



The Effect of Low Temperature on Oilseed Rape in Vegetative and Reproductive Growth Stages

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ABSTRACT

Low-temperature stress is a significant abiotic factor that adversely affects the growth and development of oilseed rape at various stages. This stress occurs in two forms: chilling and freezing. The key difference between them lies in temperature: chilling stress occurs at cold temperatures above the freezing point, while freezing stress involves exposure to sub-zero temperatures. The severity of cold damage in oilseed rape depends on several factors, including soil moisture conditions, the rate of ice melting, the plant's developmental stage, the plant's level of pre-adaptation, and the duration of the stress. Consequently, the type and intensity of cold injury can vary significantly across different growth stages, such as germination, vegetative growth, reproductive development, and seed filling. Moreover, temperature fluctuations within a single growing season can be so extreme that chilling injury in crops like oilseed rape becomes inevitable. Nevertheless, proper agronomic practices—such as ensuring adequate nutrition, selecting an optimal sowing date, utilizing cold-tolerant genotypes, and maintaining appropriate plant density—can effectively reduce or prevent chilling damage and its negative impacts.

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1. Introduction

Cold stress is one of the most important environmental stresses affecting plant survival, growth, development, and distribution. It is categorized into chilling (temperature below 15°C) and freezing stress (temperature below 0°C) (Adhikari *et al.*, 2022; Miura and Furumoto, 2013). Such cold events can occur across more than 90% of the world's arable land, particularly impacting temperate and subtropical regions (Hatfield and Prueger, 2015). Exposure to chilling temperatures (0–15°C) can disrupt physiological processes such as photosynthesis, nutrient uptake, and membrane stability, while freezing temperatures (<0°C) cause ice formation that damages cellular structures (Sanghera *et al.*, 2011). Consequently, plant growth and development in most temperate areas of the world are strongly influenced by temperature (Goering *et al.*, 2021). Management practices, including breeding for cold-

tolerant cultivars and adjusting sowing dates, are essential strategies to mitigate these effects. Morphological symptoms of cold stress in plants include chlorosis, seedling growth inhibition, surface lesions on specific plant parts, leaf curling, discoloration, tissue damage, stem cracking, weak or absent germination, low seedling vigor, metabolite leakage, leaf wilting, and necrosis (Adhikari *et al.*, 2022).

Spring oilseed rape varieties are cultivated in warm regions of the southern and northern parts of Iran, along with some western regions. Meanwhile, in cold and temperate-cold areas of Iran, the winter varieties are grown, leading to exposure to chilling or freezing conditions during critical growth stages such as germination, vegetative growth, or even reproductive growth. Generally, winter oilseed rape varieties exhibit greater cold tolerance compared to spring varieties. Cold stress resistance in oilseed rape increases

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gradually with decreasing temperatures in autumn and winter. However, a sudden rise in temperature during these seasons can significantly reduce cold tolerance (Stachurska et al., 2024).

Winter oilseed rape has developed mechanisms to withstand winter cold, enabling it to survive sub-zero temperatures (Fürtauer et al., 2019). Vernalization and cold acclimation are among the most important mechanisms for cold tolerance. Nevertheless, in some years, extreme chilling and freezing conditions can cause severe economic damage to oilseed rape cultivation, or even destroy the crop. Given the importance of low-temperature stress in oilseed rape, this chapter aims to examine the impact of cold stress, freezing, and hail at various growth stages and propose strategies for mitigating these stresses (Stachurska et al., 2024).

2. Impact of cold stress on different growth stages of oilseed rape

Cold and frost damage in oilseed rape often occurs in autumn and winter at temperatures around or below 0°C. Cold stress affects many agronomic and physiological features of oilseed rape plants, causing lower photosynthesis rates than normal conditions, resulting in lower yield and productivity. While plants adopt strategies to tolerate normal temperature fluctuations in their native environment, exposure to unfamiliar cold conditions or extreme temperature drops can result in severe damage (Miura and Furumoto, 2013).

The severity of cold stress damage in oilseed rape is influenced by soil moisture conditions, the rate of ice melting, plant growth stage, pre-adaptation to cold, and stress duration. As a result, cold damage may vary significantly across different growth stages, including germination, vegetative growth, reproductive growth, and seed filling. Temperature variations during the six growth stages of oilseed rape can significantly affect its growth and development (Feng et al., 2025; Xu et al., 2022). As shown in Table 1, the most sensitive growth stages of oilseed rape to cold stress include the cotyledon stage, the three-true-leaf stage, stem elongation, and flowering (Rezaizad et al., 2023).

2.1. Impact of cold stress on oilseed rape germination

Cold stress is the most common environmental stress affecting seed germination. Soil temperature and

moisture are the two primary factors determining oilseed rape seed germination rates. In cold and dry soils, the oilseed rape germination percentage decreases significantly. Low temperatures not only reduce germination rates but also limit seedling growth and dry matter accumulation. The primary adverse effect of cold stress during germination occurs during the water uptake phase, which is highly sensitive to chilling (Xu et al., 2022; Haj Sghaier et al., 2022).

Oilseed rape seed germination includes the following stages: water absorption, enzyme activation and synthesis, nutrient breakdown in the seed, and the transfer of breakdown products to the embryo. All these biochemical processes, except for water absorption, are temperature-sensitive (Luo et al., 2019; Haj Sghaier et al., 2022). Germination in dicotyledonous plants like oilseed rape is epigeal, meaning the hypocotyl elongates and lifts the cotyledons above the soil surface. Consequently, the growth point of new leaves is positioned above ground level (Fig. 1). In contrast, crops such as chickpeas and lentils have growth points located below the soil surface, making them less susceptible to environmental stress.

Table 1. Cold tolerance range in winter oilseed rape across different growth stages

Growth stage	Cold tolerance range (°C)
Cotyledon leaves	Up to -1°C
Two true leaves	Up to -3°C
Three true leaves	Up to -6°C
Four true leaves	Up to -10°C
Five true leaves	Up to -15°C
Six true leaves	Up to -20°C
Eight true leaves	Up to -25°C
Stem elongation	Up to -5°C
Flowering and pollination	Up to -3°C

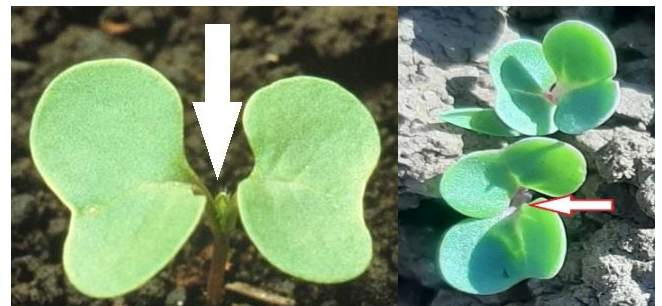


Figure 1. The growth point of oilseed rape is positioned above the soil surface, which makes the plant more vulnerable to environmental stresses, such as low-temperature stress.

Studies have shown that cold stress can negatively affect cotyledons by inducing the production of reactive oxygen species (ROS). Moreover, cold stress

also damages the cell membrane, reducing the efficiency of photosynthesis, which is why the plants may attain an abnormal morphology or exhibit retarded growth (Liu *et al.*, 2018; Cheng *et al.*, 2020). Generally, cold stress has been shown to cause dehydration, marked wilting, and chlorosis (Qi *et al.*, 2020; Raza *et al.*, 2021).

One factor that influences soil temperature and, consequently, germination and seedling establishment is the presence of crop residues. Crop residues, particularly wheat straw, reduce soil temperature, which, in addition to disrupting seed-soil contact, negatively impacts oilseed rape germination and seedling establishment (Shen *et al.*, 2018). Several studies indicate that soil temperatures below 10°C generally lead to poor oilseed rape germination.

The impact of low-temperature stress on canola (*Brassica napus* L.) germination appears to vary considerably across genotypes and experimental conditions, suggesting a complex interaction between genetic, physiological, and environmental factors. For instance, Luo *et al.* (2019) demonstrated a significant delay in seed germination under low temperatures, attributing the variability in germination rates to genetic differences among cultivars. Their transcriptomic analysis revealed the involvement of hormonal pathways and transcription factors in cold stress response, supporting the role of molecular mechanisms in cold tolerance during germination. In contrast, Wu *et al.* (2025) observed a negative correlation between cold tolerance during germination and cold tolerance in later growth stages in *B. napus*. This suggests that other post-germination traits (e.g., seedling vigor or antioxidant defense) might be more indicative of cold tolerance than germination rate alone.

Moreover, industry-based findings from the Canola Council of Canada further highlight the genetic variability in cold response. Some spring canola cultivars exhibited relatively stable germination performance at low temperatures, supporting the feasibility of breeding for enhanced cold tolerance. Taken together, these studies suggest that while low temperature generally impairs germination, the extent of this impact is genotype-dependent and may be moderated by biochemical and transcriptional regulatory networks. The inconsistency in findings regarding germination rates could stem from

differences in temperature regimes, seed pre-conditioning, or experimental design. Seeds that absorb water at cold temperatures and are later transferred to optimal temperatures exhibit significantly lower germination rates compared to seeds that initially absorb water under optimal conditions and are subsequently exposed to cold stress (Luo *et al.*, 2019; Haj Sghaier *et al.*, 2022). Cold stress during slow water uptake is less damaging to germination than stress during rapid water uptake. The primary reason for reduced germination under cold stress is the excessive leakage of solutes such as amino acids and carbohydrates from seeds (Dhaliwal and Angeles-Shim, 2022). This leakage is attributed to incomplete plasma membrane development. Future research should focus on integrating physiological assays with molecular profiling to better understand cold stress responses during early developmental stages, and to identify reliable phenotypic.

2.2. The effect of cold stress on oilseed rape in vegetative growth stage

The vegetative growth stage of oilseed rape is characterized by the emergence and development of leaves until the beginning of reproductive growth. In the early seedling establishment stage, oilseed rape exhibits relative tolerance to cold; however, during the cotyledonary and seedling phases, severe cold may result in seedling mortality (Fiebelkorn and Rahman, 2016; Jan *et al.*, 2017). Seedling growth and vigor decline at temperatures of -3°C or lower; in some cases, seedlings may perish. Cold temperatures can slow the germination rate, prolonging the emergence and establishment of seedlings. Oilseed rape seedlings can acclimate to cold if exposed to low temperatures for a few days, enabling them to withstand temperatures as low as -5°C. However, seedlings grown in warm conditions are highly susceptible to frost. If there is a risk of frost for spring oilseed rape, increasing plant density by 5–10% above the normal recommended level is advised to compensate for plant losses (Friedt *et al.*, 2018).

Oilseed rape seedlings can often recover from mild frosts, provided that the growing point remains undamaged. The severity of frost damage and plant losses is typically determined within 4 to 10 days after the freezing event. If the growing point of the plant remains green in the rosette stage, recovery is possible.

Oilseed rape is much more sensitive to frost in the cotyledonary stage than in the three- to four-leaf stage (Fiebelkorn and Rahman, 2016). If the plant retains the ability to produce green meristem tissue 5–10 days after frost, it is likely to recover (Liu et al., 2023). When oilseed rape seedlings are exposed to near-freezing temperatures for a few days at the beginning of establishment, they develop cold tolerance. This process involves biochemical changes within the plant, leading to increased accumulation of soluble compounds within cells. Research at the University of Manitoba has demonstrated that oilseed rape plants sown earlier and exposed to lower temperatures developed cold hardiness, allowing them to withstand temperatures as low as -8°C to -9°C . In contrast, late-sown oilseed rape, which did not undergo cold hardening, succumbed to temperatures of -3°C to -4°C (Meza-Basso et al., 1986).

Cold damage symptoms can sometimes be confused with symptoms of herbicide injury or soil nutrient deficiencies. However, in the cotyledonary stage, nutrient deficiencies are rare since the plant's nutritional requirements are minimal. The purpling of cotyledonary and true leaves is caused by anthocyanin production under cold conditions. This purpling may spread to the lower parts of the plant, the leaf margins, or the entire plant. As temperatures rise, these cold stress symptoms diminish or disappear. Leaf cupping is another symptom caused by cold stress, but affected leaves usually return to their normal shape once the cold subsides. In oilseed rape, blackened cotyledons are a strong indicator of frost damage (Ismaili et al., 2015).

Research has shown that oilseed rape genotypes with slower initial growth exhibit greater cold tolerance than those with rapid initial growth. This is because slow-growing oilseed rape plants can gradually acclimate to low temperatures, whereas rapid growth may prevent this acclimation process. When temperatures drop suddenly, soluble carbohydrates accumulate in the leaves, leading to the cessation of photosynthesis and the subsequent halt in seedling growth during cold seasons (Basu, 2002). In winter oilseed rape, leaf growth ceases at the rosette stage, resuming after winter dormancy when temperatures rise. In contrast, leaf growth in spring oilseed rape continues uninterrupted. The rate of leaf development and the duration of leaf area maintenance in oilseed rape are significantly influenced by temperature. Temperature

regulates the duration from germination to the end of the vegetative phase and from stem elongation to mid-flowering (Gabrielle et al., 1998). The optimal temperature for oilseed rape leaf growth is 13°C to 22°C . At higher temperatures, growth accelerates, shortening the leaf growth period. Cold temperatures during the early growth stages do not necessarily reduce seed yield (except in cases of severe frost), but they do slow down plant growth and development. During the rosette stage, when winter oilseed rape is exposed to subzero temperatures, leaf purpling occurs, affecting both the upper and lower leaf surfaces. This purpling may spread across the entire leaf surface and is a result of anthocyanin accumulation, a response to cold stress (Rathke et al., 2006). Anthocyanins act as protective pigments, accumulating in the stems and leaves under cold conditions to shield the plant from high light intensity in late autumn and winter (Fig. 2).



Figure 2. Effect of cold on oilseed rape leaves: purpling and thickening in the field.

The transition of leaf color to red-purple and the thickening of leaves indicate the completion of

vernalization in oilseed rape, which occurs due to (Swegarden, 2020): a) The accumulation of anthocyanins and phenylpropanoids in mesophyll cells exposed to cold; b) The plant's preparation for protecting cellular metabolism against cold stress; c) An increase in dry matter content, with leaf thickness up to eight times greater than in non-hardened plants; d) A rise in phenolic and anthocyanin concentrations in hardened plants by 220% and 330%, respectively.

The molecular mechanism behind the development of purple leaves in winter rapeseed (*B. napus*) during the rosette stage under cold stress involves complex biochemical and genetic pathways. Cold temperatures induce the accumulation of anthocyanins, which are pigments responsible for the purple coloration in plant tissues. Some key molecular mechanisms are the upregulation of anthocyanin biosynthesis genes, activation of transcription factors, and feedback regulation by repressor proteins (Zhou et al., 2015; He et al., 2020; Zhang et al., 2020). Thus, the color change in oilseed rape fields during winter is not a sign of frost damage, yield loss, or nutrient deficiency. As temperatures gradually rise, this color change disappears. However, severe cold during the rosette stage in winter oilseed rape or during leaf expansion in spring oilseed rape can lead to leaf wilting or bleaching (Fig. 3).



Figure 3. Leaf bleaching in oilseed rape due to severe cold.

Oilseed rape exhibits maximum cold tolerance during the rosette stage, where the central bud remains close to the soil surface and leaves surround it. After reaching this stage, sufficient nutrients have been stored in the plant's crown and root system. To achieve

maximum resistance to subzero temperatures, a fully hardened oilseed rape plant at the complete rosette stage should have 6–8 true leaves, a crown diameter of 10–12 mm, a root length of 30–35 cm, and a shoot apex positioned no more than 20 mm above the soil surface (Fig. 4). Late-emerging oilseed rape plants with poor shoot growth and weak root systems are most vulnerable to winter damage (De Meyer et al., 2023).



Figure 4. An oilseed rape plant at the complete rosette stage with well-developed shoots and roots.

For successful overwintering, oilseed rape must undergo the hardening process, which normally occurs in late autumn when winter oilseed rape is exposed to near-freezing temperatures for several days. If hardening is effective, plants develop strong cold resistance, allowing them to survive subzero temperatures without severe damage. Under these conditions, plant growth slows down, and cells become smaller with higher solute concentrations, increasing frost stress tolerance (Stachurska et al., 2024). Mild frosts, with temperatures as low as -3°C , halt leaf growth and accelerate the hardening process. The

longer the acclimation period and the more stable the temperature fluctuations, the better the hardening process and the greater the plant's cold resistance. Research suggests that oilseed rape seedlings require at least seven days of exposure to near-zero temperatures to develop cold hardiness. Well-established winter oilseed rape varieties that have undergone hardening can endure short-term temperatures as low as -15°C to -25°C . If there is green tissue present in the central point of the plant after the winter cold is over, the plant will resume growth as the temperature and day length increase (Fig. 5). In case some plants have died due to winter cold, the branching ability of oilseed rape can largely compensate for the reduced plant density (Zhang et al., 2012).



Figure 5. The start of the growth of the terminal bud occurs after the winter cold is over.

The stem elongation phase is one of the most sensitive stages of oilseed rape to frost and cold stress. Before the onset of winter and during rosette formation, the optimal stem size should be less than 2 cm. In general, the closer the crown of the oilseed rape plant is to the soil surface, the higher the cold tolerance. Plants with excessive growth (with a field cover height of more than 45 cm) and more leaves often experience stem elongation in the fall. In this case, the growth point of the plant becomes exposed to the cold, and the plant becomes vulnerable to winter frost. Frost damage during this growth stage causes serious harm to oilseed rape, as the plant moisture content is above 60%, making it susceptible to freezing (Stachurska et al., 2024). For winter varieties, this occurs when early planting or high temperatures in the fall lead to excessive plant growth or bolting (Fig. 6).



Figure 6. Bolting of oilseed rape at the beginning of winter and frost damage resulting from it.

Spring varieties, in which bolting usually occurs in late winter, are also entirely at risk. If the temperature drops below zero during the bolting stage of oilseed rape, the water inside the stem (extracellular water) freezes due to severe cold, and when the cold dissipates, it begins to thaw. This causes the stems to crack and split. However, oilseed rape can continue its natural growth. If the cracking is severe, the likelihood of plant lodging increases. Furthermore, the cracks in the stem may serve as entry points for pathogenic fungi, which can cause stem rot (Fig. 7). Oilseed rape can tolerate cold during vegetative growth, but this adaptation is lost when it is exposed to high temperatures again (Miura and Furumoto, 2013).

Optimal soil moisture helps the soil absorb solar heat during the day, which in turn preserves the heat in the soil during the night and protects it from the cold. Dry

soil quickly loses heat during the night, but moist soil cools down more slowly, reducing the likelihood of frost. Loss of moisture on sunny days or with wind, especially when the soil is frozen and moisture cannot be absorbed, may cause widespread plant death, even if the plants have had good fall growth and are fully hardened (Kourani et al., 2022).

A snow cover on the ground creates an insulating layer against cold, which can reduce damage to the plant's crown area and increase cold tolerance. Snow is an excellent insulator for protecting oilseed rape plants from severe temperature drops (Raboanatahiry et al., 2021). Oxygen and carbon dioxide have good permeability through the snow cover; the permeability of ice is normally subjected to carbon dioxide, which is up to a million times lower than that of snow. Oilseed rape plants under snow cover can sometimes tolerate temperature drops as low as -30°C . In oilseed rape, the sap in the crown does not freeze until -13°C ; however, when the soil freezes due to extreme cold, this ice efficiently conducts the outside air temperature to the surrounding environment and beneath the soil. The development of ice in the soil disrupts root respiration, and in the anaerobic respiration pathway, ethanol and malates are produced in the roots, causing significant harm to the plant (Flakelar et al., 2018).



Figure 7. Cracking of oilseed rape stems caused by severe frost (freezing) during the bolting phase.

2.3. Effect of cold stress on the reproductive growth stage of oilseed rape

The flowering stage is another phase of oilseed rape growth that is highly affected by cold stress (Zareei Siahbidi et al., 2020; Rezaizad et al., 2025). Oilseed rape is very sensitive to freezing from the time of flowering until the plant's moisture content reaches 60%. Freezing and frost during the reproductive growth

stage of oilseed rape may significantly reduce yield (Bañuelos et al., 2013). Spring frost during flowering often causes leaf discoloration and whitening, and stem and lateral branch bending may also be observed (Fig. 8). Once the frost subsides, the plants return to normal and continue their regular growth.



Figure 8. Occurrence of cold damage and stem bending at the beginning of the flowering stage of oilseed rape.

Frost during flowering can also lead to flower abortion, which results in irregular and spaced-out pod formation. The abortion of oilseed rape flowers due to cold ultimately leads to incomplete pod formation on certain parts of the oilseed rape stem, and podding occurs irregularly (Fig. 9) due to the time gap between the developed pods and flowers produced after the frost event. The flowering period of oilseed rape is 30–40 days, and this gap allows oilseed rape to continue pod formation after frost events. Open flowers are highly sensitive to frost damage, while unopened pods and buds may escape freezing damage (Kovaleski et al., 2019).



Figure 9. Flower drop and incomplete pod formation in parts of the stem due to spring frost during the flowering stage of oilseed rape.

Freezing after oilseed rape flowering can lead to a significant reduction in seed yield. Studies have shown that during freezing, only the open flowers suffer major damage. In such conditions, unopened buds can continue their natural growth after the frost. A few days after freezing, gaps between aborted pods on the stem appear. This situation indicates that the frost damage only affected the opened flowers at the time of freezing, and flowers that opened afterward were not affected by the frost (Shaffer *et al.*, 1990). Cold events during flowering can impact pod formation and seed development by destroying pollen and ovules. Open flowers on the upper main stem exhibit a higher cold sensitivity in canola reproductive structures than closed floral buds and siliques, because of reduced photoassimilate availability associated with low air temperatures in the upper canopy. In a controlled environment, air temperature of -4°C during canola anthesis reduces the number of siliques per plant and grains per silique, probably due to ovule death (Kovaleski *et al.*, 2019; Qin *et al.*, 2023). A comprehensive study examined the effects of cold and frost on the reproductive organs of oilseed rape, including pollen and ovules. In this study, plants at the reproductive growth stage (mid to late flowering) were exposed to temperatures of -3°C to 3°C for four hours. The results showed that at -3°C for four hours, morphological frost effects such as branch bending and leaf damage were visible; however, at higher temperatures, morphological effects were not noticeable. Lower temperatures at this stage caused plant death (Ismaili *et al.*, 2015).

Under normal temperature conditions, many pods form on the main and side branches of oilseed rape. Furthermore, the flowering period of oilseed rape is relatively long, about one month. Some studies have shown that less than 50% of the flowers produced turn into pods, but these flower losses are compensated for by other yield components. The first flowers appear on the lower parts of the main branches, and flowers on the side branches and the upper part of the main branch bloom later. A much smaller number of flowers from the upper part of the main branch turn into pods, but these flowers can be considered an important reserve of ovules in adverse environmental conditions. Because the flowers on the lower parts of the plant, which are affected by frost and freezing earlier, are lost, a greater number of flowers from the upper parts of the plant can

turn into pods. Research results have shown that in winter varieties, when freezing occurs early in flowering, the highest seed and pod losses occur in the lower half of the main branch (Dobrokhotov *et al.*, 2023). This may not be the case for spring varieties, as the main branch plays a more important role in determining seed yield in winter varieties compared to spring varieties. These findings indicate that, given the significant impact of cold and frost during the flowering stage, the number of days to flowering or planting date of oilseed rape varieties could be highly influential in escaping or tolerating spring frost and freezing. In an experiment in Australia, it was found that slow-growing varieties, where flowering occurred after the frost event, had higher yields compared to fast-growing varieties where the frost event occurred before or during flowering (Kniuiptyé *et al.*, 2023).

In another study, frost-related damage and benefits of cold acclimation during the reproductive phase in canola were investigated. Plants were exposed to cold acclimation and frost simulation at the start of flowering, during full flowering, and at the start of grain filling. Frost caused death in non-acclimated plants and increased abortion in siliques, floral buds, and flowers, thus reducing silique and grain dry matter content. Frost mostly prevented the development of embryos in the siliques, but viable ovules were found in the floral buds and flowers. During their reproductive phase, canola plants have only a limited ability to increase their tolerance to frost damage. Nonetheless, siliques originating from the floral buds and open flowers contained a higher number of grains than siliques after frost exposure (Kovaleski *et al.*, 2019). During the flowering stage, canola (*B. napus*) becomes particularly sensitive to low temperatures. Research indicates that frost damage begins to occur when temperatures fall to around -2°C to -3°C , which can lead to the abortion of open flowers and a potential reduction in seed set. As temperatures drop further, especially below -4°C , the likelihood of significant injury to flowers and developing pods increases, often resulting in noticeable yield losses. In more severe conditions, such as -6°C , damage extends to the death of non-acclimated plants and widespread abortion of floral structures, significantly compromising grain dry matter accumulation. These thresholds highlight the critical importance of frost risk management during the reproductive phase of canola growth (Kovaleski *et al.*,

2019). Therefore, from the start of flowering to the start of grain filling, floral buds and flowers are responsible for producing most of the grain dry matter when there is frost occurrence.

2.4. Effect of cold stress on the pod development and seed set in oilseed rape

The seed filling stage is highly sensitive to low temperatures. Cold stress during this period can disrupt the translocation of photosynthates to developing seeds, leading to poor grain filling and reduced seed weight (Kovaleski et al., 2019). Frost damage can halt seed development and reduce the thousand-seed weight of oilseed rape. Cold stress may affect a few seeds within a pod or the entire pod. If all seeds in a pod are damaged by frost, the pod will be aborted. Symptoms of cold stress and frost during pod formation and seed filling in oilseed rape include changes in pod color from green to yellow-green, the appearance of lesions and spots on the pods, pod wrinkling, pod drop, and seed shriveling. As cited in Naveed et al. (2020), frost stress can occur at any growth stage of spring oilseed rape, but pods in the early stages of growth may be severely impacted by cold and frost. In these conditions, pods will contain shriveled seeds and eventually abort. Pods that experience frost at this stage will show color changes from light green to yellow and eventually shrivel or drop. If frost occurs after this stage, the external layer of the pods or the seeds may be damaged (Perkins, 2017).

Young pods with more than 60% moisture are highly sensitive to freezing. However, these pods have received less energy for their development and therefore, if environmental conditions are favorable for compensation, the loss of these pods may not lead to a significant reduction in seed yield. The more mature the seeds are, the lower their moisture content, and consequently, they are more resistant to freezing. However, these seeds have received greater energy investment for their development and growth. The plant's ability to compensate for severe frost damage is reduced at the advanced pod development stages compared to earlier stages, and in such cases, seed yield loss becomes significant. On the other hand, drought stress during this stage of growth may intensify the impact of the damage caused by frost (McDonald and Copeland, 1997). Frost and freezing during seed growth can cause substantial damage. The number of pods per

plant, which is determined prior to the frost event, may not be affected by frost during pod formation, but seed development can be significantly impaired. Frost damage to formed seeds is highly dependent on the growth stage and moisture content. The quality and viability of mature and dry seeds are rarely impacted by frost and freezing. Seeds with less than 20% moisture typically tolerate frost. In general, the higher the moisture content of the seeds, the more severe the frost damage will be. A short-term freezing event is sufficient to destroy seeds with 60% moisture content. Frost damage to seeds is not uneven due to asynchronous development of seeds from the lower parts of the plant to the upper parts a result of continuous flowering in oilseed rape (Buntin et al., 2007).

At 20% moisture, seeds may suffer considerable frost damage. The higher the moisture content of the seeds, the more severe the frost damage will be. At 50-60% moisture, a temperature of -3°C may cause the death of developing seeds. However, mature and dry seeds are generally protected from frost and freezing and do not experience damage. Frost also affects the chlorophyll content of seeds. Temperatures between 0°C to 1°C may disrupt the enzymatic system, leading to a reduction in chlorophyll levels in seeds during maturity. Sudden frost may cause plant death, and if this happens just before maturity, seeds with high chlorophyll content may be produced. Even light freezing may stabilize the green color of seeds and prevent processes that lead to the degradation of chlorophyll. High chlorophyll levels may reduce seed vigor and increase seedling mortality in oilseed rape. The chlorophyll content of oilseed rape seeds should be below 35 mg per kilogram to maintain optimal seed quality (Fiebelkorn and Rahman, 2016).

3. Conclusion and future prospects

This comprehensive review demonstrates that cold stress, encompassing both chilling and freezing temperatures, poses a significant threat to oilseed rape productivity, particularly in regions like Iran, where both spring and winter varieties are cultivated. The severity of cold-induced damage varies considerably depending on the growth stage, with germination, the cotyledon stage, stem elongation, flowering, and early pod development being the most vulnerable. The temperature thresholds for frost damage in canola at different growth stages are presented in Table 2.

Table 2. The temperature thresholds for frost damage in canola at different growth stages

Growth stage	Approximate critical temperature (°C)	Description of potential damage
Germination / Seedling	-4°C to -6°C	Damage to cotyledons, growth inhibition, and possible seedling mortality under severe frost
Rosette Stage (8–12 leaves)	-10°C to -15°C (with full acclimation)	Winter canola can tolerate very low temperatures after cold acclimation in autumn
Stem Elongation (Bolting)	-6°C to -8°C	Risk of damage to apical meristem, leading to shortened stems or deformed growth, yield reduction
Flowering	-3°C to -4°C	High sensitivity; open flowers may be aborted, reducing pod set and final yield
Early Pod Formation / Early Seed Set	-4°C to -5°C	Damage to ovules and embryos, leading to pod abortion or malformed pod development
Seed Filling / Ripening	-2°C to -3°C	Shriveling of seeds and reduced seed weight; however, damage is usually less severe at this stage

Cold stress negatively impacts various physiological and morphological processes, reducing germination rates, seedling vigor, photosynthetic activity, and yield. Key damaging effects include membrane damage, solute leakage, reduced water uptake, disrupted enzyme activity, flower abortion, impaired pollination, and arrested seed development. While winter oilseed rape possesses some degree of cold tolerance through mechanisms like vernalization and cold acclimation, extreme cold events can still cause substantial crop loss. The interaction of cold stress with other environmental factors, like soil moisture and the presence of crop residues, further complicates the situation. Previous studies in this area have clarified many issues related to cold stress in oilseed rape; however, there are still issues that require more research. The following are some prospects that the researchers in this area can consider.

- **Developing Cold-Tolerant Varieties:** A primary focus should be on breeding and developing oilseed rape varieties with enhanced cold tolerance. This could involve utilizing advanced techniques like marker-assisted selection, genomic selection, and gene editing to identify and incorporate genes associated with cold hardiness. Research should prioritize identifying and understanding the complex genetic and physiological mechanisms underlying cold tolerance in oilseed rape.
- **Optimizing Planting Dates and Agronomic Practices:** Adjusting planting dates to minimize exposure to frost-prone periods can be a crucial strategy. Further research is needed to determine optimal planting windows for different regions and varieties, taking into account local climate patterns and the specific cold tolerance of the cultivars. Investigating the effects of other agronomic

practices, such as seed priming, nutrient management, and the use of biostimulants, on cold tolerance is also warranted.

- **Understanding Cold Acclimation and Deacclimation:** A deeper understanding of the molecular and physiological processes involved in cold acclimation and deacclimation is essential. Research should focus on identifying the key triggers and signaling pathways that regulate these processes. This knowledge could be used to develop strategies to enhance cold hardening and prevent premature deacclimation.
- **Investigating the Role of Crop Residues:** Further research is needed to fully understand the impact of crop residues on soil temperature and oilseed rape germination. Studies should investigate the optimal management of crop residues to minimize their negative effects on germination and seedling establishment in cold conditions.
- **Developing Predictive Models:** Integrating climate data, soil information, and oilseed rape growth models can help develop predictive tools for assessing cold stress risk. These tools can aid farmers in making informed decisions about planting, crop management, and even the selection of appropriate varieties.
- **Exploring the Interaction of Cold with Other Stresses:** Given the complex interplay of environmental stresses, future research should investigate the combined effects of cold stress with other factors like drought, heat, and disease. Understanding these interactions is crucial for developing comprehensive strategies for improving oilseed rape resilience in a changing climate.
- **Utilizing Advanced Technologies:** Integrating advanced technologies like remote sensing,

phenotyping platforms, and metabolomics can accelerate research on cold tolerance in oilseed rape. These tools can enable the rapid and non-destructive assessment of plant responses to cold stress, facilitating the identification of superior genotypes and the development of effective mitigation strategies.

Conflict of interests

The authors declare no conflict of interest.

Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

Consent for publications

All authors read the final version of this manuscript and approved it for publication in this journal.

Availability of data and material

The authors declare that they embedded all required data in the manuscript.

Authors' contributions

A.R. prepared the main draft and provided the pictures, and A.S. finalized the paper and prepared it for publication.

Informed consent

The authors declare not to use any patients in this research.

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