 0.843** | 0.848** | 0.863** | −0.930** | 0.897** | 0.835** |
| IAA content | −0.989** | 1.000 | 0.881** | 0.966** | −0.922** | 0.953** | −0.916** | 0.889** | 0.844** | 0.941** |
| $GA_3$ content | −0.979** | 0.962** | 1.000 | 0.973** | −0.727** | 0.731** | −0.709** | 0.597* | 0.558 | 0.747** |
| ($IAA + GA_3$) content | −0.987** | 0.975** | 0.999** | 1.000 | −0.844** | 0.862** | −0.832** | 0.757** | 0.714** | 0.865** |
| ABA content | −0.963** | 0.965** | 0.917** | 0.932** | 1.000 | −0.984** | 0.988** | −0.948** | −0.878** | −0.972** |
| ($IAA + GA_3$)/ABA | −0.961** | 0.950** | 0.985** | 0.984** | 0.873** | 1.000 | −0.970** | 0.961** | 0.890** | 0.965** |
| CAT activity | −0.952** | 0.932** | 0.895** | 0.908** | 0.916** | 0.895** | 1.000 | −0.971** | −0.933** | −0.993** |
| APX activity | −0.955** | 0.934** | 0.899** | 0.911** | 0.930** | 0.890** | 0.978** | 1.000 | 0.975** | 0.971** |
| SOD activity | −0.962** | 0.937** | 0.883** | 0.899** | 0.937** | 0.880** | 0.967** | 0.980** | 1.000 | 0.950** |
| GR activity | −0.975** | 0.962** | 0.936** | 0.947** | 0.938** | 0.937** | 0.984** | 0.982** | 0.983** | 1.000 |

Upper triangle: based on UMC; lower triangle: all treatments based on UMC.

$R_{0.05} = 0.553$; $R_{0.01} = 0.684$.

** indicates extremely significant correlation ($P < 0.01$).

Embryo abortion percentage unit: %; Plant hormone content unit: ng/g FW; The activity units of CAT, APX, SOD and GR: μmol $H_2O_2$/(min · mg protein), μmol/(min · mg protein), U/mg protein and mol NADPH/(min · mg protein), respectively.

**Table 2 Regression analysis of endogenous hormone contents and antioxidant enzyme activities and EAP**

| Action factor ($X$) | EAP//% ($Y$) | | | |
|---|---|---|---|---|
| | Regression equation | $R^2$ | Se | F |
| IAA activity//ng/g FW | $Y = 62.247\ 73 - 0.342\ 92X - 0.000\ 52X^2$ | 0.978 6** | 1.788 73 | 229.058** |
| $GA_3$ activity//ng/g FW | $Y = 47.773\ 75 - 0.081\ 65X - 0.000\ 06X^2$ | 0.959 0** | 2.477 72 | 116.986** |
| ABA activity//ng/g FW | $Y = 137.646\ 67 - 0.654\ 66X + 0.000\ 71X^2$ | 0.931 6** | 3.200 75 | 66.098** |
| ($IAA + GA_3$) activity//ng/g FW | $Y = 51.859\ 16 - 0.076\ 42X - 0.000\ 02X^2$ | 0.973 9** | 1.977 59 | 186.487** |
| ($IAA + GA_3$)/ABA | $Y = 50.182\ 15 - 5.618\ 71X - 4.478\ 26X^2$ | 0.9273** | 3.299 79 | 63.776** |

(Continued)

(Table 2)

| Action factor ($X$) | EAP//% ($Y$) | | | |
|---|---|---|---|---|
| | Regression equation | $R^2$ | Se | F |
| CAT activity//μmol $H_2O_2$/(min · mg protein) | $Y=57.451\ 06+10.254\ 13X-28.549\ 53X^2$ | 0.912 0** | 3.630 15 | 51.828** |
| APX activity//μmol/(min · mg protein) | $Y=64.513\ 04-10.244\ 13X-1.036\ 48X^2$ | 0.914 5** | 3.578 05 | 53.495** |
| SOD activity//U/mg protein | $Y=58.817\ 32-0.518\ 83X-0.044\ 18X^2$ | 0.9029** | 4.005 24 | 41.883** |
| GR activity//μmol NADPH/(min · mg protein) | $Y=45.444\ 09+0.560\ 39X-0.012\ 34X^2$ | 0.969 6** | 2.134 60 | 159.353** |

$R^2_{0.01}=0.6019$; $F_{0.01}=7.56$.

** indicates extremely significant correlation ($P<0.01$).

**Table 3 Path analysis of endogenous hormone contents and antioxidant enzyme activities and EAP**

| Action factor | Direct path | Indirect path | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | IAA content | $GA_3$ content | ABA content | (IAA + $GA_3$) | (IAA + $GA_3$)/ABA | CAT activity | APX activity | SOD activity | GR activity | Σ |
| IAA content | −309.624 | 0 | 72.598 | 0.195 | −383.848 | 0.563 | 0.027 | −0.362 | −0.484 | 0.708 | −310.603 |
| $GA_3$ content | −75.478 | 297.807 | 0 | 0.205 | −374.889 | 0.547 | 0.028 | −0.376 | −0.514 | 0.728 | −76.464 |
| ABA content | 0.212 | 72.801 | 284.059 | 0 | −358.383 | 0.499 | 0.028 | −0.374 | −0.514 | 0.71 | −1.174 |
| (IAA + $GA_3$) | −384.411 | 73.609 | 309.170 | 0.198 | 0 | 0.563 | 0.027 | −0.367 | −0.493 | 0.717 | 383.424 |
| (IAA + $GA_3$)/ABA | −0.572 | 71.732 | 304.918 | 0.185 | −378.263 | 0 | 0.027 | −0.358 | −0.482 | 0.709 | −1.532 |
| CAT activity | −0.030 | 70.315 | 277.166 | 0.194 | −348.987 | 0.512 | 0 | −0.394 | −0.530 | 0.745 | −0.979 |
| APX activity | −0.402 | 70.513 | 278.198 | 0.197 | −350.206 | 0.509 | 0.030 | 0 | −0.537 | 0.743 | −0.553 |
| SOD activity | −0.548 | 70.691 | 273.478 | 0.199 | −346.642 | 0.503 | 0.029 | −0.394 | 0 | 0.744 | −1.002 |
| GR activity | −0.757 | 72.617 | 289.791 | 0.199 | −363.970 | 0.536 | 0.030 | −0.395 | −0.539 | 0 | −1.731 |

## Conclusions and Discussion

After the formation of the zygote in angiosperms, a series of programmed cell divisions, tissue differentiation and organ formation must occur for the development of a mature seed embryo. In the study of the morphology, genetics, and molecular biology of plant embryonic development, *Arabidopsis thaliana* has been the most extensively researched. Its morphological development can be divided into five stages: proembryo, globular embryo, heart-shaped embryo, torpedo embryo, and mature embryo[19]. The fertilized egg undergoes embryonic development, differentiating into distinct cell populations with specific properties, locations, and states, and forming particular organ primordia and tissues. It is a directional, orderly, and strictly genetically regulated process of cell division and differentiation, governed by complex gene expression regulation. Numerous factors can influence this process, leading to the interruption or even termination of embryonic development[20]. The results of this study clearly demonstrated that the EAP in Red sandalwood was highly significantly negatively correlated with seed IAA content. Se, particularly Se (IV), significantly reduced the EAP, and its most pronounced effect on endogenous hormones was observed in IAA content, which is an important discovery in the scientific cultivation of Red sandalwood, holding significant scientific implications and practical value.

The relationship between endogenous hormones and plant embryo abortion has attracted significant attention from researchers, though most related studies to date have focused on fruit trees. The research on embryo abortion in jujube has found that early-stage embryo development requires relatively high levels of growth-promoting hormones to support growth, and the decrease in IAA content, the increase in ABA content and the reduction in the ($GA_3$ + IAA)/ABA ratio during embryo development are key factors leading to embryo abortion[21]. A study on 'Jinhuang' mango (*Mangifera indica*) resported that 20 − 30 d after fruit set was a critical period for embryo development. During this phase, aborted embryos exhibited higher IAA and ABA contents but lower $GA_3$ and ZT levels than normal embryos. High $GA_3$ and ZT contents coupled with low ABA levels in the embryo favored normal development. The key factors leading to embryo abortion included decreased ZT content, continuously elevated ABA levels, and a ($GA_3$ + IAA + ZT)/ABA ratio in the embryo that was lower than that in the fruit flesh. The critical reasons leading to seed abortion and small fruit size were the low ratio of ($GA_3$ + IAA + ZT)/ABA in both the embryo and the flesh[22].

Regarding embryo abortion in forest trees, a study on the mangrove species *Aegiceras* corniculatum found that changes in the $GA_3$/ABA content ratio could clearly characterize the occurrence of its vivipary. Meanwhile, this ratio also reflected the synergistic regulatory role of endogenous $GA_3$ and ABA in its viviparous process[23]. A study on *Catalpa bungei* showed that the content of endogenous hormones dynamically changes during seed development along with embryonic development. Differences in IAA content and the IAA/ABA ratio were the main reasons for the variation in embryonic development rates between two clones. Early embryonic development required higher levels of growth-promoting hormones, and subsequently, the proportion of growth-inhibiting hormones increased significantly, promoting embryo and seed maturation[24]. A study on the seed development process of Korean pine (*Pinus koraiensis*) indicates that the levels of endogenous hormones changed dynamically along with embryonic morphological development, exhibiting distinct patterns. IAA, ABA, and ZR played significant regulatory roles in the embryonic development of

Korean pine, whereas GAs showed no obvious effect on the development process[25]. These findings indicate that from fruit set to the early stages of growth and development, endogenous hormones in fruits and seeds are closely related to embryo abortion. However, the specific hormones involved, their levels and compositional relationships may vary or even differ considerably among different tree species regarding embryo abortion.

Based on the test results of endogenous hormone contents and the EAP in Red sandalwood seeds during the same period, all fertilization treatments increased the levels of IAA, $GA_3$, ABA, (IAA + $GA_3$), and the (IAA + $GA_3$)/ABA ratio. However, the four treatments involving Se application showed the greatest increases in IAA, $GA_3$, ABA, and (IAA + $GA_3$) contents, significantly surpassing other treatments. Notably, the Se nutritional status had a substantial impact on the (IAA + $GA_3$)/ABA ratio, particularly before the mid-stage of seed development. Meanwhile, statistical analysis results indicated that the EAP at different developmental stages of Red sandalwood seeds showed a highly significant negative correlation with the contents of the three aforementioned endogenous hormones and (IAA + $GA_3$), the (IAA + $GA_3$)/ABA ratio, and the activities of the four antioxidant enzymes. The optimal regression equations for various factors with the EAP were all polynomial regressions. In the absence of human management intervention, among the effects of the three types of hormones and their balance, the IAA content level was the most critical.

The overall results of this study support the aforementioned previous research findings, but one point requires special emphasis, that is, Se application significantly increased the levels of all three endogenous hormones in Red sandalwood seeds as a whole, rather than suppressing the rise in ABA content or its ratio to growth-promoting hormones. Regarding the relationship between GA and seed and fruit growth and development, common understanding mostly focuses on its roles in inducing flowering and parthenocarpy, promoting seed germination, and stimulating stem elongation. In fact, GA not only promotes cell division and accelerates cell growth but also enhances IAA levels in plants. Therefore, it is also a crucial hormone in embryogenesis, and the assurance of fruit set and the proper development of seed embryos and seeds[26-27]. Bioactive GAs regulate various aspects of plant growth and development by promoting cell proliferation and expansion. To date, there have been no reports on the effects of Se application on endogenous hormones in plants.

The production of ROS in living organisms is inevitable, and under oxidative stress, their levels can sharply increase, causing severe damage to cellular structures. Developing seeds are highly susceptible to ROS-induced harm. Therefore, an efficient antioxidant system is essential to ensure normal embryogenesis, preventing oxidative degradation, browning, and death. Antioxidant enzymes such as CAT, APX, SOD and GR possess strong ROS-scavenging capabilities and have been demonstrated to play prominent protective roles in the somatic embryogenesis of tree species such as *Lycium chinense*, *Hevea brasiliensis*, and *Catalpa bungei*[28]. The findings of this study indicated that improving the Se nutrition level in forest soils significantly enhanced the activity of these antioxidant enzymes in Red sandalwood seeds at all developmental stages. Moreover, the EAP at different developmental stages showed a highly significant negative correlation with the activities of these four enzymes, with the order of importance being GR > SOD > APX > CAT. The selenoenzyme GR is even more important, and its implications are particularly significant.

It is generally accepted that Se acts as an antioxidant in plants, primarily functioning to enhance their antioxidant capacity[29]. However, the mechanism by which appropriate levels of Se participate in the plant antioxidant process remains unclear. According to current hypotheses, Se operates through three potential mechanisms: mediating the disproportionation of superoxide anions into $H_2O_2$, directly scavenging superoxide anions and hydroxyl radicals, and regulating the activity of the antioxidant enzyme system. Furthermore, Se can directly or indirectly regulate the formation of antioxidant substances in plants, such as small molecules including reduced glutathione (GSH), ascorbate (AsA), and tocopherol. It is imperative to elucidate the mechanism by which selenium regulates the antioxidant process during seed abortion in Red sandalwood at the molecular level. Therefore, the authors intend to pursue this in future studies.

In summary, Se application may enhance the content and balance of IAA and $GA_3$ during seed growth and development in Red sandalwood through the following regulatory pathways: promoting tryptophan synthesis to provide precursors for IAA, inhibiting IAA oxidase activity to reduce IAA degradation, and upregulating the expression of key enzyme genes involved in $GA_3$ synthesis. It is noteworthy that Se simultaneously increased ABA content but achieved a significant elevation in the (IAA + $GA_3$)/ABA ratio by raising IAA and $GA_3$ levels to a greater extent, which is key to improving embryo development. The role of GR as a core antioxidant enzyme: GR plays a critical role in the AsA-GSH cycle. It maintains glutathione in its reduced state through NADPH-dependent reactions, which is essential for scavenging ROS and preserving cellular redox homeostasis. Se may enhance GR activity through the following mechanisms: serving as a key cofactor in the active center of GR, promoting GR gene expression and protein synthesis, and improving chloroplast function to increase NADPH supply. The potential reasons for the differential mechanisms between Se (IV) and Se (VI) include the fact that Se (IV) is more readily absorbed and reduced by plants, binds to proteins more efficiently, and is more easily incorporated into selenoproteins via the sulfur assimilation pathway.

Se is the core mineral element that mitigates embryo abortion in Red sandalwood induced by relatively low temperatures during fruit development. Application of $Na_2SeO_3$, particularly $Na_2SeO_3$, significantly reduced the EAP, with efficacy far surpassing that of individual applications of KCl, $H_3BO_3$, $CO(NH_2)_2$, $Ca(H_2PO_4)_2$, NPK compound fertilizer, or enzyme-microbe fermented organic fertilizer. The synergistic effect of $Na_2SeO_3$ combined with compound fertilizer, EFOF, or both further significantly enhanced this improvement. Se mitigates embryo abortion in Red sandalwood through a dual regulatory pathway: by enhancing IAA and $GA_3$ levels as well as the (IAA + $GA_3$)/ABA ratio to optimize the hormonal signaling network, and by improving the activity of antioxidant enzymes such as GR to alleviate oxidative stress in-

duced by low temperatures during the cool season. These findings provide a theoretical basis and technical strategy for precision fertilization and stress resistance management in the cultivation of Red sandalwood in tropical regions of China.

## *References*


[1] DEPAEPE T, HENDRIX S, VAN RENSBURG HCJ, *et al.* At the crossroads of survival and death: The reactive oxygenspecies-ethylene-sugar triad and the unfolded protein response[J]. Trends Plant Science, 2021, 26: 338 – 335.

[2] WU Y, SHI L, LI LW, *et al.* Integration of nutrient, energy, light, and hormone signaling via TOR in plants[J]. Journal of Experimental Botany, 2019, 70: 2227 – 2238.

[3] LI N, XU R, LI Y. Molecular networks of seed size control in plants[J]. Annual Review of Plant Biology, 2019, 70: 435 – 463.

[4] QI H, XIA FN, XIE LJ, *et al.* TRAF family proteins regulate autophagy dynamics by modulating AUTOPHAGY PROTEIN6 stability in *Arabidopsis*[J]. Plant and Cell, 2017, 29: 890 – 911.

[5] GONG XF, XU Y, LI H, *et al.* Antioxidant activation, cell wall reinforcement, and reactive oxygen species regulation promote resistance to waterlogging stress in hot pepper (*Capsicum annuum* L.)[J]. BMC Plant Biology, 2022, 22: 425

[6] XIN GL, EVENSON JK, SUNDE RA. Glutathione peroxidase and phospholipid hydroperoxide glutathione peroxidase are differentially regulated in rats by dietary selenium[J]. J Nutr, 1995, 125: 1438 – 1446.

[7] SHI TR, YANG YJ, LIU Q, *et al.* Selenoprotein R: A unique methionine sulfoxide reductase[J]. Progress in Chemistry, 2018, 30(10): 1496 – 1502. (in Chinese).

[8] TINGGI U. Essentiality and toxicity of selenium and its status in Australia: A review[J]. Toxicology Letters, 2003, 137: 103 – 110.

[9] DJANAGUIRAMAN M, DEVI DD, SHANKER AK, *et al.* Selenium: An antioxidative protectant in soybean during senescence[J]. Plant and Soil, 2005, 272: 77 – 86.

[10] ZHANG MM, HAN SH, WANG YN, *et al.* The effect of selenium on the antioxidaut enzyme system of radicle root of *Vicia faba*[J]. Journal of Sichuan Normal University: Natural Science, 2010, 33(2): 239 – 242. (in Chinese).

[11] XU CX, ZENG J, CUI TC, *et al.* Introduction, growth performance and ecological adaptability of Hongmu tree species (*Pterocarpus* Spp.) in China[J]. Journal of Tropical Forest Science, 2016, 28(3): 260 – 267.

[12] XU CX, MA YP, DAN SY, *et al.* Effects of silicon on mineral element absorption, micro-distribution and ion pump activity of Red sandalwood seedlings[J]. Scientia Silvae Sinicae, 2019, 55(10): 1 – 9. (in Chinese).

[13] ZENG QQ, CHEN HB, LU CH, *et al.* An optimized HPLC procedure for analyzing endogenous hormones in different organs of litchi[J]. Journal of Fruit Science, 2006, 23(1): 145 – 148. (in Chinese).

[14] JIANG M, ZHANG J. Effect of abscisic acid on active oxygen species, antioxidative defence system and oxidative damage in leaves of maize seedlings[J]. Plant and Cell Physiology, 2001, 42: 1265 – 1273.

[15] AEBI HE, Catalase. In: Bergmeyer Hu eds. Methods of enzymatic analyses[M]. Weinheim: Verlag Chemie, 1983.

[16] DONAHUE JL, OKPODU MC, CRAMER CL, *et al.* 1997. Responses of antioxidants to paraquat in pea leaves[J]. Plant Physiology, 113: 249 – 257.

[17] HALLIWELL B, FOYER CH. Properties and physiological function of a glutathione reductase purified from spinach leaves by affinity chromatography[J]. Planta, 1978, 139: 9 – 17.

[18] BRADFORD MM. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding[J]. Analytical Biochemistry, 1976, 72: 248 – 254.

[19] CUI KM. Plant development biology[M]. Beijing: Peking University Press, 2022. (in Chinese).

[20] UEDA M, AICHINGER E, GONG W, *et al.* Transcriptional integration of paternal and maternal factors in the *Arabidopsis zygote*[J]. Genes & Development, 2017, 31(6): 617 – 627.

[21] REN HY, WANG YK, ZHAO AL, *et al.* Changes of endogenous hormones during fruit development and their relationship with embryo abortion in *Ziziphus jujuba* 'Lengbaiyu'[J]. Scientia Silvae Sinicae, 2020, 56(4): 55 – 63. (in Chinese).

[22] HE JH, MA FW, SHU HR, *et al.* The change of endogenous hormones in 'Jinhuang' mango fruit with normal and aborted embryo[J]. Acta Horticulturae Sinica, 2012, 39(6): 1167 – 1174. (in Chinese).

[23] YANG SC, LU L, ZHU H, *et al.* Changes in the contents of endogenous ABA, $GA_3$ and carbohydrates during the vivipary of *Aegiceras corniculatum*[J]. Journal of Applied Oceanography, 2021, 40(4): 608 – 613. (in Chinese).

[23] HAN DH, YANG GJ, XIAO Y, *et al.* Dynamic changes of endogenous hormone content in *Catalpa bungei* seeds during their developmental periods[J]. Forest Research, 2021, 34(1): 56 – 64. (in Chinese).

[25] LIANG Y, SHEN HL, GAO ML, *et al.* Content dynamics of endogenous hormones in different seed developmental stages of korean pine[J]. Scientia Silvae Sinicae, 2016(3): 105 – 111. (in Chinese).

[26] OKABE Y, YAMAOKA T, ARIIZUMI T, *et al.* Aberrant stamen development is associated with parthenocarpic fruit set through up-regulation of gibberellin biosynthesis in tomato[J]. Plant Cell Physiol, 2019; 60(1): 38 – 51.

[27] JI XZ, LI HL, WANG G, *et al.* Activity during somatic embryogenensis of two litchi cultivars[J]. Chinese Journal of Tropical Crops, 2018, 39(4): 681 – 686. (in Chinese).

[28] ELKELISH AA, SOLIMAN MH, ALHAITHLOUL HA, *et al.* Selenium protects wheat seedlings against salt stress-mediated oxidative damage by up-regulating antioxidants and osmolytes metabolism[J]. Plant Physiology and Biochemistry, 2019, 137: 144 – 153.

[29] DI XR, QIN X, ZHAO LJ, *et al.* Selenium distribution, translocation and speciation in wheat (*Triticum aestivum* L.) after foliar spraying selenite and selenite[J]. Food Chemistry, 2023, 400: 134077.

[30] HASANUZZAMANA M, BORHANNUDDIN BHUYANB MHM, RAZAC A, *et al.* Selenium in plants: Boon or bane[J]. Environmental and Experimental Botany, 2020, 178: 104170.


Editor: Yingzhi GUANG Proofreader: Xinxiu ZHU