Dynamic Changes in Endogenous Hormones in Terminal Buds from Different Crown Positions in *Sequoia sempervirens* (Lamb.) Endl

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Abstract. Endogenous hormones can improve plant resistance and regulate growth and development. To obtain the basis of chemical control technology for improving *Sequoia sempervirens* resistance in Xuzhou, China, the current study probed the dynamic changes of endogenous hormones in terminal buds from different crown positions in *S. sempervirens*. Enzyme-linked immunosorbent assay (ELISA) was used to measure changes in the contents of endogenous hormones in terminal buds from the upper, middle, and lower lateral branches. The results were as follows: Indole acetic acid (IAA) in all terminal positions had a similar change trend of “rise–drop–rise.” Gibberellic acid (GA) in the upper and middle terminal buds showed similar trends of “drop–rise,” but GA in the lower lateral branches presented a “rise–drop” trend. Zeatin–riboside (ZR) in all terminal positions had similar change trends of “drop–rise.” Abscisic acid (ABA) in all terminal positions had similar change trends of “drop–rise–drop.” the trend of (IAA + GA + ZR)/ABA in all terminal positions was the same as that of IAA. Our results confirmed that, in autumn, the high content and ratio of stimulatory endogenous hormones in the terminal bud of *S. sempervirens* induced the terminal bud cells to continue to divide and grow, and the new branches could not be fully lignified and deeply dormant before the onset of low temperatures in winter, which led to a decrease in cold resistance and even the death of the terminal buds.

Sequoia sempervirens belongs to cedar, a relict plant. Natural forests of *S. sempervirens* in North America are now found only in a narrow strip along the California coast. *S. sempervirens*, which grows quickly and lives for many years (Chang et al., 2015), is one of the five largest ornamental tree species in the world, and has high value for cultivation and

promotion (Ju et al., 2009). Therefore, in past years, *S. sempervirens* has been introduced to various parts of the world. It was first introduced to China in 1972 and has been now cultivated in many southeastern areas (Sheng et al., 2017). *S. sempervirens* was first planted in Xuzhou on a trial basis in 2000. During the process of cultivation in autumn and winter, its terminal buds were lost and, the next spring, the lateral buds sprouted into new branches. Considering the habitable environment of *S. sempervirens* and the living environment in Xuzhou (Ju et al., 2019; Zhang et al., 2015), the causes of terminal bud death were analyzed. There are three possible explanations. First, terminal bud death in *S. sempervirens* can be the result of low temperatures in winter (Luo et al., 2013). In addition, before the arrival of cold air, the *S. sempervirens* buds are not fully lignified, which contributes to their death. Observation of trees under cultivation has shown that not all terminal buds are dead; the rate of death is 30%. When the degree of lignification is high, a bud does not die. Second, this problem may be a result of a water deficit in *S. sempervirens*. The weather is dry and windy during the winter in Xuzhou, which impairs lignification in *S. sempervirens* branches, so

terminal buds die because of a shortage of water (Luo et al., 2013). Observation of trees under cultivation has shown that *S. sempervirens* planted beneath shelter performed better than those planted in the open ground in terms of the death of terminal buds. Third, and last, low temperatures and the shortage of water may combine to cause terminal bud death in *S. sempervirens* (Zuo et al., 2000).

These options indicate directions for exploring the mechanism of bud death of *S. sempervirens*. However, the death of the terminal bud is a complicated process, and can be influenced by many internal and external factors (Wang et al., 2012). The concentration and ratio of hormones have a significant regulatory effect on plant resistance (Karimi, 2017; Wang et al., 2012; Yuan et al., 2020). Studies have shown that cells resisted freezing temperatures by dehydration or the accumulation of sugar and protein complexes bound to water, thereby avoiding freezing, which destroys cells and leads to death, and all processes are coordinated by hormones and the perception of temperature (Chen et al., 2006; Karimi, 2017). At the same time, most researchers thought that endogenous hormone signaling could adjust the growth and development of buds, and affect woody plant adaptation mechanisms such as bud death (Arora et al., 2003; Pan and Dong, 1998; Wang et al., 2012). During the annual growth cycle of *S. sempervirens*, there are obvious growth rhythms resulting from the influences of the internal environment and external factors that lead to the formation of multiple new branches (Lochard and Schneider, 1981). For plant endogenous hormones, it is generally acknowledged that IAA, GA, and ZR are stimulatory hormones; ABA is a suppressive hormone. IAA is the most ubiquitous auxin in higher plants, which affects cell division, cell elongation, and cell differentiation (Mwange et al., 2005; Sivaci and Yalcin, 2008). ABA is associated with plant dormancy, meaning that high levels lead to plant dormancy and low levels benefit the plant by releasing dormancy and promoting growth and germination (Sivaci and Yalcin, 2008; Zhang et al., 2020). The hormones GA and ZR not only stimulate the growth of plants, but also are linked to the differentiation of plant buds (Peng et al., 2013; Wu et al., 2017). The regulation of plant endogenous hormones on plant growth and development is related to a certain type of hormone and the ratio between different hormones. Studies have shown that an increased ABA/GA ratio is closely related to enhanced cold resistance (Zheng et al., 2009).

Numerous studies have explained the physiological mechanisms of endogenous hormones on plant stress resistance, and growth and development (Shi et al., 2006). Currently, no research describes the dynamic changes of endogenous hormones in the terminal buds of *S. sempervirens*. The purpose of our study was 1) to determine the content of endogenous hormones in the terminal buds of *S. sempervirens* in different seasons; 2) to analyze the variation characteristics of

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Table 1. Mean meteorological conditions during the sampling periods (1981–2010).

Meteorological parameters	Mo.											
	1	2	3	4	5	6	7	8	9	10	11	12
Mean temperature (°C)	0.7	3.5	8.6	15.6	21.1	25.4	27.3	26.4	22.1	16.2	8.8	2.8
Humidity (%)	66	64	62	61	64	67	79	81	75	69	69	66
Total rainfall (mm)	18	20	36	47	66	107	241	133	72	52	27	14

endogenous hormones in different seasons, combined with the climatic characteristics of Xuzhou; and 3) to explore the relationship between the content or proportion of endogenous hormones and terminal bud death to provide a theory for the technology of chemical control in the production of *S. sempervirens* in Xuzhou.

Materials and Methods

Test site location. The test site was located at the Xuzhou Institute of Technology nursery base in Xuzhou, Jiangsu Province, China (lat. 34°15'N, long. 117°11'E), which has a warm temperate and semihumid monsoon climate. The annual average temperature is 14.58 °C, the annual average lowest temperature is -10.52 °C (1960–2018), and the extreme minimum temperature is -22.6 °C (noted in 1969, which is in our study range of 1960–2018). The annual sunshine duration is 2284 to 2495 h, and the relative sunshine duration is 52% to 57%. The annual accumulated temperature is 5143.5 °C, the average annual frost-free period is ≈210 d, and the average annual precipitation is 853.1 mm. The soil at the test site is a sandy soil, and the pH is 8.3 (Ju et al., 2020; Wang et al., 2010). Some of the meteorological conditions encountered during the sampling period are presented in Table 1.

Experiment materials. We used 6-, 8-, and 9-year-old *S. sempervirens* as experiment materials. The sampling times were spring (15 Apr.), summer (15 July), autumn (15 Oct.), and winter (15 Jan.). In case of rain, the sampling time was adjusted by 3 d, so the weather was observed in advance. During sampling, three samples were taken from each plant, and the sampling sites were mainly the upper terminal bud (the terminal bud of the second-layer branch from the top to the bottom of the crown), the middle terminal bud (the terminal bud of the middle-layer branch of the crown), and lower terminal bud (the terminal bud of the bottom-layer branch of the crown). Samples were taken from four directions and each material was equivalent.

Determination of endogenous hormone content. Measurement of the endogenous hormones IAA, GA, ZR, and ABA of *S. sempervirens* terminal buds was performed using ELISA (Wu et al., 1993). The ELISA kit was purchased from China Agricultural University. It measured optical density at 490 nm and drew a calibration curve, then calculated the IAA, GA, ZR, and ABA levels. Each sample assay was repeated three times and, after excluding abnormal data, the data were averaged for analysis (Zhou et al., 2014). Calculation was performed using the regression method to establish a logit curve.

Data processing. SPSS 19.0 analysis software (SPSS Inc., Chicago, IL) was used to analyze the measurement data. Differences between different treatments were analyzed using one-way analysis of variance with Tukey's test at a significance level of $P < 0.05$. Origin 8.0 software (OriginLab Corp., Northampton, MA) was used to produce a plot.

Results

Changes in IAA content in different terminal positions in *S. sempervirens*. As shown in Fig. 1, the trend of IAA in terminal buds from different crown positions was “rise-drop-rise.” In winter, IAA content in terminal buds was low, and plants were in a period of dormancy. In spring, IAA content was generally high, which indicates active bud growth. In summer, IAA content at the different positions was decreasing, which indicates that bud growth had declined. However, IAA content increased again, showing that the plants had an additional growing season in autumn. In addition, at that time, IAA content of the upper terminal bud was greater than that of the middle and lower terminal buds.

Changes in GA content in different terminal positions in *S. sempervirens*. As shown in Fig. 2, the trends of GA in the upper, middle, and lower terminal buds were obviously different. In winter, the GA content in the upper and middle terminal buds were greater than those of the lower buds. From winter to summer, GA content in the upper and middle terminal buds decreased gradually, whereas those of the lower terminal buds increased gradually. From summer to autumn, GA content in the upper and middle terminal buds increased gradually; however, those of the lower terminal buds decreased gradually. In autumn, GA content of the upper terminal buds were the greatest; those of the lower terminal buds were the lowest.

Changes in ZR content in different terminal positions in *S. sempervirens*. As shown in Fig. 3, changes in ZR content in the upper, middle, and lower terminal buds resembled a “V” shape, or a “drop-rise” trend. In winter, ZR content in the middle and lower terminal buds was generally high. From winter to summer, ZR content in the upper, middle, and lower terminal buds increased gradually, reaching its lowest point of the year when *S. sempervirens* is dormant in summer. From summer to autumn, ZR content from the different crown positions increased gradually, and not much difference was observed among the three locations. The basic biological function of ZR is to promote cell division. Because ZR content in terminal buds at different positions was not low in autumn, *S. sempervirens* was still growing quickly in autumn.

Fig. 1. Change in indole acetic acid (IAA) content in different terminal positions in *S. sempervirens*. Different letters indicate significant differences at $P < 0.05$. FW, fresh weight.

Fig. 2. Change in gibberellic acid (GA₃) content in different terminal positions in *S. sempervirens*. Different letters indicate significant differences at $P < 0.05$. FW, fresh weight.

Changes in ABA content in different terminal positions in S. sempervirens. As shown in Fig. 4, the trend of ABA content in terminal buds from different crown positions was “drop–rise–drop.” In winter, when the plants were dormant, ABA content in the upper terminal bud was the lowest, and those in the middle and lower terminal buds were generally greater. From winter to spring, ABA content in terminal buds from different crown positions decreased significantly, reaching

the first minimum of the year, which indicates that *S. sempervirens* began its period of growth. From spring to summer, the terminal buds in all three positions showed a gradually increasing ABA content, and that of the middle terminal bud showed a major change. From summer to autumn, ABA content from all three positions decreased gradually and reached the second minimum of the year, which indicates these plants grow vigorously in autumn.

Fig. 3. Change in zeatin-riboside (ZR) content in different terminal positions in *S. sempervirens*. Different letters indicate significant differences at $P < 0.05$. FW, fresh weight.

Changes in the ratio (IAA + GA + ZR)/ABA in different terminal positions in S. sempervirens. As shown in Fig. 5, the trend in the ratio of (IAA + GA + ZR)/ABA in terminal buds from different crown positions in *S. sempervirens* was similar to that of IAA. From winter to spring and from summer to autumn, the ratios increased, and they reached a peak in spring. From spring to summer and from autumn to winter, the ratios of the upper, middle, and lower terminal buds were all decreasing, and they reached a minimum. In winter and summer, the ratios were all less than one, indicating that inhibitory hormones dominated and the plant was dormant. However, in spring and autumn, the ratios were more than one, which shows that growth-promoting hormones dominated and the plant was actively growing.

Discussion

Ecological factors such as temperature, drought, photoperiod, and so on affect endogenous hormones levels (Sivaci and Yalcin, 2008; Zhang et al., 2020). Plant physiology studies have shown that the effect of external factors on plant growth and development is realized through the regulation mechanism of endogenous hormones (Pan and Dong, 1998). Our study shows that endogenous hormones levels vary with the seasons (Figs. 1–5). After the introduction of *S. sempervirens* to Xuzhou, IAA content in terminal buds from different crown positions showed a similar change trend of “rise–drop–rise” (Fig. 1), which was consistent with the growth type of a double peak in spring and autumn. Some studies have shown that IAA content in scales of *Lilium longiflorum* (Okubo et al., 1988), leaves of *Cinnamomum pauciflorum*, and terminal buds of *Paulownia* (Wang et al., 2012) also demonstrate a similar seasonal variation trend. Considering the climate characteristics of the introduced region (Xuzhou, East-central China; Table 1) and provenance region (Eureka, western North American) (Zhang et al., 2015), the growth patterns of a double peak were influenced by climate and regulated by IAA (Bai and Yu, 2005). In the cool autumn in Xuzhou, a rapid growth of *S. sempervirens* led to new branches being unable to become sufficiently lignified and deeply dormant before the onset of low temperatures in winter, which may reduce cold resistance and be one of the mechanisms of bud death in winter. Rajagopal et al. (1988) showed that a low auxin (1-naphthyl acetic acid) content promoted lignification of *Cuscuta*. Hang and Wang (1982) suggested that for the strongly cold-resistant varieties of *Malus* sp., the lignification of the branches was greater in degree and occurred at a faster rate.

GA has the effects of promoting high growth, enhancing apical dominance, and delaying senescence (Yan et al., 2010). Studies of the seasonal dynamic change of GA content in plants such as *Actinidia arguta* (Yuan et al., 2020) and *Lilium longiflorum* (Sivaci and Yalcin, 2008) showed that low-temperature stress in winter

Fig. 4. Change in abscisic acid (ABA) content in different terminal positions in *S. sempervirens*. Different letters indicate significant differences at $P < 0.05$. FW, fresh weight.

reduced GA content, which induced dormancy, inhibited plant growth, and was conducive to safe overwintering of plants. However, our study showed inconsistent results. In the upper and middle terminal buds, GA content in winter was significantly greater than that in spring and summer, which is not conducive to *S. sempervirens* hibernation and safe overwintering. *S. sempervirens* could have inherited

from its ancestors this growth and germinate characteristic that acts during the winter wet season in western North America in December and January (Zhang et al., 2015). Mwange et al. (2005) showed that *Eucommia ulmoides* introduced to the north temperate zone could have inherited from its tropical ancestors this dormant characteristic that acts during the dry and hot season. In our study, in autumn, GA content of the

lower terminal bud reached its lowest point of the year, but GA content of the upper and middle terminal buds was very high, which shows that *S. sempervirens* continued to grow by rapid elongation in autumn. This situation was unfavorable for the formation of a dormant bud. Patel and Franklin (2009) believed that reducing GA concentration could limit plant elongation and thus improve plant cold resistance.

The basic physiological function of ZR is to promote cell division (Wang et al., 2012). Studies by Lisabeth (1971) on *Populus tremula*, *Acer platanoides*, and *Betula verrucosa*; by Kong et al. (2009) on *Pseudotsuga menziesii*; and by Pan et al. (2000) on *Camellia sinensis* showed that ZR content in buds increased obviously at the bud initiation stage. Studies on the dynamic change of ZR content showed that low-temperature stress reduced ZR content in plants in winter, as seen in *Ginkgo biloba*, *Salix babylonica*, *Acer mono*, and *Cotinus coggygria* (Zhang et al., 2020), and *Lilium longiflorum* (Sivaci and Yalcin, 2008), which reduced cell division of terminal buds, induced plant dormancy, and was beneficial to safe overwintering. However, our study showed inconsistent results. ZR content in winter was significantly greater than that in spring, summer, and autumn. *S. sempervirens* could have inherited from its ancestors this growth and germinate characteristic that acts during the winter wet season in western North America during December and January (Zhang et al., 2015). A high concentration of ZR in winter was not conducive to hibernation and safe overwintering of *S. sempervirens*.

ABA is a well-known stress hormone (Yang et al., 2008; Zheng et al., 2009). Studies have shown that ABA plays an important role in balancing growth and climate adaptation (Yu et al., 2019). In our study, ABA content in terminal buds of *S. sempervirens* showed a trend of “drop-rise-drop-rise.” High temperatures in summer and low temperatures in winter induced an increase in ABA content in buds, which improved resistance to temperature stress. Previous studies showed that high temperatures in summer can increase ABA content significantly in the terminal buds of *Paulownia* (Wang et al., 2012), and low temperatures in summer can increase ABA content significantly in the buds of *Acer saccharum* (Dumbroff et al., 1979). In our study, ABA content from different terminal bud positions reached its lowest value of the year in autumn, which shows that the plants grew well during this period and were not prepared for dormancy.

The effects of endogenous hormones on plant growth and development depend not only on the absolute contents of some endogenous hormones, but also on the dominant hormone during a certain period, which assumes a guiding role (Brenner, 1989). The ratio of (IAA + GA + ZR)/ABA could reflect plant growth conditions. A low ratio indicates that suppressive hormones are dominant and plants are dormant; a high ratio indicates that stimulatory hormones are dominant and plants are actively growing (Li et al., 2007; Wang et al., 2012). In

Fig. 5. Change in the ratio [(indole acetic acid + gibberellic acid + zeatin-riboside)/abscisic acid] in different terminal positions in *S. sempervirens*. Different letters indicate significant differences at $P < 0.05$.

our study, on the whole, the range of change from winter to spring was greater than that from summer to autumn. From summer to autumn, the ratio of (IAA + GA + ZR)/ABA increased. According to the previous single-hormone analysis, this was mainly a result of a greater IAA, GA, and ZR content, rather than a decrease in ABA content in autumn. The larger ratio of (IAA + GA + ZR)/ABA indicates that *S. sempervirens* was still in the active growth period in autumn, which is also consistent with the peak growth of *S. sempervirens* in the autumn. This made the branches unable to be sufficiently lignified and deeply dormant before the onset of low temperatures in winter, which might be one of the mechanisms of bud death in winter. Practices have also proved this point in reverse. The application of the growth inhibitor paclobutrazol and calcine during autumn could inhibit significantly the growth of redwood branches and improve the cold resistance of the tree (Ju et al., 2019, 2020).

The regulation of endogenous hormones in plant morphology is a complicated process. One kind of hormone can participate in multiple physiological processes (Culter and Vltos, 1962). Our study showed that the death of terminal buds of *S. sempervirens* was closely related to endogenous hormones, and confirmed that, in autumn, the high content and ratio of stimulatory endogenous hormones in the terminal bud of *S. sempervirens* induced the terminal bud cells to continue to divide and grow. This did not allow the new branches to become fully lignified and deeply dormant before the onset of low temperatures in winter, which led to a decrease in cold resistance and even the death of the terminal buds.

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