

Response of Endogenous ABA, GA and Their Ratio to Cold Resistance in *Brassica rapa* and *Brassica napus* Winter Rapeseed under Low Temperature Stress: Postprint

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Date: 2017-11-07T00:00:00+00:00

Abstract

To elucidate the regulation of leaf withering period and the response to cold resistance by hormone content under low temperature stress in winter rapeseed, and to provide a basis for research on cold resistance in winter rapeseed, eight accessions of winter rapeseed of different cold resistance levels, including *Brassica rapa* and *Brassica napus* types, were used as materials in a pot experiment. When seedlings grew to 5–6 true leaves, low temperature treatments (25 °C, 10 °C, 2 °C, -5 °C) were conducted in an artificial climate chamber, and changes in endogenous ABA, GA content, and chlorophyll in winter rapeseed after low temperature stress were analyzed. Regression analysis showed a significant negative correlation between temperature and ABA content, with the regression equation conforming to $y = ax + b$. As temperature decreased, endogenous ABA content exhibited a trend of initially slow increase (at 10 °C) followed by rapid increase (at 2 °C and -5 °C), and differences among temperature treatments and temperature \times cultivar interactions were highly significant; due to antagonistic effects between hormones, GA content changed in the opposite direction. When temperature was above 0 °C, there was no significant difference in ABA content among cultivars; when temperature dropped to -5 °C, ABA content in *Brassica rapa* winter rapeseed was significantly higher than that in *Brassica napus*, and cultivars with strong cold resistance had higher ABA content than those with weak cold resistance. The increase in ABA content led to changes in chlorophyll content. As temperature decreased, chlorophyll content showed a trend of initial decrease followed by increase, but overall exhibited a declining trend, and different response mechanisms existed between *Brassica rapa* and *Brassica napus* winter rapeseed. This effect resulted in chlorophyll content in

Brassica rapa winter rapeseed being lower than that in Brassica napus, causing the leaf withering period in Brassica rapa winter rapeseed to occur earlier and entry into the overwintering stage to be advanced, thereby increasing tolerance and avoidance to low temperature freezing damage. Therefore, as temperature decreased, ABA content in winter rapeseed leaves increased and chlorophyll degraded, with Brassica rapa winter rapeseed entering the leaf withering period earlier. Earlier leaf withering period and high ABA content after temperature reduction are the main reasons for the stronger cold resistance of Brassica rapa winter rapeseed.

Full Text

Response of Endogenous ABA and GA to Cold Resistance in Brassica rapa L. and Brassica napus L. Under Low Temperature Stress

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Abstract

To elucidate the regulatory effects of hormone content on the leaf wilting period and the response to cold resistance in winter rapeseed under low temperature stress, we conducted a pot experiment using eight winter rapeseed cultivars with different cold resistance levels from *Brassica rapa* L. and *Brassica napus* L. Seedlings at the 5-6 true leaf stage were subjected to low temperature treatments (25 °C, 10 °C, 2 °C, -5 °C) in an artificial climate chamber, and changes in endogenous ABA, GA content, and chlorophyll were analyzed. Regression analysis revealed a significant negative correlation between temperature and ABA content, following the equation $y = -ax + b$. As temperature decreased, endogenous ABA content increased slowly at 10 °C and then rose rapidly at 2 °C and -5 °C, with highly significant differences among temperature treatments and temperature × cultivar interactions. Due to antagonistic effects between hormones, GA content showed the opposite trend. No significant differences in ABA content among cultivars were observed above 0 °C; however, at -5 °C, *B. rapa* showed significantly higher ABA content than *B. napus*, and cold-resistant cultivars exhibited higher levels than susceptible ones. Elevated ABA content induced changes in chlorophyll content, which initially decreased and then increased with declining temperature, but showed an overall decreasing trend.

Different response mechanisms existed between *B. rapa* and *B. napus*, resulting in lower chlorophyll content in *B. rapa* than in *B. napus*. This caused earlier leaf wilting in *B. rapa*, advancing the onset of the wintering period and enhancing both avoidance and tolerance of freezing injury. Therefore, decreasing temperature increased leaf ABA content and promoted chlorophyll degradation in winter rapeseed. Earlier leaf wilting and higher ABA content after temperature reduction represent the primary mechanisms underlying the superior cold resistance of *B. rapa* compared with *B. napus*.

Keywords: *Brassica rapa* L.; *Brassica napus* L.; Winter rapeseed; Endogenous ABA; Endogenous GA; Chlorophyll; Low temperature stress; Cold resistance

Introduction

Among the three major types of rapeseed in China, only *Brassica rapa* L. and *Brassica napus* L. contain strong winter-type varieties. Strong winter-type *B. rapa* is the most suitable winter rapeseed type for cultivation in the severe cold regions of northern China, serving as a major oil and ecological crop in this region, whereas strong winter-type *B. napus* struggles to survive the winter in these areas. Strong cold resistance is a prerequisite for adaptation to the harsh cold environment of northern China. The plant hormone ABA (abscisic acid) acts as a signaling molecule for cold resistance gene expression and plays a crucial role in regulating plant cold tolerance, earning it the designation “stress hormone” that enhances plant stress resistance. Exogenous ABA application can induce cold resistance gene expression and improve cold tolerance by altering the hormonal balance within plants, as demonstrated in maize (*Zea mays* L.), rice (*Oryza sativa* L.), and sugarcane (*Saccharum officinarum* L.), where it effectively alleviates low temperature damage to cell membranes, reduces MDA and GA content, and increases proline and ABA content. During cold acclimation, cold-resistant varieties accumulate more ABA than susceptible ones. For example, cold-tolerant banana (*Musa nana* Lour.) accumulates higher ABA levels under low temperature stress than cold-sensitive varieties; plateau cold-resistant rice cultivars show greater ABA accumulation than sensitive varieties; and the ABA/GA ratio correlates with cold resistance in grape (*Vitis vinifera* L.) and gardenia (*Gardenia jasminoides* Ellis), with higher leaf ABA/GA ratios in resistant varieties making this ratio a useful indicator for evaluating cold resistance. Previous studies have shown that foliar application of $20 \text{ mg} \cdot \text{L}^{-1}$ ABA at the six-leaf stage of *B. rapa* winter rapeseed can reduce low temperature damage by increasing protective enzyme activities and osmolyte content, enhancing chlorophyll content and photosynthetic rate under low temperature, and stimulating root growth, particularly root thickening, thereby improving winter survival and cold resistance. Additionally, *B. rapa* winter rapeseed exhibits earlier leaf wilting than *B. napus*, and this phenological shift may be related to changes in leaf hormones and chlorophyll. However, the regulatory effects of endogenous hormone content on the leaf wilting period and cold resistance in winter rapeseed

under low temperature stress remain poorly documented. This study investigated changes in leaf endogenous ABA, GA, and chlorophyll content in eight winter rapeseed cultivars with different cold resistance levels from *B. rapa* and *B. napus* under low temperature stress to clarify the hormonal regulation of the leaf wilting period and the response to cold resistance, providing a foundation for future research on winter rapeseed cold resistance.

1.1 Experimental Materials

The experimental materials consisted of eight representative winter rapeseed cultivars with different cold resistance levels, selected from breeding and demonstration trials conducted by the Gansu Rapeseed Engineering Research Center across 12 provinces and municipalities in northern China from 2002–2015. The characteristics of these materials are presented in Table 1 .

1.2 Experimental Design

A pot experiment was conducted with seeds sown in nutrient pots (18 cm height, 15 cm diameter) at four plants per pot. Pots were placed in an artificial climate chamber (PRXD-300) under 25 °C with 14 h light (6,000 lx) and 10 h dark, with daily watering. When seedlings reached the 5–6 true leaf stage, four temperature treatments were applied: 25 °C (control), 10 °C, 2 °C, and -5 °C, with four pots per treatment. After 3 days of treatment, the third functional leaf from the center was sampled, placed in an ice box, and immediately used for relevant index determination.

1.3.1 Determination of Endogenous ABA and GA Content

Leaf ABA and GA contents were measured using ELISA kits. Fresh leaves were weighed, homogenized in PBS buffer (pH 7.4), centrifuged at 3,000 r · min⁻¹ for 20 min, and the supernatant was collected. Measurements were performed according to the ELISA kit instructions.

1.3.2 Determination of Leaf Pigment Content

Leaf pigments were extracted using 80% acetone. Fresh leaf samples (0.5 g) were immersed in 25 mL of 80% acetone, sealed, and extracted in darkness until leaves became colorless (approximately 48 h). Absorbance was measured using a UV-1601 spectrophotometer at 663 nm, 646 nm, and 470 nm. Chlorophyll contents were calculated using the following formulas:

$$\text{Chlorophyll a (Chl a)} = (12.21A_{663} - 2.81A_{646}) \times V / 1,000W \quad (1)$$

$$\text{Chlorophyll b (Chl b)} = (20.13A_{663} - 5.03A_{646}) \times V / 1,000W \quad (2)$$

where A represents absorbance values, V is the total extraction volume (mL), and W is the fresh leaf weight (g). Values for Chl a + Chl b and Chl a/Chl b ratio were calculated with four replications.

1.4 Data Processing

Microsoft Excel 2003 was used for graphing, table preparation, and regression analysis. SPSS 19.0 was used for analysis of variance.

Results

2.1 Changes in Winter Rapeseed Leaf Morphology Under Low Temperature Stress

After 3 days of treatment, leaves at 25 °C, 10 °C, and 2 °C remained dark green with vigorous growth and no obvious low temperature injury symptoms, likely because short-term above-zero temperatures caused no significant damage. However, after 3 days at -5 °C, leaves exhibited obvious freezing injury characteristics, including petiole bending, leaf drooping, and dark, lusterless appearance (Fig. 1 [Figure 1: see original paper]).

2.2 Variance in Endogenous ABA and GA Content of Winter Rapeseed Under Low Temperature Stress

Combined variance analysis of ABA and GA contents across different winter rapeseed cultivars and temperatures showed that ABA content, GA content, and ABA/GA ratio differed highly significantly among temperature treatments ($P < 0.001$) but not among cultivars ($P > 0.05$), while temperature \times cultivar interactions were highly significant. This indicates that changes in endogenous ABA, GA, and ABA/GA ratio among cultivars were primarily induced by temperature variation.

2.6 Changes in Chlorophyll Content of Winter Rapeseed Under Low Temperature Stress

Variance analysis of leaf pigment content across different winter rapeseed cultivars and temperatures revealed significant differences ($P < 0.05$) among temperature treatments for chlorophyll a, chlorophyll b, and total chlorophyll content (chlorophyll a + chlorophyll b), with no significant differences among cultivars ($P > 0.05$) but highly significant temperature \times cultivar interactions ($P < 0.001$). Chlorophyll a/chlorophyll b ratio showed highly significant differences for both temperature and temperature \times cultivar interactions, decreasing with temperature reduction, with more dramatic changes observed in *B. napus* (Table 7). The chlorophyll a/chlorophyll b ratio reflects the stacking degree of thylakoids in chloroplasts; lower values indicate more severe chloroplast damage and greater photoinhibition. This study showed that as temperature decreased, the chlorophyll a/chlorophyll b ratio declined, but the reduction was smaller in *B. rapa*, suggesting less chloroplast damage compared with *B. napus*. Chlorophyll a, chlorophyll b, carotenoid, and total chlorophyll contents initially decreased and then increased with declining temperature, with *B. napus* showing faster decreases and more rapid increases (Table 7).

2.7 Regression Analysis of Temperature, ABA Content, and Chlorophyll Content

Regression analysis indicated that within the temperature range of -5°C to 25°C , temperature and ABA content were negatively correlated, following the equation $y = -ax + b$ (Fig. 2a [Figure 2: see original paper]). Different linear relationships existed between temperature and chlorophyll content for *B. rapa* and *B. napus* (Fig. 2b [Figure 2: see original paper]). As temperature decreased, chlorophyll content in *B. rapa* declined according to the equation $y = 0.0019x + 0.9775$, whereas *B. napus* showed an increasing trend following $y = -0.0065x + 1.2552$. Different linear relationships also existed between ABA and chlorophyll content for the two species (Figs. 2c, 2d [Figure 2: see original paper]). Within a certain ABA range, increasing ABA content caused only slight chlorophyll increases in *B. rapa*, while *B. napus* showed rapid chlorophyll elevation.

Discussion

3.1 Temperature as the Primary Factor Inducing Changes in Endogenous ABA and GA in Winter Rapeseed

Normal plant growth and development require specific temperature ranges; when environmental temperature falls below the optimum, plant growth is affected and may result in death. Abscisic acid (ABA) plays important roles in plant growth, development, and environmental stress responses. Under various abiotic stresses including drought, cold, heat, salinity, waterlogging, hypoxia, and pathogen infection, ABA content increases rapidly. This study demonstrated that endogenous ABA content increased significantly with decreasing temperature, while GA content decreased due to hormonal antagonism, leading to changes in the ABA/GA ratio. Variance analysis showed significant differences among temperature treatments and temperature \times cultivar interactions, but not among cultivars, indicating that differences in endogenous ABA, GA, and ABA/GA ratio among cultivars were primarily temperature-induced. Similar results have been reported for lavender (*Lavandula angustifolia* Mill.) and winter wheat (*Triticum aestivum* L.), where temperature was the main factor causing changes in endogenous hormone content.

3.2 ABA Regulation of Cold Resistance in *B. rapa* and *B. napus*

As winter approaches and temperature decreases, plants cease growth and enter dormancy. Leaf yellowing and wilting are regulated by ABA, which promotes leaf senescence and dormancy—an adaptive response to low temperature stress. In northern China, *B. rapa* winter rapeseed stops growing in mid-to-late December, with leaves yellowing and entering the wilting period. Different cultivars show variation in wilting time, particularly between cold-resistant and susceptible varieties, with significant differences between *B. rapa* and *B. napus*. This study showed that ABA content increased significantly with decreasing temperature. At 25°C , 10°C , and 2°C , no significant differences in ABA content were

observed among cultivars within the same temperature treatment. However, at -5°C , *B. rapa* showed significantly higher ABA content than *B. napus*, and cold-resistant cultivars exhibited higher levels than susceptible ones, demonstrating that ABA plays a crucial regulatory role in winter rapeseed cold resistance, particularly during sub-zero temperatures. These findings align with reports that ABA is the key endogenous hormone for lavender winter survival and that ABA content increases significantly in cold-tolerant maize and cucumber seedlings under low temperature stress, with greater increases in more tolerant materials.

3.3 Early Leaf Wilting as a Biological Characteristic of Superior Cold Resistance in *B. rapa*

Chlorophyll is essential for photosynthesis in plant leaves, and its content correlates with photosynthetic efficiency. Low temperature impairs light energy utilization through photosynthesis and inhibits chlorophyll synthesis, reducing chlorophyll content. This study showed that chlorophyll content decreased at 10°C , primarily due to inhibited synthesis and accelerated degradation. However, at lower temperatures, chlorophyll content increased, likely because winter rapeseed transitions to cold resistance mechanisms or activates cold resistance genes after initial low temperature stress, enhancing cold resistance and promoting continued chlorophyll synthesis. The increased ABA content simultaneously promoted leaf yellowing, an effect more pronounced in *B. rapa*, resulting in lower chlorophyll content compared with *B. napus*. Regression analysis revealed a positive linear correlation between ABA content and chlorophyll content in *B. napus*, whereas this relationship was not evident in *B. rapa*, reasonably explaining the earlier leaf wilting in *B. rapa*. After freezing injury, *B. rapa* leaves remain open, producing ineffective photosynthesis without generating organic matter. Aboveground growth requires nutrient supply from roots—the only winter-surviving organ. Early leaf wilting in cold-resistant varieties avoids consumption of underground nutrients, allowing greater organic matter storage in roots before winter. This substantial root reserve provides energy for maintaining basic metabolism and resisting low temperature during the long winter period, forming the material basis for strong cold resistance and safe winter survival. This represents a self-regulating mechanism in *B. rapa* for cold avoidance and tolerance, demonstrating that ABA significantly regulates the leaf wilting period and that early wilting is a biological characteristic of superior cold resistance in *B. rapa* compared with *B. napus*.

3.4 Future Perspectives on Cold Resistance Research in *B. rapa* and *B. napus*

Extensive research on winter rapeseed breeding and cold resistance has investigated morphological, physiological, biochemical, anatomical, and molecular aspects. Cold-resistant varieties exhibit prostrate seedling growth, dark green leaf color, small palisade ratios, and small stomatal areas, with photosynthates preferentially allocated to underground parts to establish extensive root systems

for safe wintering and timely spring regrowth. Under low temperature stress, these varieties show high antioxidant enzyme activity and osmolyte content, and several stress-regulated genes have been cloned. Suitable cultivation techniques for cold and arid regions in northern China have also been developed. However, these epigenetic characteristics cannot fundamentally elucidate the mechanisms of cold resistance. Therefore, we propose the following future research directions for winter rapeseed cold resistance:

- 1) The early leaf wilting period in cold-resistant varieties is primarily regulated by ABA. This study demonstrates that increased ABA content and decreased chlorophyll content after low temperature stress cause early leaf wilting in *B. rapa*, representing an objective manifestation of its superior cold resistance over *B. napus*.
- 2) Cold-resistant varieties exhibit depressed growth points. The long, severe winters in northern China demand exceptional cold resistance. Cold-resistant seedlings show prostrate growth with growth points recessed below the soil surface, avoiding direct cold air damage, whereas susceptible varieties grow erect with elevated growth points vulnerable to freezing.
- 3) The root system is the sole nutrient organ for winter rapeseed survival. *B. rapa* possesses a taproot system with long roots and large root collars, while *B. napus* has smaller, more lignified roots. During winter, aboveground parts wither and cease growth, but growth points continue developing and flower bud differentiation proceeds. The ability to utilize limited pre-winter light and heat resources for photosynthesis to establish an extensive root system is prerequisite for safe wintering and post-winter vegetative reconstruction.
- 4) Antifreeze protein research. Low temperature stress may induce new antifreeze proteins that modify ice crystal morphology in cells to resist freezing injury.
- 5) Cold resistance gene research. Identifying specific cold resistance genes or those activated through low temperature acclimation represents an important research topic.

In conclusion, decreasing temperature significantly increased endogenous ABA content, with higher levels in cold-resistant varieties. Variance analysis showed significant differences among temperature treatments and temperature \times cultivar interactions, but not among cultivars, indicating that temperature was the primary factor causing variation. Increased ABA content induced changes in chlorophyll content, resulting in lower chlorophyll levels in *B. rapa* than in *B. napus* and causing earlier leaf wilting. Early leaf wilting and elevated ABA content after low temperature stress are the main reasons for the superior cold resistance of *B. rapa* compared with *B. napus*.

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