Foliar spraying of plant growth regulators can alleviate high-temperature stress in late-sown spring potatoes to improve yield and quality

Chao Wu

wuchao9382@163.com

Sichuan Agricultural University

Wensen Huang

Sichuan Agricultural University

Xiaoting Fang

Sichuan Agricultural University

Haiyan Ma

Sichuan Agricultural University

Wenwen Song

Sichuan Agricultural University

Kaiqin Zhang

Sichuan Agricultural University

Zhitong Ren

Sichuan Agricultural University

Muhammad Amir Shahzad

Sichuan Agricultural University

Dawa Dolker

Sichuan Agricultural University

Cuiqin Yang

Sichuan Agricultural University

Shunlin Zheng

Sichuan Agricultural University

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Abstract

In practice, late sowing of spring potatoes is commonly adopted to bridge crop rotation and mitigate natural disasters, inadvertently facilitating high-temperature conditions during the latter growth phase, leading to diminished tuber yield and quality. To avert these setbacks, this experiment explored the influence foliar applications of plant growth regulators like Diethyl aminoethyl hexanoate (DTA-6), Uniconazole (S3307), Abscisic acid (S-ABA), and Salicylic acid (SA) on Zhongshu Zao 45 (ZZ45), a late-sowing tolerant variety, and Yunshu 902 (Y902), a sensitive variety. The findings indicated that spraying growth regulators can effectively upgrade the agronomic attributes of late-sown spring potatoes: They curbed the above-ground part of growth, boosted the root-top ratio, promoted dry matter accumulation in the below-ground part, and regulated leaf area index. Physiologically, they increased leaf SPAD value and net photosynthetic rate, reduced MDA and proline content, ultimately increasing yield and improving quality. In the case of the late sowing tolerant variety Zhongshu Zao45 and sensitive variety Yunshu902, S-ABA and S3307 respectively produced the most effective results. A further investigation discovered that S-ABA and S3307 both pitch in endogenous hormone regulation, augmenting antioxidant enzyme activity to bolster plant resilience and alleviate adversity stress from late-sown high temperatures. By selecting appropriate growth regulators for different varieties, it is possible to achieve stable yield and improved quality for late-sown spring potatoes. This study furnishes theoretical insights into the field production of late-sown potatoes.

1. Introduction

Potato (*Solanum tuberosum* L.) uses tubers as its main economic organ, with temperature playing a crucial role in tuber formation (Mokrani et al. 2022). Potatoes prefer cool environments but are not tolerant to high temperatures. The suitable temperature for aboveground plant growth is 20–25 ℃, and for underground tuber formation is 15–20 ℃ (Tang et al. 2018). However, in agricultural practice, potato planting times are typically staggered to align with crop rotations, previous crops such as vegetables may be harvested later than the spring potato sowing time (Gao et al. 2022; Blecharczyk et al. 2023). At the same time, potatoes may be affected by natural disasters such as cold waves and cold temperatures in late spring, leading to the withering and death of potato plants (Yan et al. 2021). To avoid this phenomenon, spring potato sowing time is intentionally delayed to incorporate crop rotation and mitigate seedling cold exposure (Shimoda et al. 2018). Unfortunately, although this strategy is suitable for seedling development, it can lead to sustained high-temperature conditions during tuber formation, hindering tuber size and quantity formation (Trapero-Mozos et al. 2018). It can also lead to deformed and secondary tubers, causing yield loss and diminished harvest returns (Paul et al. 2017). Notably, elevated temperature impairs plant photosynthesis, which disrupts dry matter accumulation, diminishing starch and protein levels in potato tubers, and impairing tuber quality (Hancock et al. 2014). Recently, research has intensified on late-sown thermal strain on potatoes, yet field-based adaptations remain limited, leading to substantial yield losses.

Plant growth regulators exert similar effects on plant hormones and can effectively regulate every reproductive process of plants, including enhancing crop resistance, stabilizing yields, and improving quality (Głosek-Sobieraj et al. 2018). Diethyl aminoethyl hexanoate (DTA-6) can increase the nutritional content of crops, including protein, amino acids, vitamins, etc. It also promotes potato creeping and tuber formation (Liu et al. 2018). Uniconazole (S3307), primarily inhibits apex meristem cell elongation, controlling plant apex overgrowth, and thickening dark green foliage (Keshavarz and Khodabin 2019). Abscisic acid (S-ABA) rebalances plant endogenous hormones, attaining an optimal root-top ratio, accelerates ripening, improves quality, and amplifies fruit size (Rehman et al. 2018). Salicylic acid (SA) can reduce the damage caused to plants under adversity stress and is widely used to improve plant stress tolerance (Faried et al. 2017). Topical sprays of these growth regulators at plausible ranges can enhance potato productivity and quality (Ahmadi-Lahijani et al. 2021; Pavlista 2011; Thornton et al. 2013), but the application effect on late-sown spring potatoes has not yet been reported.

The objective of this research is to analyze the effects of four growth regulators (DTA-6, S3307, S-ABA, and SA) on the development, photosynthetic capacity, stress resistance, quality, and yield of late-sown spring potatoes. Two ideal regulators were selected to dynamically detect endogenous hormones and antioxidant enzyme activities, thereby, assessing the response of potato plants to growth regulator manipulation. These results provide a theoretical foundation for the application of field production technologies that promote consistent yield and harvest of late-sown spring potatoes.

2. Materials and methods

2.1. Site description

The experiment ran from Dec. 2020 to Dec. 2022 at Sichuan Agricultural University's experimental base (30° 42'57.80" N, 103° 52'25.65" E), sub-tropical and humid. The terrain is relatively level with uniform plots and soil fertility. The soil texture is sandy with 29% sand, 50% silt, and 21% clay in the topsoil. Basic fertility data for the field are in Table 1, and the daily mean temperatures during growth are displayed in Fig. 1. First-year sowing produced an average temperature of 11.8°C for normal and 16.4°C for late. Second-year sowing rendered an average temperature of 13.1°C for normal and 18.5°C for late.

Table 1
Soil base fertility in the field.

Time	Total nitrogen (g/kg)	Total phosphorus (g/kg)	Total potassium (g/kg)	Alkali-hydro nitrogen (mg/kg)	Olsen-P (mg/kg)	Available-K (mg/kg)	Organic matter (g/kg)	pH value
2020-2021	2.16	1.59	14.01	136.71	19.01	111.25	26.82	6.02
2021-2022	2.02	1.45	19.33	125.19	17.11	117.39	25.09	5.94

2.2. Experimental materials

Experimental Materials In 2019, 15 test varieties were selected, including Zhongshu18 (Z18), Zhongshu19 (Z19), Zhongshu26 (Z26), Zhongshu28 (Z28), Zhongshu Zao35 (ZZ35), Zhongshu Zao39 (ZZ39), Zhongshu Zao45 (ZZ45), Zhongshu Zao47 (ZZ47), Zhongshu zao660 (ZZ660), Zhongshu Hong1 (ZH1), Zhongshu Hong (ZH3), and Zhongshu Purple No.4 (ZP4), Yunshu 304 (Y304), Yunshu 902 (Y902), Hongmei (HM). By measuring agronomic traits, starch, net photosynthetic rate, and yield under normal and late sowing conditions, late-sowing tolerant potato Zhongshu Zao45 and intolerant potato Yunshu 902 were selected (Fig. 2). The growth regulators chosen included DTA-6, S3307, S-ABA, SA, all provided by Sichuan Guoguang Agrochemical Co., Ltd (China).

2.3. Experimental design

2.3.1. Experimental design Year 1

Year 1 explored the effect of growth regulators on the development of late-sown spring potatoes. A two-factor randomized block design was adopted in this experiment, with the treatment factors being variety and growth regulators. Normal sowing of ZhongshuZao 45 and Yunshu 902 on Dec. 15, 2020, was used as CK1 treatment. Each variety was sown in three small plots, and the experiment adopted single-row planting in the field. Each plot had 9 rows, a ridge height of 30 cm, a planting depth of 10–15 cm, a length of 3.6 m, a width of 4 m, an area of 14.4 m^2, a row spacing of 0.9 m, a plant spacing of 0.2 m, and 55556 plants per hectare. Compound fertilizer (N: P: K = 16:6:18) and herbicides were applied after sowing. The same varieties of potatoes were late-sown on February 27, 2021, and the field management measures were consistent with the last December sowing. For the late-sown potatoes, four growth regulators were sprayed when the plants were in the bud, with distilled water serving as the control (CK2). The spraying took place on the surface of the potato leaves in the evening on a sunny day with no rain and no strong winds. Each growth regulator was sprayed until the leaf surface was wet, and the leaf edges had water droplets. DTA-6 was applied at 30 mg/L, S3307 at 40 mg/L, S-ABA at 10 mg/L, and SA at 25 mg/L.

2.3.2. Experimental design Year 2

Year 2 screened two growth regulators from year 1 that could effectively alleviate late-sown high-temperature stress. The activity of endogenous hormones and antioxidant enzymes in potato leaves was dynamically detected to explore the response of plants to growth regulators. Simulated late sowing high temperatures were used in the experiment, which was conducted on August 26, 2022, by planting potted plants in the climate room of the second teaching building of Sichuan Agricultural University. The light temperature cycle was 12 hours with 25 °C light and 12 hours with 20 °C darkness. Four treatments were established, Zhongshu Zao45 sprayed with S-ABA and no spray (CK); Yunshu902 sprayed with S3307 and no spray (CK). Growth regulators were sprayed during the budding stage of each variety. Planting 6 pots per treatment, totaling 24 pots, with a pot size of 24 cm × 23 cm, cultured in a matrix, V (vermiculite): V (perlite) = 3:1. After sowing, water thoroughly with clean water, and then water every 7 days with 250 mL of Hoglan nutrient solution until seedlings emerge.

2.4. Plant sampling and measurements

2.4.1. Agronomic traits and dry matter accumulation.

Plant samples were collected post-spraying growth regulators (at 0 and 20 days) to differentiate consistent growth, pest/disease-free specimens. Plant height was determined by measuring the length from its stem base to its apex. The stem diameter was calculated as the average of the lateral and longitudinal widths at the base. 20 fresh leaves were collected, drilled, and their weights relative to the entire plant were recorded to calculate leaf area. Leaf Area Index (LAI) – a ratio of leaf area to land area – was computed using these values (Wei et al. 2020). For data collection, the entire plant was excavated, cleaned, and divided into four parts (stem, leaf, root, and tuber). All tissue was killed at 105 °C for 30 min, dried at 80 °C to a constant weight, and weighed. Following this, the dry weight of each organ was documented, and the ratio of above and belowground parts was calculated as the root-top ratio.

2.4.2. Measurement of physiological indices

LI-6400 portable photosynthesizer (USA) measured net photosynthetic rate (Pn) between 9:30 – 11:30 on sunny days at 0, 10, and 20 post-regulator spraying days. Using SPAD-502 chlorophyll rapid analyzer (Japan) to determine SPAD value. Determination of malondialdehyde (MDA) content using a two-component spectrophotometer method (Dogan et al. 2016). Determination of proline (Pro) by sulfosalicylic acid extraction method (Liu et al. 2022).

2.4.4. Yield and its components

Harvest when 50% of the leaves in the entire field turn yellow. First, count the number of plants in each plot, and then weigh and calculate the yield after harvesting all the plants (excluding diseased, rotten, and insect-infested potatoes). In addition, observe the number of potatoes per plant, average weight per plant, commodity rate, and average yield. The commodity potato yield adopts the three-level commodity potato classification according to the GB/T 31784 – 2015 standard (China), which means that no less than 75 g of potato blocks are classified as commodity potatoes. On average, 1.5% of the gross weight of harvested potato pieces is deducted for impurities and soil content.

2.4.5. Endogenous hormone and antioxidant enzyme activity

Post-day-1, -7, -14, and – 21 growth regulator application, extract the penultimate fully expanded leaf from the main stem and store it in liquid nitrogen. ELISA kits (Jiangsu Enzyme Immunoassay Industry Co., Ltd., China) were employed for plant hormone analysis including indole-3-acetic acid (IAA), cytokinin (CTK), gibberellin (GA), abscisic acid (ABA), and jasmonic acid (JA). Superoxide dismutase (SOD) using the nitrogen blue tetrazole photoreduction method (Che et al. 2020), Peroxidase (POD) using the guaiacol method (Minaeva et al. 2022), Catalase (CAT) using the UV absorption method (Zhang et al. 2017).

2.5. Statistical analyses

We employed Microsoft Excel 2021 for data processing and calculations, IBM SPSS Statistics (Windows version 27.0) for $P < 0.05$ significance testing and ANOVA, and Origin2022 for plotting and correlation analysis.

3. Results

3.1.Effect of growth regulators on agronomic traits in late-sown spring potatoes

The plant height and stem diameter of late-sown potatoes (CK2) were significantly increased compared to normal-sown potatoes (CK1), and the root-top ratio was significantly reduced compared to normal-sown potatoes. However, after spraying growth regulators on late-sown potatoes, plant height and stem diameter decreased compared to CK2, and root-top ratio increased (Fig. 3). At Zhongshu Zao 45, S-ABA and S3307 treatments had a better effect than DTA-6 and SA, and S-ABA treatment had the best effect. After 20 days of S-ABA treatment, compared with CK2, plant height was significantly reduced by 16.40%, stem diameter was significantly reduced by 20.18%, and root-top ratio was significantly reduced by 31.05% (Fig. 3A). In Yunshu 902, the treatment with S3307 had the best effect. On the 20th day of spraying, the plant height and stem diameter were significantly reduced by 20.53% and 10.27%, respectively, compared to CK2, and the root-top ratio was significantly increased by 57.37% (Fig. 3B).

3.2. Effect of growth regulators on dry matter accumulation in potatoes

The accumulation of roots, stems, leaves, tubers and total dry matter in late sown potatoes (CK2) showed significant differences compared to normal sowing (CK1). However, after spraying with growth regulators, dry matter accumulation in different organs of late-sown potatoes reached an ideal effect (Fig. 4). At Zhongshu Zao45, the dry matter accumulation of roots, stems and leaves hardly changed with four growth regulators compared to CK2. However, the total dry matter and tuber dry matter of late-sown potatoes increased the most under S-ABA treatment compared with CK2, with a significant increase of 10.58% and 18.28% on the 20th day of treatment, respectively (Fig. 4A). In Yunshu 902, the four growth regulators had minimal impact on the accumulation of stems, leaves, and total dry matter, but significantly impacted tubers and roots. S3307 had the best treatment effect, with a significant increase of 63.18% and 33.21% in dry matter accumulation of roots and tubers compared to CK2 on the 20th-day post-spraying, and a significant decrease of 20.23% and 11.48% in stems and leaves, respectively (Fig. 4B).

3.3. Effect of growth regulators on the physiology in potato leaves.

The leaf Pro content, MDA content and LAI of Zhongshu Zao 45 and Yunshu 902 showed an increasing trend with the lengthening of the growing season. The SPAD content and Pn of Yunshu 902 showed an increasing trend, while these two indicators of Zhongshu Zao 45 first showed an increasing trend and then a decreasing trend (Fig. 5). In the four growth regulator treatments, the levels of SPAD and Pn were higher than CK2 over time, while the levels of Pro, MDA and LAI were generally lower than CK2. At day 10, SPAD and Pn levels of Zhongshu Zao 45 and Yunshu 902 increased the most compared to CK2 under DTA-6 treatment, while Pro and MDA levels decreased the most. LAI levels did not differ significantly between treatments. On day 20, SPAD, Pn and LAI values of Zhongshu Zao 45 were highest under S-ABA treatment and significantly higher than CK2, while Pro and MDA values were lowest, also significantly lower than CK2 (Fig. 5A). The SPAD and Pn values of Yunshu 902 were the highest under S3307 treatment, significantly higher than CK2, while the Pro values were the smallest and significantly different. Under the DTA-6 treatment, the MDA values decreased the most compared to CK2 (Fig. 5B). The LAI values of the two varieties showed no differences between the treatments, but both had the lowest values under the S3307 treatment.

2.4.3. Tuber quality

Take the dry matter from the tubers and use the anthrone colorimetric method to determine the starch content (Kumar et al. 2018). Measurement of reducing sugar content using the 3,5-dinitro salicylic acid method (Muttucumaru et al. 2017). Using a fully automatic Kjeltec 8400 nitrogen analyzer, the total nitrogen content was first measured, and the total protein content was 6.25 times the total nitrogen. Determination of ascorbic acid content using molybdenum blue colorimetric method (Tang et al. 2023).

3.4. The effect of growth regulators on the quality of potatoes

The starch and protein content of late-sown potatoes (CK2) was significantly reduced compared to normal-sown potatoes (CK1), while the content of reducing sugars and ascorbic acid was significantly increased. However, after spraying four growth regulators on late-sown potatoes, the starch, protein and ascorbic acid contents were increased compared to CK2, and the reducing sugar content was suppressed, which improved the overall quality of the potatoes (Fig. 6). In Zhongshu Zao 45, S-ABA treatment showed the highest increase in starch, protein and ascorbic acid content compared to CK2, with significant increases of 32.26%, 43.53% and 12.26%, respectively. The content of reducing sugars decreased significantly by 13.25% (Fig. 6A). In Yunshu 902, the S3307 treatment showed the highest increase in starch content and ascorbic acid compared to CK2, with a significant increase of 11.43% and 22.41%, respectively. DTA-6 treatment showed the highest decrease in reducing sugar compared to CK2 at 7.33%. The S-ABA treatment showed the highest increase in protein content compared to CK2, with a significant increase of 22.08% (Fig. 6B).

3.5. The effect of growth regulators on potato yield and its composition.

According to Table 2, the single tuber weight, tuber number per plant, commodity potato rate, and average yield of late-sown potatoes (CK2) were significantly reduced compared to normal-sown potatoes (CK1). However, yield and its composition of late-sown potatoes were improved after being treated with four growth regulators. For Zhongshu Zao 45, under S-ABA treatment, the single tuber weight, commodity potato rate, and average yield increased the most compared to CK2, by 13.72%, 8.34%, and 15.26%, respectively. Tuber number per plant under DTA-6 treatment increased the most compared to CK2, by 6.14%. For Yunshu 902, single tuber weight, tubers number per plant, commodity potato rate, and average yield under S3307 treatment all showed the most significant improvement compared to CK2, with significant increases of 65.52%, 29.40%, 174.92%, and 46.48%, respectively. The influence of variety on yield composition was highly significant ($P < 0.01$), while the effect of growth regulators on commodity potato yield and average yield was highly significant ($P < 0.01$). The effect on single tuber weight and tuber number was not significant. Overall, except for tuber number per plant, the interaction between variety differences and growth regulators on yield composition was highly significant ($P < 0.01$).

Table 2
The effect of different growth regulators on yield and its composition of late-sown spring potatoes.

Treatment		Single tuber weight (g)	Tuber number ($plant^{-1}$)	Commodity potato rate (%)	Average yield ($kg\ ha^{-1}$)
ZZ45	CK1	119.95 ± 7.29a	5.93 ± 0.81a	81.84 ± 2.68a	30166.35 ± 1347.33a
	CK2	96.67 ± 8.21bc	4.40 ± 0.72b	65.56 ± 1.89b	25379.85 ± 808.89d
	DTA-6	99.06 ± 7.59bc	4.67 ± 0.61b	69.57 ± 4.48b	27582.90 ± 921.68bc
	S3307	96.77 ± 8.51bc	4.60 ± 0.21b	69.58 ± 1.33b	26658.90 ± 894.68cd
	S-ABA	109.94 ± 7.84ab	4.53 ± 0.83b	71.03 ± 3.04b	29253.60 ± 1175.96ab
	SA	95.27 ± 5.09c	4.47 ± 0.42b	66.95 ± 2.62b	25737.45 ± 716.71bc
	Average	102.94b	4.77b	70.76b	27463.18bc
Y902	CK1	77.55 ± 4.71a	7.87 ± 0.99a	65.54 ± 4.25a	29152.50 ± 1017.81a
	CK2	30.10 ± 2.07c	5.00 ± 0.69b	15.73 ± 4.05c	9017.55 ± 839.40e
	DTA-6	47.50 ± 2.39b	5.60 ± 0.35b	32.57 ± 5.78b	12013.80 ± 688.66bc
	S3307	49.22 ± 4.35b	6.47 ± 0.99ab	43.28 ± 7.18b	13208.70 ± 1044.31bc
	S-ABA	33.50 ± 2.61c	4.87 ± 1.17b	20.78 ± 4.98c	9959.55 ± 764.35de
	SA	43.57 ± 5.67b	5.53 ± 1.14b	38.68 ± 2.51b	10906.05 ± 1004.71cd
	Average	46.91b	5.89b	36.10b	14043.03bc
F-value	Variety	661.205**	10.698**	385.844**	2133.539**
	Reagent	2.550Ns	1.118Ns	8.027**	9.413**
	V×R	5.754**	0.787Ns	6.856**	8.010**

Note: Data are means of four replicates. CK1 stands for normal sowing and CK2 represents late-sown control group. Different lowercase letters in the row represent significant differences between different treatments (*P* < 0.05). Ns, not significant, '*' *P* < 0.05, '**' *P* < 0.01.

3.6.Response of endogenous hormones and antioxidant enzymes in potato leaves to growth regulators

3.6.1. Response of endogenous hormones

After spraying Zhongshu Zao45 with S-ABA, the ABA and JA content increased significantly by 15.70% and 16.24% on day 14 and 21, respectively, compared to CK (Fig. 7A-[illegible], [illegible]); GA content and IAA content decreased compared to CK, but the difference was not significant (Fig. 7A-[illegible], [illegible]), while CTK content showed no remarkable change before and after treatment (Fig. 7A-[illegible]). After spraying S3307 on Yunshu 902, there was no significant change in ABA and CTK content compared to CK (Fig. 7B-[illegible], [illegible]). GA content decreased significantly compared to CK, with a significant decrease of 40.63%, 50.15%, 46.71% and 28.11% on days 1, 7, 14 and 21 compared to CK, respectively (Fig. 7B-[illegible]). The IAA content decreased slightly compared to CK and decreased significantly by 16.53% on day 21 (Fig. 7B-[illegible]). The JA content increased compared to the CK content and increased significantly by 20.83% on day 21 (Fig. 7B-[illegible]).

3.6.2. Response of antioxidant enzyme.

Overall, after spraying growth regulators, the activities of SOD, POD and CAT increased in Zhongshu Zao 45 and Yunshu 902 compared to CK (Fig. 8). In Zhongshu Zao 45, SOD activity increased significantly ($P < 0.05$) by 9.20% on day 7 compared to CK. The SOD activity of Yunshu 902 showed a significant difference ($P < 0.05$) compared to CK on day 7, with highly significant differences ($P < 0.01$) on days 14 and 21, with an increase of 17.14%, 32.39% and 35.35%, respectively, compared to CK (Fig. 8A). On the 7th, 14th and 21st days, the POD activity of Zhongshu Zao 45 increased significantly by 31.72%, 33.09% and 26.80%, respectively, compared with CK. For Yunshu 902, POD activity showed a significant difference compared with CK ($P < 0.05$), increasing by 44.25%, 67.84% and 57.50% on the 7th, 14th and 21st days, respectively (Fig. 8B). In Zhongshu Zao 45, CAT activity showed a significant difference ($P < 0.05$) on day 21 compared to CK, namely an increase of 17.44%. For Yunshu 902, CAT activity showed a significant difference ($P < 0.05$) compared to CK on the first day and a highly significant difference ($P < 0.01$) on the 7th, 14th and 21st days, i.e. an increase of 17.35%, 26.74%, 48.85% and 54.30%, respectively, compared to CK (Fig. 8C).

4. Discussion

4.1. Growth regulators alleviate plant stress in late-sown spring potatoes and promote photosynthesis

The above-ground and underground parts of the plant must be coordinated and mutually supportive, especially in the case of potatoes. Overgrowth of the aboveground part can severely impair tuber formation in the underground part (Lindqvist-Kreuze et al. 2023). The root-top ratio reflects a correlation between the below-ground and above-ground parts of the crop. Since it is a crop that harvests underground tubers, a higher root-top ratio is beneficial for increasing yield (Tengli et al. 2022). A study on corn seedlings sprayed with S-ABA promoted root growth to increase the root-top ratio in response to drought stress (Qiao et al. 2023). Our experimental results also showed that after the application of four growth regulators, the plant height and stem diameter of late-sown potatoes were controlled; the growth morphology of the aboveground parts of potatoes was effectively regulated, and the root-top ratio was significantly improved. The accumulation of dry matter is the basis for yield formation (Li et al. 2022). In addition, the dry matter must be rationally distributed between the nutrient organs and the economic organs, which is the key to increasing crop yields and economic returns (Silva-Díaz et al. 2020). Our findings indicated the dry matter and total dry matter of the potato increased in the underground part after spraying the growth regulator. Specifically, this hormone prompts potato growth center alteration and helps channel photosynthesis into tubers.

Leaf area index and SPAD are important factors affecting photosynthesis in plant populations (Pham and Chun 2020). Previous studies on Poaceae plants have found that both S3307 and DYA-6 can increase SPAD content and net photosynthetic rate (Zhao et al. 2019; Sun et al. 2022). Our research results also showed that after the application of four growth regulators to late-sown potatoes, the net photosynthetic rate and SPAD content were increased to varying degrees and the leaf area index was inhibited, but there were certain differences among varieties. S-ABA and S3307 had the best effects on Zhongshu Zao45 and Yunshu 902, respectively, maintaining the high net photosynthetic rate and SPAD level at the later growth stage.

Plants undergo lipid peroxidation of membranes under unfavorable conditions and accumulate a large amount of MDA, which may reflect the severity of plant damage (Gao et al. 2017). Proline is a good osmotic regulator, and plants often accumulate proline to a considerable extent under high-temperature stress (Zhuo et al. 2018). In this experiment, potatoes effectively inhibited the accumulation of MDA and free proline after treatment with growth regulators compared to the control group. This reduces the damage to the plants under high-temperature stress.

4.2. Growth regulators increase yield and improve tuber quality in late-sown spring potatoes.

High temperatures have a serious impact on the development and growth of potato tubers, causing a decrease in both the number and individual weight of tubers. This also affects the composition of starch, protein, and other substances in the tubers, resulting in reduced yield and quality (Singh et al. 2015; Kim et al. 2017). In our experiment, all four growth regulators increased the single potato weight, tuber number, commodity potato rate, and average yield to varying degrees. The results were consistent with Głosek-Sobieraj et al. (Głosek-Sobieraj et al. 2018) on using growth regulators to spray potatoes. Zhongshu Zao 45 and Yunshu 902 showed the most significant increase in yield under S-ABA and S3307 treatments, respectively. Research has indicated that the application of S3307 and DTA-6 on potato leaves regulates the activity of key enzymes involved in starch synthesis and sucrose invertase, leading to an increase in starch content and a decrease in reducing sugar accumulation (Jiang et al. 2021). Additionally, in studies on cereal crops, growth regulators have been shown to increase the levels of ascorbic acid and protein in plants under high-temperature stress (Wakchaure et al. 2016; Fahad et al. 2016). Rehman et al. (Rehman et al. 2018) applied S-ABA to navel oranges, which also increased protein content. All four growth regulators in our study were equally effective in enhancing potato tuber starch, ascorbic acid, and protein content, while decreasing reducing sugar content.

4.3. Growth regulators can balance endogenous hormone levels and increase antioxidant enzyme activity

In terms of the impact of growth regulators on the growth, yield, and quality of potatoes, it was observed that S-ABA treatment was most effective for the late-sowing tolerant variety Zhongshu Zao 45; While S3307 showed the best treatment effect for the late-sowing sensitive variety Yunshu 902. Therefore, there is potential to investigate the response of potato plants to growth regulators by evaluating endogenous hormones and antioxidant enzymes in leaves. In this study, we revealed that late-sown Zhongshu Zao45 and Yunshu 902 exhibited increased ABA and JA contents, with suppressed GA contents, after being sprayed with S-ABA and S3307, respectively. It is widely accepted that ABA can enhance the stress resistance of potatoes, thereby promoting tuber formation (Wang et al. 2022), while JA can also promote tuber formation and serve as a positive regulatory factor (Miyawaki et al. 2021). The decrease in GA content can inhibit cell elongation, resulting in dwarfing of potato plants and enhancing their ability to resist lodging (Wang et al. 2018). Moreover, after the application of S-ABA, the IAA content of Zhongshu Zao45 was slightly lower than that of the control group, with no significant change in CTK content. On the other hand, after spraying S3307, the IAA content of Yunshu 902 was significantly lower ($P<0.05$) than that of the control group on the 21st day, with no significant change in CTK content. The interactions and effects of IAA and CTK in tuber formation may require synergy with other hormones to be more clearly manifested.

Late planting of potatoes is subject to high-temperature stress, which produces large amounts of reactive oxygen species that are toxic to growth and development(Gong and Chen 2021). S-ABA and S3307 have the ability to increase antioxidant enzyme activity, thereby mitigating the damage caused by reactive oxygen species (He et al. 2017; Qiao et al. 2023). This is evidenced by the heightened activities of stress-responsive antioxidant enzymes, namely SOD, POD, and CAT (Batool et al. 2020). In our experiment, after spraying S-ABA, all three enzymes' activity was higher than the control group, and the effect on POD enzyme activity was highly significant ($P<0.01$), while SOD and CAT were not significant. Spraying S3307 also increased the activity of all three enzymes, and the effects were highly significant ($P<0.01$). These findings suggest that application of growth regulators induces the synthesis of antioxidant enzymes in plants, with variations observed among different plant varieties. It is clear that these regulators can attenuate the impact of adverse stress on plants to varying degrees, ultimately leading to increased yields.

5. Conclusions

The growth regulators DTA-6, S-ABA, S3307, and SA significantly enhanced the agronomic characteristics of late-sown spring potatoes under high-temperature stress. They improved photosynthetic capacity, reduced stress substance accumulation, and ultimately increased yield and quality. For the late-sown tolerant variety Zhongshu Zao45 and the not-tolerant variety Yunshu 902, S-ABA and S3307 were the most effective treatments, respectively. The mechanism of these growth regulators involves balancing plant endogenous hormones, increasing antioxidant enzyme activity, and regulating plant growth and development in response to damage caused by late-sown high-temperature stress. Choosing suitable growth regulators for different varieties can achieve stable yield and improved tuber quality in late-sown spring potatoes.

Declarations

Authorship contributions

Chao Wu: Conceptualization, Formal analysis investigation, Writing—original draft, Software, Writing—review & editing. **Wensen Huang:** Resources, Formal analysis investigation, Writing—review & editing. **Xiaoting Fang:** Software, Writing—original draft, Visualization. **Haiyan Ma:** Methodology. **Wenwen Song:** Validation. **Kaiqin Zhang:** Formal analysis. **Zhitong Ren:** Methodology, Validation. **Muhammad Amir Shahzad:** Writing – review & editing. **Dawa Dolker:** Visualization. **Cuiqin Yang:** Writing—original draft, Project administration. **Shunlin Zheng:** Project administration, Resources, Writing—review & editing. All authors have read and agreed to the published version of the manuscript.

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Declarations of interest

The authors declare no conflict of interest.

Data Availability Statement

The data presented in this study are available within the article.

Declaration of Competing Interest

This manuscript has not been published or presented elsewhere in part or entirety and is not under consideration by another journal. We have read and understood your journal’s policies, and we believe that neither the manuscript nor the study violates any of these. There are no conflicts of interest to declare.

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Figures

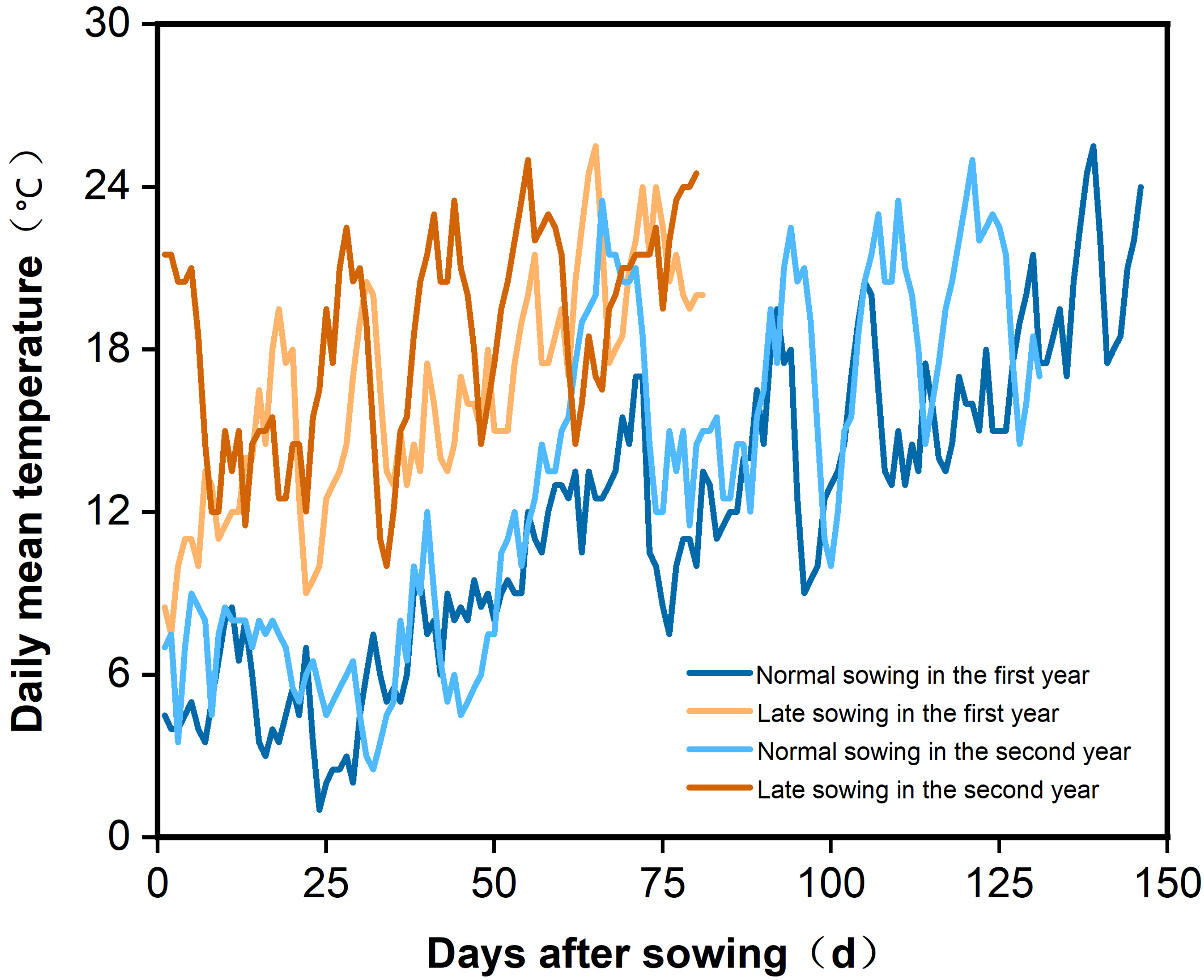

Figure 1

Changes in mean daily temperature during potato fertility, with warm lines representing late sowing and cool lines representing normal sowing. The dates are for the two years 2020-2022.

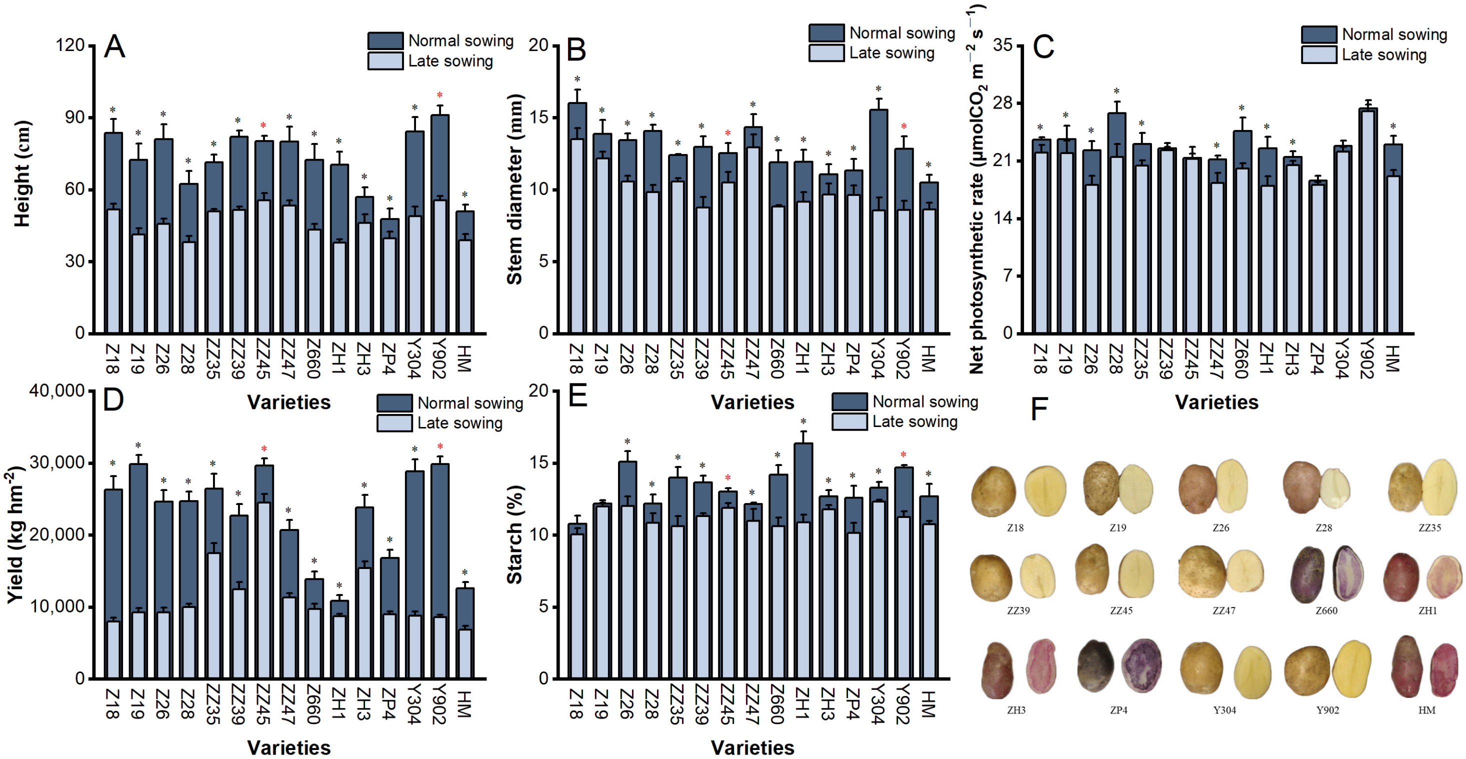

Figure 2

Comparison of plant height **(A)**, stem diameter **(B)**, net photosynthetic rate **(C)**, yield **(D)**, and starch **(E)** content of the tested varieties under normal and late sowing conditions, as well as display of tuber slices of each variety **(F)**.

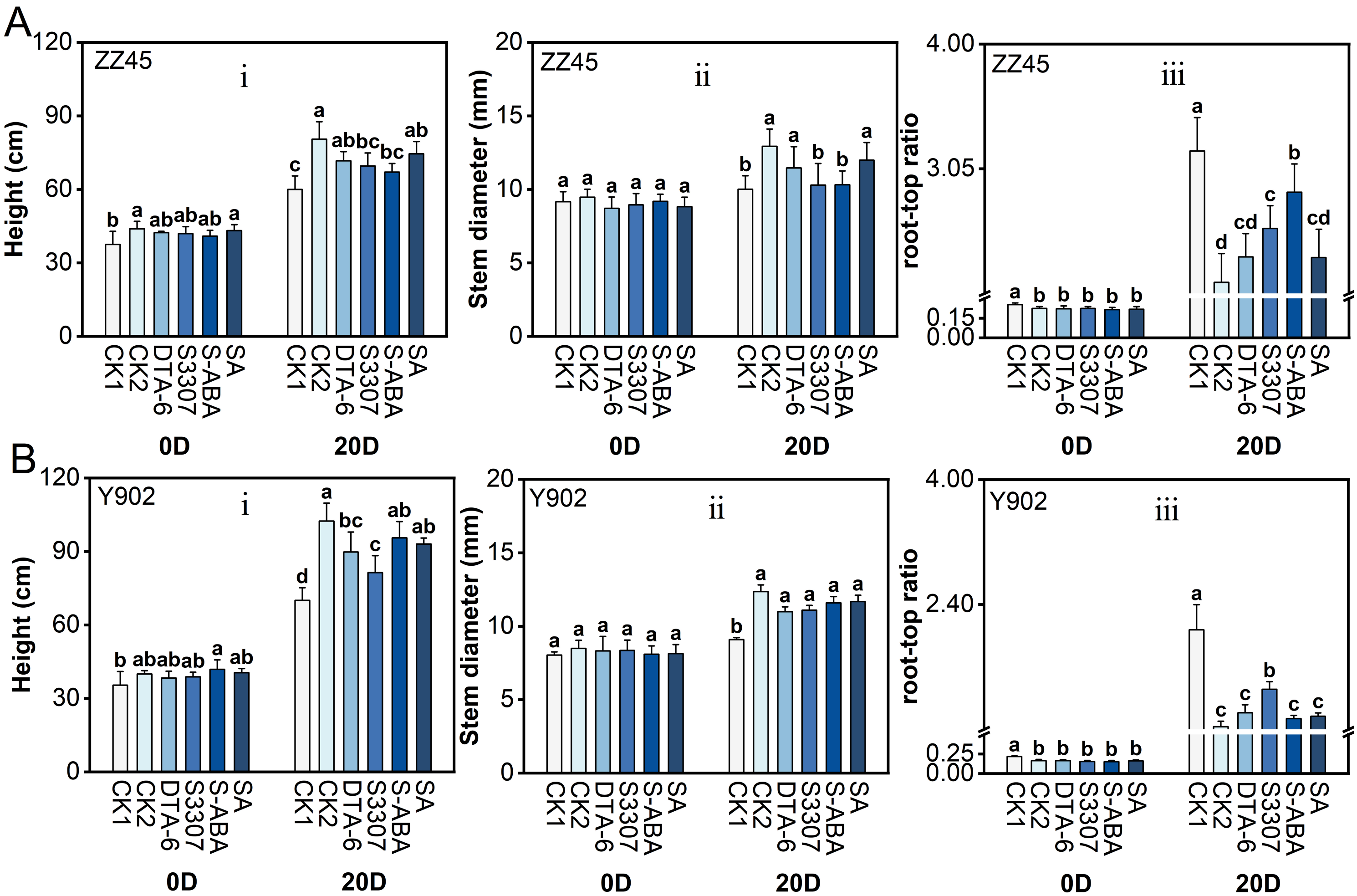

Figure 3

Effects of different growth regulators on plant height (Ⅰ), stem diameter (Ⅱ) and root-top ratio (Ⅲ) of late-sown spring potatoes. CK1 stands for normal sowing and CK2 for late-sown control group. **A** corresponds to Zhongshu Zao45, while **B** corresponds to Yunshu 902, and different lowercase letters represent significant differences between treatments (*P*<0.05).

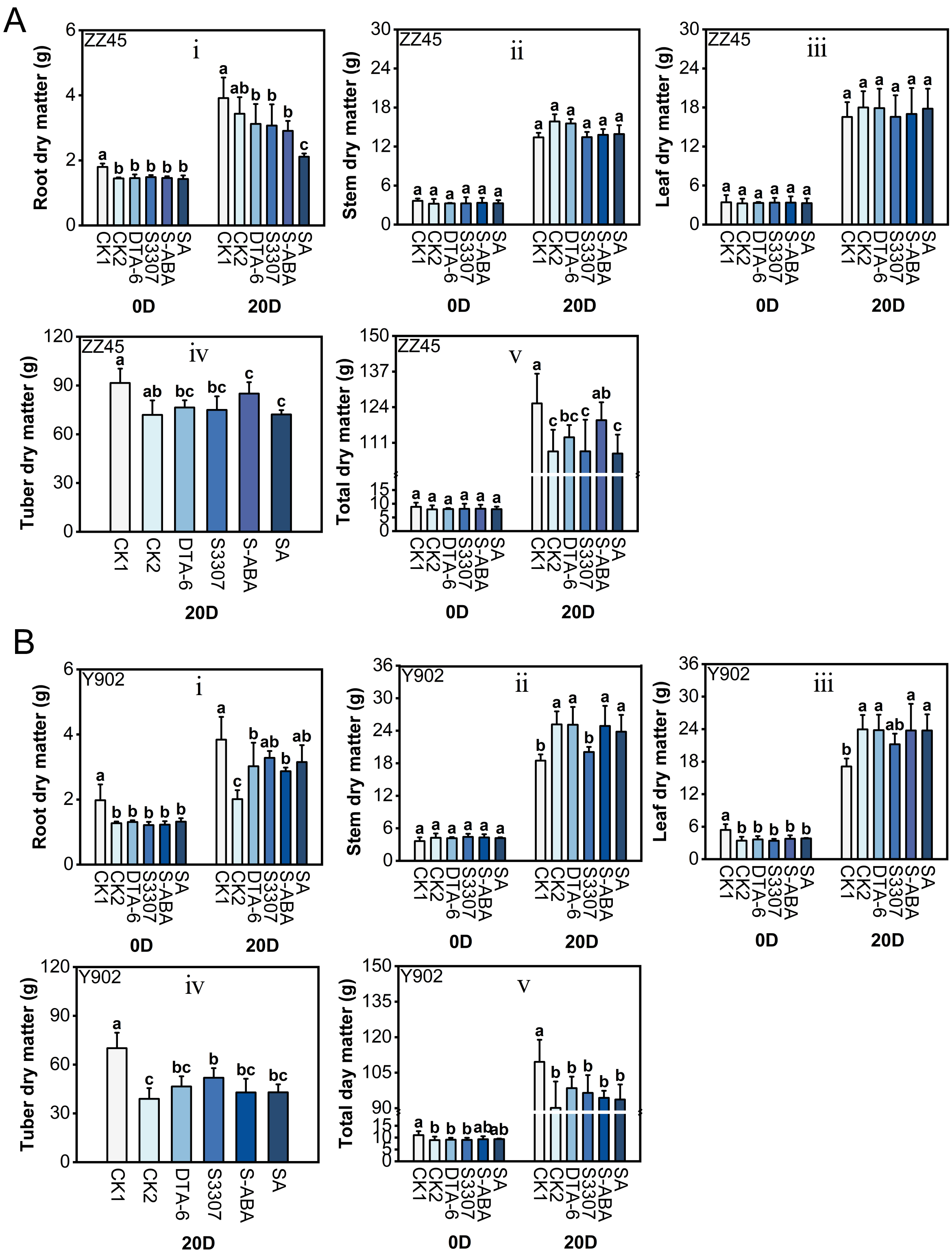

Figure 4

Effects of different growth regulators on root dry matter (**i**), stem dry matter (▯), leaf dry matter (▯), tuber dry matter (▯), and total dry matter accumulation (▯) in late-sown spring potatoes. CK1 stands for normal sowing and CK2 for late-sown control group. **A** represents Zhongshu Zao45, and **B** represents Yunshu 902. Different lowercase letters represent significant differences between treatments (P<0.05).

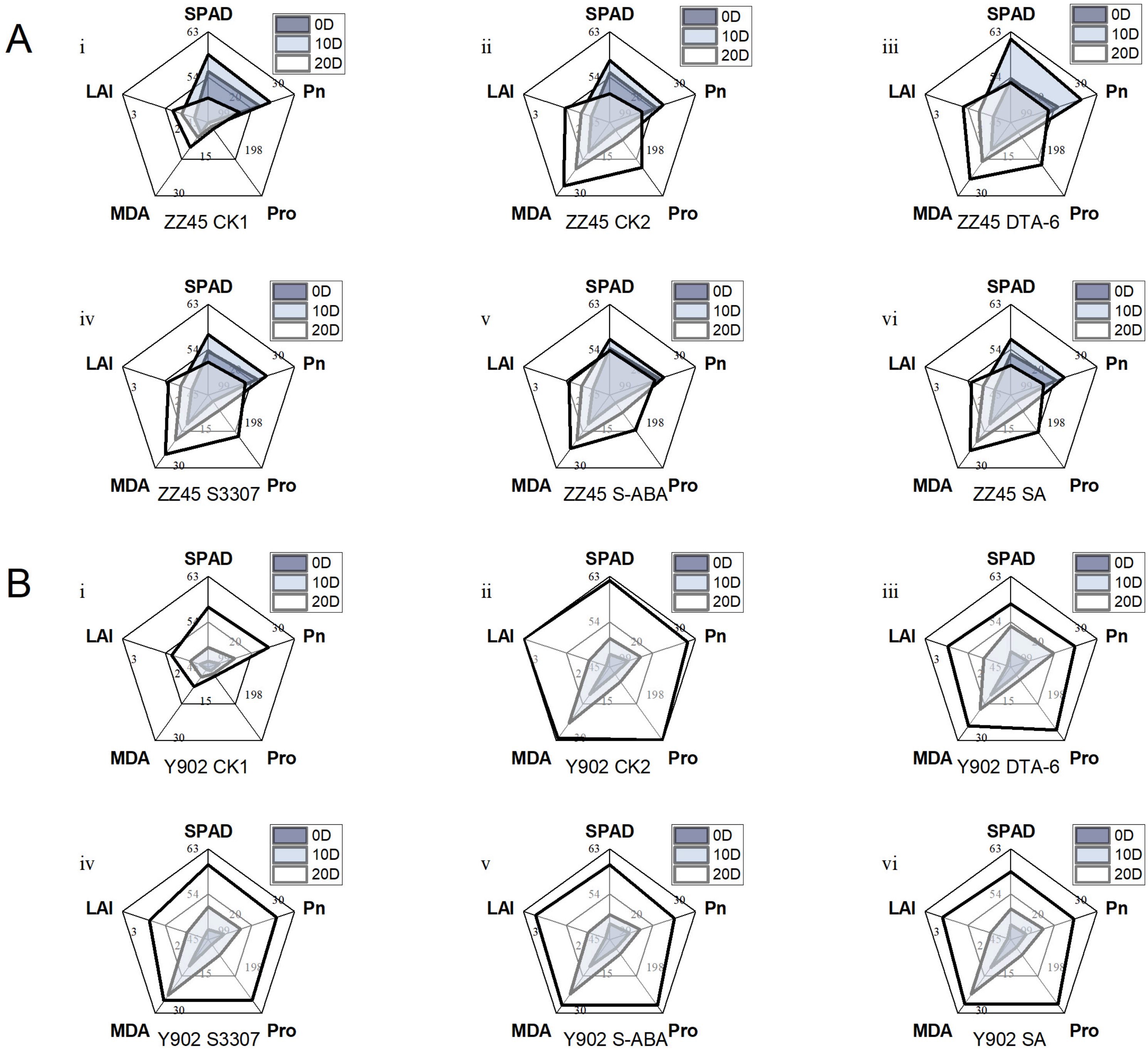

Figure 5

The effects of different growth regulators on the physiology of late-sown spring potato leaves showed, that CK1 stands for normal sowing and CK2 for late-sown control group. **A** corresponds to Zhongshu Zao45, while **B** corresponds to Yunshu 902. Different indices for each angle of the pentagon, including SPAD, Pn, Pro, MDA, and LAI respectively.

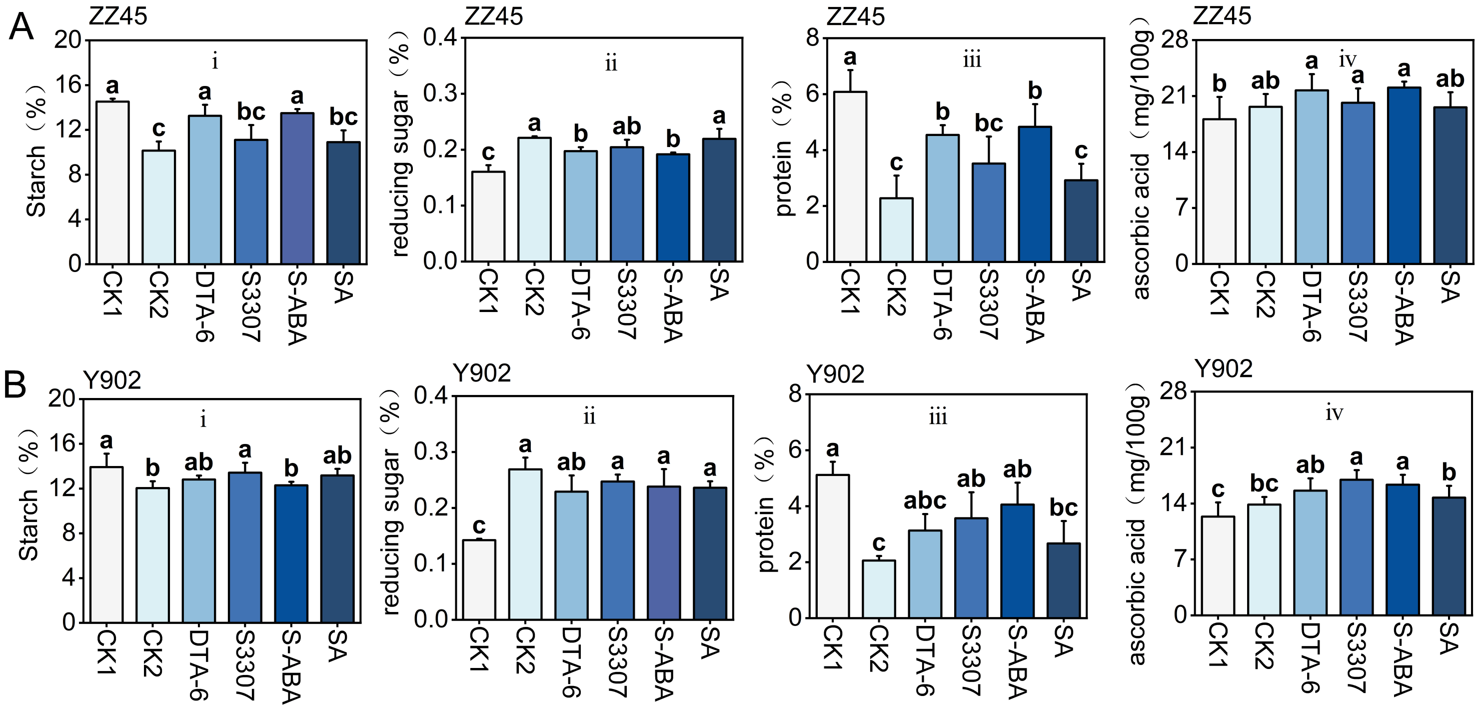

Figure 6

Effects of different growth regulators on starch (), reducing sugar (), protein () and ascorbic acid () of late-sown spring potatoes. CK1 stands for normal sowing and CK2 represents late-sown control group. **A** corresponds to Zhongshu Zao45, while **B** corresponds to Yunshu 902, and different lowercase letters represent significant differences between treatments (*P*<0.05).

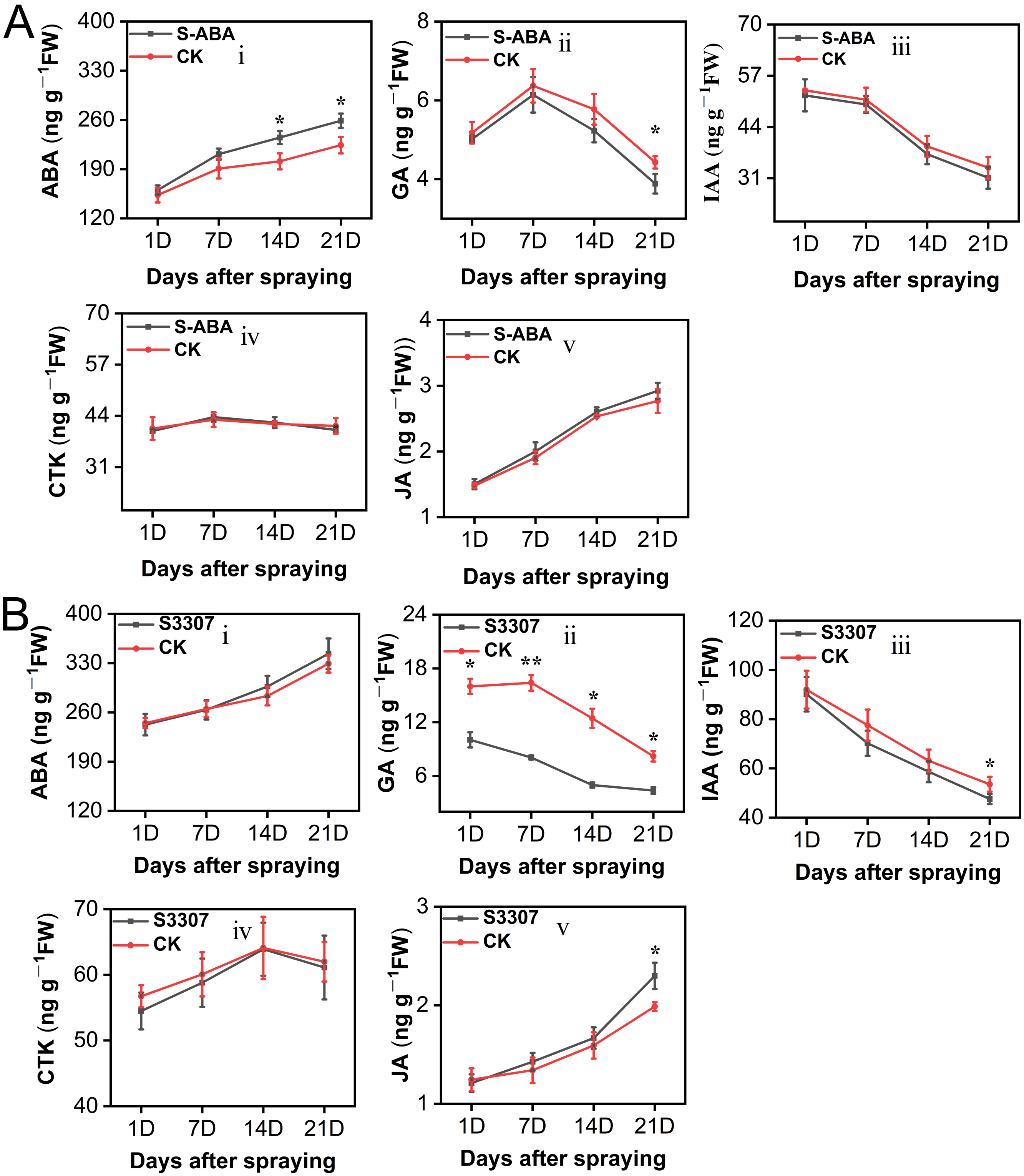

Figure 7

Response of endogenous ABA(□), GA(□), IAA(□), CTK(□), and JA(□) in leaves to growth regulators. CK indicates the late-sown control group. The above figure shows the effect of S-ABA on hormone content in Zhongshu Zao45 **(A)**, and the following figure shows the effect of S3307 on Yunshu 902 **(B)**. '*' $P < 0.05$, '**' $P < 0.01$.

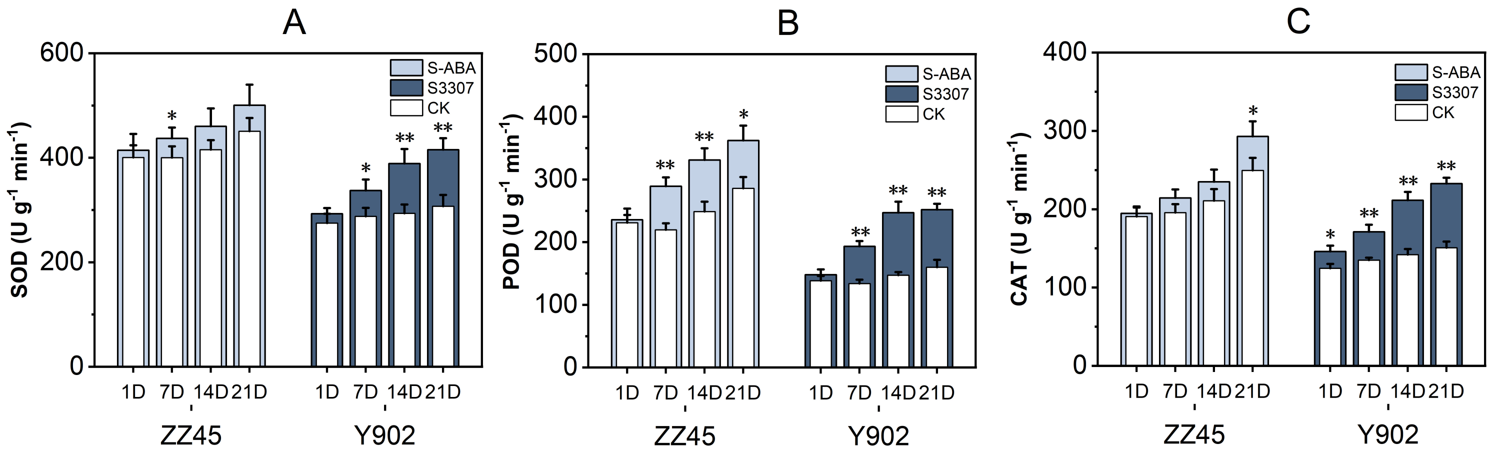

Figure 8

Response of leaf SOD **(A)**, POD **(B)**, and CAT **(C)** to growth regulators. The data shows 1-21 days after spraying growth regulators. CK indicates the late sowing control group. The light image represents the impact of S-ABA on Zhongshu Zao45, while the dark image represents the impact of S3307 on Yunshu 902, and the white image represents CK.'*' $P < 0.05$, '**' $P < 0.01$.