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Transcriptional Networks in Rapeseed Development and Stress Responses

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Abstract Rapeseed (*Brassica napus* L.) is a globally significant oil crop, and its development and stress responses are precisely controlled by a complex transcriptional regulatory network to adapt to diverse environmental conditions. Key transcription factors (such as the AP2/ERF, MYB, and WRKY families) play a core role in the formation of plant stress resistance by coordinating the regulation of hormone signaling, reactive oxygen species scavenging, and osmotic adjustment pathways. Meanwhile, long non-coding RNAs and epigenetic modifications (such as DNA methylation) further enhance the gene regulatory capacity of plants under abiotic stress conditions like drought, salt stress, and low temperature. With the development of CRISPR/Cas9 technology, precise editing of key transcription factors has become possible, providing an effective strategy for the breeding of stress-resistant rapeseed varieties. By integrating multi-omics data and genetic variation analysis, the breeding process can be significantly accelerated, opening up new paths for sustainable rapeseed production in the context of climate change.

Keywords Transcriptional networks; Rapeseed; Stress responses; Transcription factors; Epigenetic regulation

1 Introduction

Speaking of it, rapeseed (*Brassica napus* L.) looks ordinary, but don't underestimate it. It can be regarded as the "top star" among oil crops worldwide. Oil can be eaten, meal can be fed, and biodiesel cannot do without it (Xiong et al., 2022). If you ask what special ability it has, it does have one-strong adaptability. It can endure both the north and the south, cold and warm, dry and wet conditions. Except for extremely bad weather, it is not very picky about the environment. It is precisely for this reason that many places are willing to grow it. Not to mention the economic benefits it brings. This is very direct for farmers. Crops that can make money, naturally, no one finds them troublesome.

When it comes to vegetable oil, many people might first think of soybean oil or palm oil. But in fact, rapeseed is not a nobody. It has consistently ranked third in global vegetable oil production (Wang et al., 2022). Why is it so popular? The reason is not complicated. Using it for stir-frying or processing food is relatively healthy-it has low saturated fat and is rich in omega-3 fatty acids. After oil extraction, the remaining rapeseed meal is not wasted either. It has a high protein content and is most suitable to be directly used as feed. And now a new use is beginning to emerge: making biodiesel. Although it is not used much at present, when it comes to reducing reliance on traditional energy sources, this path is indeed worthy of attention.

Rapeseed, if you say it's delicate, is actually not fragile at all. It can survive cold weather, drought and even a little saline-alkali soil (Pu et al., 2019). This story begins with its "origin"-it was originally a hybrid of brassica and cabbage, and its genome is particularly complex (Zhou et al., 2022). It is precisely this complex "foundation" that has provided more operational space for breeding. Whether it is for yield or oil quality, targeted improvements can be made. Of course, it is not made of iron. In the event of extreme weather, its output will still be affected. Looking at it now, the reason why it can be so "resilient" is that it relies on a group of transcription factors and stress genes responsible for coping with adverse conditions in the body. They act like switches, activating when necessary and mobilizing resistance.

When it comes to how plants cope with harsh environments, the key lies in those invisible genetic regulations. For example, when rapeseed is exposed to conditions such as cold and drought, a complex emergency mechanism will be activated in its body. It's not a single gene at work, but rather transcription factor families like AP2/ERF and WRKY are engaged in a coordinated battle (Xue et al., 2022). They are like the conductors of an orchestra, regulating physiological activities such as hormone signals and sugar metabolism. Interestingly, although the coping methods for different stresses have their own focuses, they basically cannot bypass the process of reactive oxygen species scavenging (Liu et al., 2022). Of course, these molecular-level changes will eventually be reflected in the stress resistance of the plants, enabling the crops to survive in harsh environments (Raza et al., 2021).

We conducted this research precisely to figure out what mechanism rapeseed relies on to withstand various environmental pressures. At present, transcription factors such as AP2/ERF and WRKY have indeed been confirmed to be involved, but in the final analysis, these are just the tip of the iceberg. What exactly does the entire regulatory network look like? Which links are the most crucial? It's still a fog now. The goal this time is to thoroughly review the existing research results and see if we can piece together a relatively complete map. If one is lucky, perhaps a few nodes with strong control can really be identified-then in the future, when breeding, there will be a direction and focus for improvement. In fact, increasing production is one aspect. What is more crucial is to ensure that rapeseed can remain stable in the context of unstable and even increasingly extreme climate, which is of great significance for food security. However, it must be admitted that the stress resistance mechanism of plants is indeed rather complex, and different stresses often interweave and influence each other. Therefore, clarifying these relationships is not something that can be achieved overnight; it requires a gradual process.

2 Transcriptional Regulatory Mechanisms in Plants

2.1 Basics of gene expression and transcription factors

The gene regulation of plants is actually quite like a multi-level circuit system. Which gene and when it starts working are all scheduled by a set of "instructions". The most crucial role in this system is undoubtedly the transcription factors-they are like precise identifiers that can target specific DNA fragments to initiate reactions. Take rapeseed as an example. There is a transcription factor family called GARP, which is particularly active when the plant is deficient in nutrients (Hua et al., 2022). Members like BnaA9.HHO1 and BnaA1.HHO5 (Figure 1) can be regarded as emergency response centers during nutritional stress. But nutrient deficiency is only one of the problems. When drought or soil salinization occurs, it's the turn of the NF-Y family to step in. This type of transcription factor is composed of three different subunits that work together to help plants survive the difficult times. Interestingly, although they seem to be responsible for different tasks respectively, once multiple stresses occur simultaneously, these "independent" factors will also join forces to form more complex regulatory responses.

2.2 Regulatory elements in plant genomes

To understand how plants regulate genes, it is not enough to just look at the genes themselves; one also needs to pay attention to those unremarkable "accessories"-regulatory regions like promoters and enhancers, which are the ones that truly control the switches of genes. Take rapeseed as an example. The promoter region of the GARP family genes is quite interesting. There are many regulatory loci related to growth and stress response distributed in it (Hua et al., 2022). These sites are like pre-set buttons. As soon as there is any movement from the outside world, the transcription factors can find them immediately and start a response. Interestingly, the "operation methods" of different gene families are indeed not the same. For instance, the protein structures of several subunits of NF-Y and some transcription factors related to plant hormones have not changed much during evolution, indicating that their functions are indeed stable and crucial (Wang et al., 2020). Recently, it has also been discovered that gene families like BnLTP are quite special. Their DNA sequences contain a type of "sensing element" that can recognize external stress. When drought or pests and diseases occur, these genes can respond quickly.

2.3 Role of transcriptional networks in development and stress responses

The gene regulatory network within plants is indeed complex. It's somewhat like a huge symphony orchestra, with each "musician"-that is, the transcription factor-doing their own job, but they also have to work in perfect harmony. Take rapeseed as an example. When it gets cold, it doesn't rely on a single gene to survive. Instead, transcription factors like WRKY and bZIP work together (Luo et al., 2019) to jointly ensure that the seeds can germinate even in an unfriendly climate. The most "worried" ones are still the WRKY family, especially members like BnaWRKY56 and BnaWRKY60 (Ma et al., 2022). They have to deal with heavy metal pollution and saline-alkali stress at the same time. They almost have to rush wherever there is an incident. Interestingly, some transcription factors take an unconventional path, such as BnaMYB111L, which is a member of the R2R3-MYB family and specializes in regulating reactive oxygen species balance (Yao et al., 2019). Once a pathogen invasion is detected, it will trigger that "suicidal" defense mechanism-directly causing the infected cells to self-destruct to protect the entire plant. It sounds quite ruthless, but for plants, this is one of the means to save their lives.

You might not expect that among the "heroes" behind rapeseed's drought resistance are some lncrnas that are not very prominent in daily life. Recent studies have found that when drought occurs, these long non-coding Rnas collaborate with transcription factors like BnaC07g44670D to initiate a set of mechanisms specifically for responding to drought. Even better, even after the drought ended and water was restored, this system continued to operate, somewhat like a plant's "memory"-as if it had remembered the stress it had experienced before. Such reactions can now be seen more clearly through genome-wide analysis. Some lncrnas directly regulate target genes, while others function by being embedded in more complex co-expression networks. But to say it thoroughly is far from enough. The lncRNA combinations initiated by each drought are quite different, and the mechanisms cannot be simply copied. Ultimately, these new discoveries have indeed provided us with a lot of inspiration, but to figure out exactly how these molecules "communicate" with each other, we still need to dig deeper.

3 Key Transcription Factors in Rapeseed Development

3.1 Auxin-related Transcription Factors

When it comes to the growth regulation of rapeseed, auxin is definitely an indispensable role. It is like a global dispatcher, overseeing the entire process from germination to fruiting. However, it is the transcription factors responsible for responding to it that are actually "working" on the front line. For example, BnerF114a1, a member of the AP2/ERF family, mainly manages the terminal bud part-once it is activated, the plant will sprout more lateral branches and the number of corner fruits it bears will also increase significantly. However, if the environment deteriorates, such as encountering salt or alkali or drought, the plot will have to be written by someone else. At this point, it is the turn of WRKY46 (Ding et al., 2015). It not only regulates the level of auxin but also activates the ABA signaling pathway, helping plants grow strong lateral roots under stress conditions. One interesting point is that although all these transcription factors cannot bypass auxin, their division of labor is very clear: one is in charge of the branches and the other focuses on the root system. The boundaries are distinct, yet they cooperate very naturally.

3.2 Ethylene and cytokinin-responsive transcription factors

The "interaction" among plant hormones is always quite interesting. Like ethylene and cytokinin, which seem to be doing their own thing on the surface, they often work together in the growth of rape. When encountering low temperatures, ethylene will join forces with H_2O_2, allowing the seed cell wall to "relax" so that the embryo can extend smoothly. What's more interesting are the transcription factors of the ERF family, such as BnerF114A1 (Lyu et al., 2022). Although they are ethylene response factors, they can regulate the distribution of auxin-as a result, the plants have more branches and plumper kerberries. However, these hormone signals do not act alone; they interweave into a complex network, taking into account everything from daily growth to coping with environmental stress. Sometimes the same transcription factor has to deal with several hormone signals simultaneously, which is indeed quite busy.

3.3 MYB and WRKY families in rapeseed growth

When rapeseed is coping with environmental pressure, the transcription factors of the two major families, MYB and WRKY, are extremely busy. Take the MYB family as an example. BnaMYBL17 mainly focuses on frost resistance (Luo et al., 2023), and can precisely regulate the expression of those genes related to cold resistance. The most interesting one is BnMRD107 (Figure 1) (Li et al., 2021).

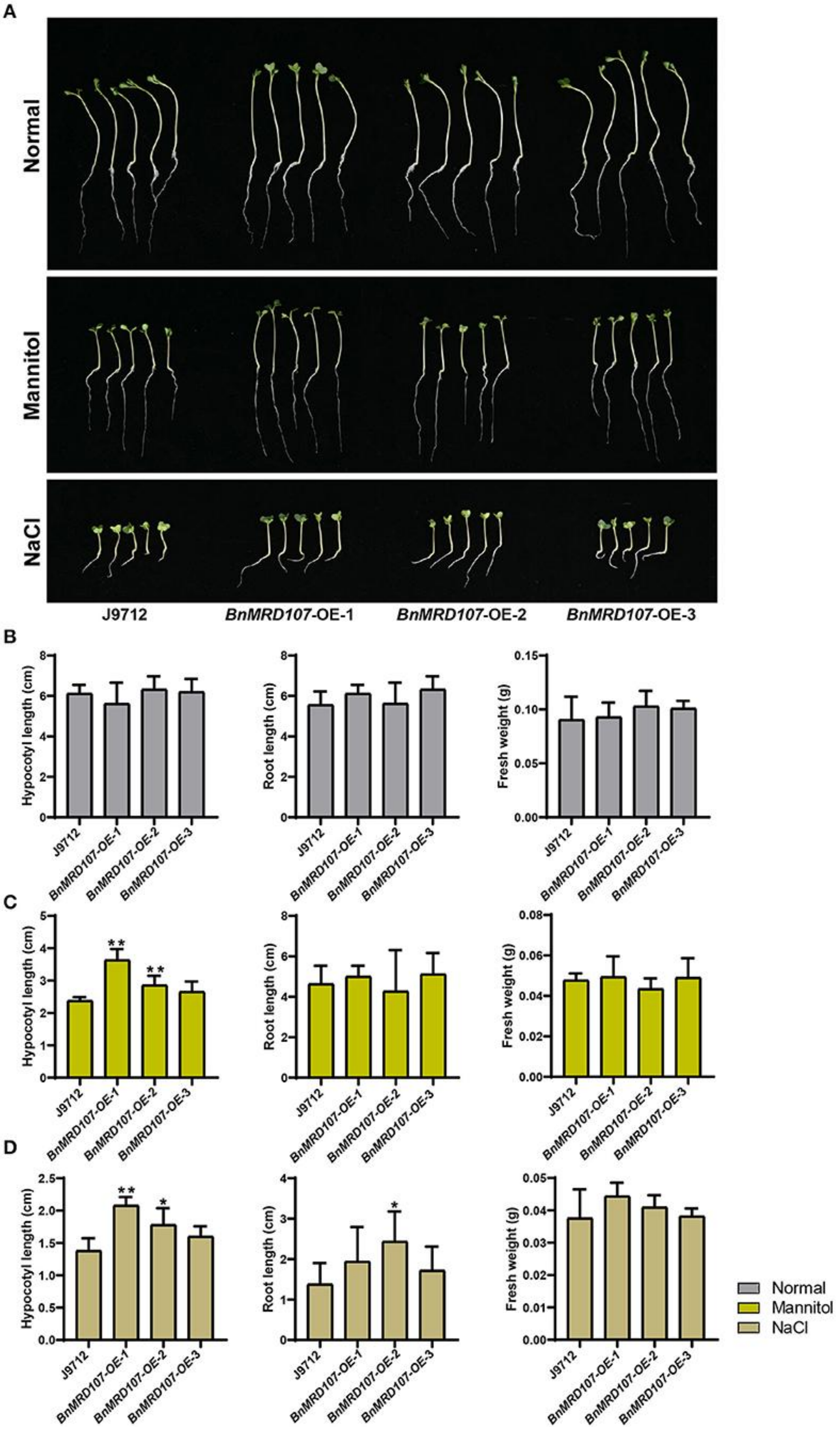

Figure 1 Phenotype of BnMYBR107-OE plants under normal conditions, osmotic stress, and salt treatments. (A) Growth performance of J9712 and BnMYBR107-OE plants under normal conditions, osmotic stress, and salt treatments. (B-D) Hypocotyl length, root length, and fresh weight under normal conditions, osmotic stress, and salt treatments. Data are presented as means±SD (n=5). Asterisks (*) indicate significant differences between the transgenic lines and J9712 based on Duncan's multiple range test (**p*<0.05, ***p*<0.01) (Adopted from Li et al., 2021)

It is also a MYB family, but it is responsible for osmotic stress, that is, it helps the seedlings to hold up when there is a lack of water. Interestingly, although these factors belong to the same family, the "business" they are responsible for varies greatly, just like colleagues in the same department who are in charge of different projects. They each perform their own duties while also cooperating with each other, jointly building a defense system for rapeseed to deal with various environmental challenges.

The transcription factors of the WRKY family are truly all-round players. They can be seen in almost every stage of the growth and development of rapeseed. For example, WRKY6, although the research data are from *Arabidopsis thaliana* (Song et al., 2020), is likely to play a similar role in rapeseed oil synthesis. Even more remarkable is WRKY46 (Ding et al., 2015), which can simultaneously regulate both ABA and auxin signaling pathways, helping plants grow more lateral roots to absorb water in saline-alkali or arid environments. The most interesting aspect of the WRKY family lies in their "social skills" (Jiang et al., 2017; Wani et al., 2021)-When subjected to stress such as drought or high temperature, they can not only rapidly adjust their own gene expression, but also act in conjunction with other transcription factors. Speaking of this, it has to be mentioned that although MYB and WRKY are good at different tasks respectively, they cooperate quite well in helping rapeseed adapt to environmental stress (Khoso et al., 2022), almost like an emergency response team within the plant.

4 Transcriptional Networks in Rapeseed Flowering and Reproductive Development

4.1 Regulatory pathways influencing flowering time

The flowering time of rapeseed is not something that can be determined casually. Behind it lies a complex regulatory network. It is quite surprising that homologues of genes such as VIN3 and FUL have developed new functions in rapeseed (Shah et al., 2018). Through genome-wide scanning, scientists identified 55 key regions affecting flowering time (Li et al., 2018a), among which the most notable ones included genes such as BnaC03g32910D (CO) and BnaA02g12130D (FT). These genes each have their own responsibilities-some are responsible for sensing the length of daylight, some process low-temperature signals, and others are related to the gibberellin pathway. However, the most troublesome thing is that they always like to go against each other. For instance, BnaA03g13630D (FLC) is particularly fond of going against other genes. It is no wonder that the flowering time of rape is always difficult to predict. There are simply too many regulatory pathways involved. Just considering the signals such as photoperiod, vernalization and circadian rhythm is complex enough.

The regulatory mechanism of the flowering time of rapeseed has become increasingly fascinating with further research. For instance, the 14-3-3 protein BnGF14-2c (Figure 2) (Fan et al., 2022) can actually promote flowering through the vernalization pathway in semi-winter rapeseed, and it also interacts closely with flowering regulatory factors such as BnFT.A02 and BnFLC.A10. What's more interesting is the small RNA miR156 (Wang, 2014), which regulates the SPL transcription factor to ensure that the plant flowers at the right time and can survive even in less than ideal environments. When it comes to fine control, RNA-binding proteins such as AtGRP7 and AtGRP8 (Steffen et al., 2019) cannot be overlooked. They specifically prune the mRNA of flowering inhibitory factors such as FLC with the precision of a gardener pruning. These findings suggest that the flowering of rapeseed is not determined by a single path, but rather is the result of various molecules "showing their unique abilities"-some are responsible for vernalization, some for age control, and others specifically for splicing regulation, ultimately converging into a complex regulatory network.

4.2 Transcriptional control of floral organ development

The mystery of rape flowering actually lies in the meticulous regulation of the development of its flower organs. Transcription factors like LFY and AP1 (Winter et al., 2015) are like the conductors of a band, controlling the major transition from vegetative growth to flowering. Interestingly, they not only directly regulate flowering genes, but also involve the expression of hormone signaling and substance transportation-related genes (Wils and Kaufmann, 2017). As a result, a phenomenon emerged-different regulatory pathways would "connect" with each other, hormone signals might unexpectedly affect the flowering time, and material transport might change the morphology of flower organs. Although this complex network increases the difficulty of research, it precisely reflects the wisdom of plants in flexibly responding to the environment.

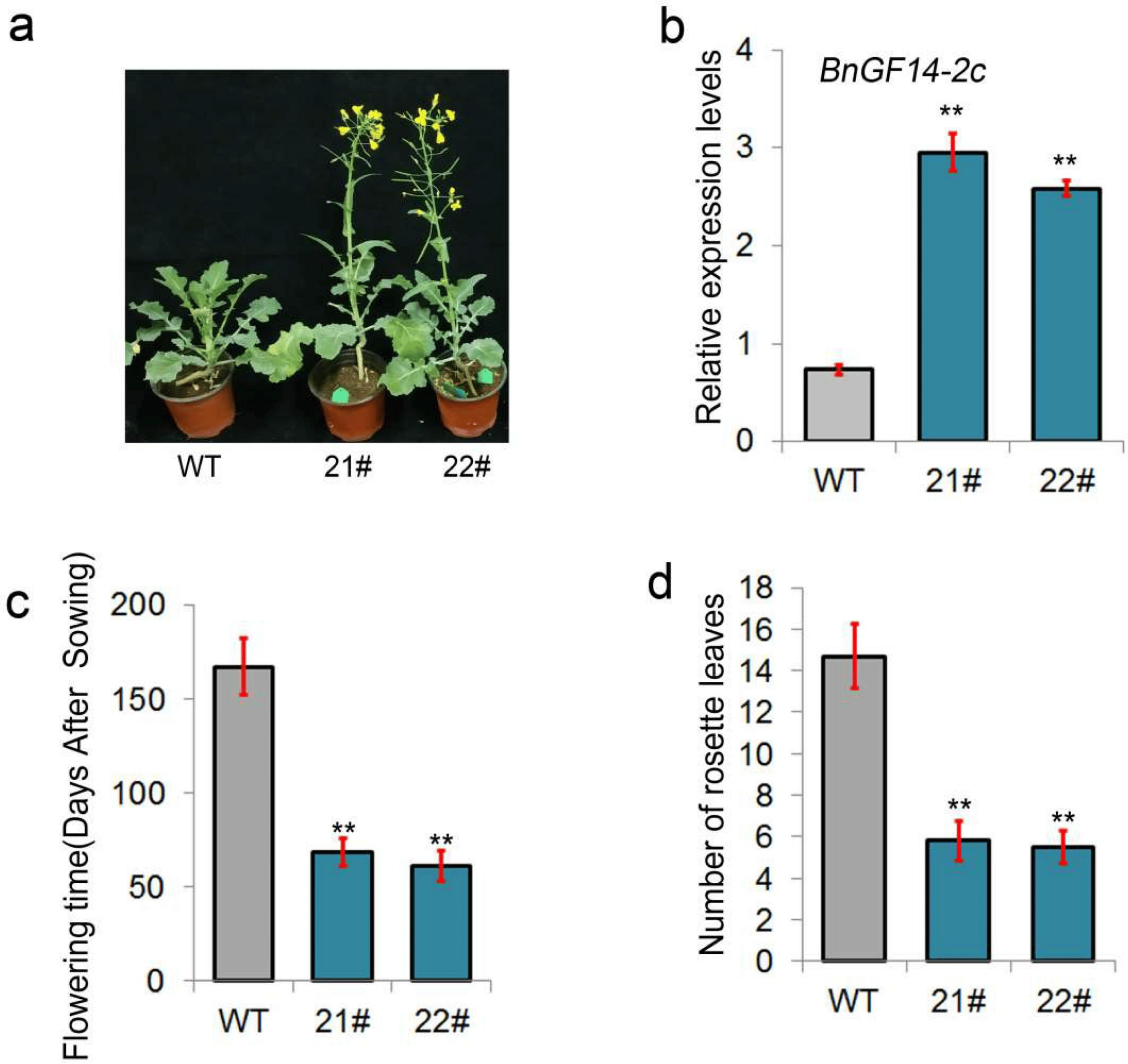

Figure 2 Phenotypic observation and qPCR validation of 35S::BnGF14-2c transgenic rapeseed. Two positive BnGF14-2c transgenic lines (OE21#, OE22#) and wild type (93275) were selected and analyzed in the greenhouse at 22 °C-24 °C with 55% relative humidity under long-day (LD) conditions (16 h light/8 h dark). (a): Phenotypic differences in flowering between 35S::BnGF14-2c transgenic plants and wild-type plants. Photographs were taken at 85 day-after-sowing. (b): Expression analysis of BnGF14-2c by qRT-PCR. (c): The statistical analysis of the flowering time (day-after-sowing) in T3 35S::BnGF14-2c transgenic plants and wild-type plants. (d): The number of rosette leaves in T3 35S::BnGF14-2c in transgenic plants and wild-type plants at 85 day-after-sowing. All the experiments were repeated for three times. Asterisk '**' indicates extremely significant differences ($p < 0.01$, Student's t-test) between the transgenic lines and WT (Adopted from Fan et al., 2022)

The driving forces behind plant flowering are not just a few "star" transcription factors. The C_2H_2 zinc finger protein family is a low-key yet powerful role (Lyu and Cao, 2018). They can not only adjust chromatin structure but also interact with hormone pathways, participating in the entire process from flowering induction to flower organ maturation. Interestingly, these proteins are particularly active in pollen and pistil development and can be regarded as "experts" in reproductive development. Even more amazing are those tiny mirnas (Luo et al., 2013). Despite their small size, they are highly conserved in various plants and specifically regulate the critical transition from vegetative growth to flowering. These findings suggest that the development of floral organs is not accomplished by just a few genes, but rather a symphony played by multiple mechanisms including chromatin modification, hormone signaling and small RNA regulation.

4.3 Gene networks in seed development and maturation

The process of rapeseed from flowering to seed production is like a meticulously planned performance, with various "staff members" both on and off the stage. The transcription factors and mirnas in the cells are extremely busy (Pajoro et al., 2014), having to handle hormone signals and adjust chromatin states to ensure that each developmental stage is closely connected. Interestingly, this regulatory system is surprisingly similar in different plants, and even the details are well preserved, indicating that it is indeed the core procedure of plant reproduction. From the falling of petals to the maturation of seeds, each step is closely linked-the floral organs must first develop fully before laying the foundation for the subsequent formation of seeds. These molecular regulatory networks are like precise assembly lines, with clear division of labor and mutual cooperation, jointly completing the life relay from flowering to seed production.

5 Rapeseed Response to Abiotic Stresses

5.1 Drought-induced transcriptional responses

The impact of drought on rapeseed is not merely the wilting of leaves as seen on the surface. Once water is lacking, the plant will immediately activate the emergency plan (Wang et al., 2019)-quickly synthesize more proline and reduce its decomposition at the same time, thereby maintaining the osmotic balance within the cells. Even more surprisingly, those lncrnas that were originally considered "useless" are extremely active under drought (Figure 3) (Tan et al., 2020), especially in drought-resistant varieties, they participate together with mRNA to regulate various metabolic pathways. When it comes to drought resistance experts, DREB transcription factors (Dong et al., 2017) can be regarded as commanders, capable of simultaneously regulating the expression of multiple stress-resistant genes. Interestingly, different rapeseed varieties have different strategies when facing drought-some are good at water retention, while others are proficient in restoration. This diversity provides rich options for breeding.

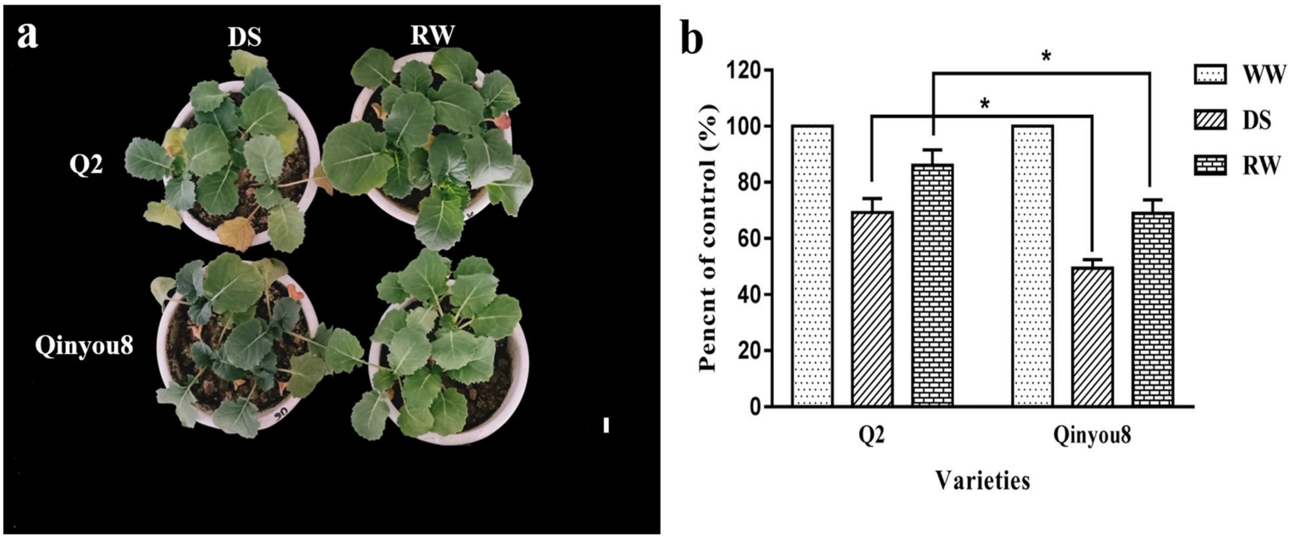

Figure 3 Phenotypes of seedlings under different treatments. a The picture show seedlings under DS and RW treatments, respectively. Bar = 1 cm. b Comparisons of fresh weight among the treatments. Experiments were repeated three times and vertical bars indicate standard errors. “*” indicates the significance of the difference at the 0.05 level. WW = well-watered; DS = drought stress; RW = re-watering (Adopted from Tan et al., 2020)

5.2 Heat stress and transcriptional regulation

The strategy of rapeseed in dealing with high temperatures is quite ingenious. Various transcription factors are like an emergency response team working hard on the spot. The factor DREB2A, which is usually responsible for drought resistance and cold protection (Schramm et al., 2007), actually temporarily "shifts" during high temperatures-it first activates HsfA3, the "high-temperature alarm", and then triggers the production of heat shock proteins in a chain reaction. However, what is even more surprising is the performance of the NF-Y family, especially BnNF-YA3, which is mainly responsible for seed germination and root growth at high temperatures. It is worth mentioning that these pathways have never worked alone. DREB2A and HsfA3 act like a relay, one activating the other, and ultimately jointly enhancing the plant's heat tolerance. Although high temperatures may delay seed germination by a few days, at least they can preserve life. This is the wisdom of plants in responding to environmental stress.

5.3 Cold stress and the role of CBF/DREB networks

Rapeseed is not passively exposed to low temperatures; it has a complete "cold-resistant system". These transcription factors such as CBF/DREB are like cold resistance commanders (Agarwal et al., 2006), specifically recognizing the DRE/CRT elements on the promoters of cold stress genes. Interestingly, this system is more pronounced in transgenic plants (Ito et al., 2006)-overexpression of these factors causes the plants to frantically accumulate proline and sugar, just like putting on a "cold-proof suit" for themselves. Even more astonishingly, from *Arabidopsis thaliana* to rapeseed, the strategies used by different plants are almost the same (Lata and Prasad, 2011), indicating that this is a universal overwintering wisdom in the plant kingdom. However, this system is not omnipotent. It will still fail in extremely low temperatures, but it can basically handle daily frosts.

6 Rapeseed Response to Biotic Stresses

6.1 Pathogen recognition and signal transduction

The defense system of rape against pathogens is quite ingenious, as if it were equipped with multiple alarms. Transcription factors like BnaGRF are particularly interesting (Sun et al., 2022)-they do not show up in normal times, but immediately adjust their expression and activate the defense program once pathogen invasion such as scltinomycosis is detected. Even more astonishingly, the nsLTPs protein (Xue et al., 2022), named "non-specific", shows high specificity when resisting fungi such as sclerotinia and Leptospirosis spotted. In fact, the immune system of rape is much more complex than imagined. Different pathogens will activate completely different signaling pathways when they attack. Some are responsible for early warning, while others are specifically responsible for subsequent defense. This flexible and versatile strategy enables rapeseed to effectively resist the threats of various pathogens without consuming excessive energy.

6.2 Transcriptional regulation of disease resistance genes

The immune system of rapeseed is like a precise regulatory network, where various signal molecules and transcription factors interact in a complex way. The transcription factors of the GARP family are versatile (Hua et al., 2022), not only involved in growth and development, but also mobilizing defense genes when pathogens invade. Interestingly, the salicylic acid (SA) and jasmonic acid (JA) signaling pathways have a subtle relationship (Caarls et al., 2015)-SA often regulates the expression of JA-related genes, just like two departments of the immune system that both divide the labor and cooperate. This cross-regulation enables rapeseed to flexibly adjust its defense strategies according to different pathogens. The most remarkable part is that this system can automatically balance defense and growth. It neither wastes energy on excessive defense nor focuses solely on growth while neglecting protection, demonstrating the survival wisdom that plants have evolved over a long period of time.

6.3 Role of salicylic acid and jasmonic acid pathways

The immune defense system of rapeseed is like two well-coordinated combat troops-the SA and JA signaling pathways each have their own specialties. The SA pathway excels in protracted battles (Beckers and Spoel, 2006), especially against pathogens that rely on living organisms. It dispatches NPR1, this "messenger", to contact TGA transcription factors and rapidly activate the production line of disease-resistant proteins. The JA pathway excels in emergency response and is specifically designed to deal with highly destructive necrotic pathogens and pests, rapidly activating defense genes through the COI1 protein. Interestingly, these two channels will also "snatch channels" from each other (Liu et al., 2021)-SA often hides or directly degrades the transcription factors of JA. The seemingly contradictory regulation is actually very smart. It not only avoids the waste of defense resources but also flexibly adjusts strategies according to different threats, enabling rapeseed to deal with various biological stresses calmly.

7 Epigenetic Regulation in Rapeseed Development and Stress Response

7.1 DNA methylation and its impact on gene expression

DNA methylation acts like a "gene switch" in rapeseed's adaptation to adverse conditions, with a very ingenious regulatory approach. When nitrogen deficiency occurs, rapeseed will reprogram gene expression by adjusting the methylation pattern (Hua et al., 2020)-just like labeling different genes as "enabled" or "disabled", especially those involved in nitrogen metabolism, thereby improving nitrogen utilization efficiency. Interestingly, when facing salt stress, this system plays new tricks, and the methylation markers are specifically adjusted for the transcription factors that regulate stress resistance. In fact, the effect of methylation is entirely dependent on the location-in some places, methylation activates genes, while in others it silenced them. This flexible regulation enables rapeseed to quickly respond to various environmental pressures without altering its DNA sequence, saving energy and being highly efficient. It can be regarded as an "intelligent regulation system" in the plant kingdom.

7.2 Histone modifications in transcriptional control

When rapeseed responds to environmental stress, histones are like regulatory masters wearing various chemical "hats", and these modifications directly determine the on-off state of genes. Interestingly, the histone deacetylase HDA9 and the transcription factor WRKY53 are like a pair of rivals (Zheng et al., 2019), with the former "removing the label" from the latter, resulting in a decline in resilience. The phenomena found in soybeans (Song et al., 2012), such as H3K4 trimethylation and H3K9 acetylation, are also likely to play a similar role in rapeseed. In fact, these histone modifications are like precise tuning knobs-when methyl or acetyl groups are added, the chromatin structure undergoes subtle changes, thereby precisely regulating gene expression levels. This regulatory approach that does not alter the DNA sequence but can quickly respond to environmental changes demonstrates the survival wisdom formed by plants during their long-term evolution.

7.3 Small RNAs and transcriptional silencing mechanisms

Those insignificant small RNAs (sRNAs) in rapeseed actually hold significant regulatory power. These little ones, including miRNA and siRNA, collectively "switch positions" when nitrogen is deficient-some adjust leaf development, some manage amino acid metabolism, and some specifically regulate hormone signals. Work together to help the plants get through the difficult times. Even more amazing is the ability of siRNA (Simon and Meyers, 2011), which can directly mark methylation on DNA or change histone modifications, just like a small conductor precisely controlling gene switches. In fact, this system is particularly adept at dealing with "junk DNA" in the genome, silencing these potentially dangerous regions by forming heterochromatin. These findings suggest that rapeseed's adaptation to the environment is not achieved through the individual efforts of a few star genes, but rather through a sophisticated regulatory network jointly constructed by "behind-the-scenes workers" such as sRNA, DNA methylation, and histone modification.

8 Case Study: Transcriptional Response to Drought Stress in Rapeseed

8.1 Overview of drought-stress challenges in rapeseed cultivation

When rapeseed encounters drought, the water in the cells is the first to be affected-just like a sudden water cut-off. At this time, the plant will activate the emergency plan: on the one hand, it will vigorously accumulate "water-retaining agents" such as proline; on the other hand, it will increase the level of antioxidant enzymes to eliminate free radical damage. Interestingly, different varieties have different coping strategies-some are busy adjusting the opening and closing of stomata, while others focus on changing the root structure. From a molecular perspective, drought can cause a major reshuffle of the entire transcriptome (Zhang et al., 2019), the expression of thousands of genes has changed, as if rewriting the survival program. These findings indicate that the drought resistance of rapeseed does not rely on a single mechanism, but rather maintains its life activities through a comprehensive strategy that involves multiple approaches.

8.2 Key transcriptional changes observed under drought

When drought strikes, the genetic activity within rape plants undergoes a complete transformation. Genome-wide scanning revealed that the differences in gene expression between drought-tolerant varieties and sensitive varieties were very significant; In 2020, tens of thousands of mrnas and lncrnas were either abnormally active or simply on strike. In this genetic "chaos", transcription factors such as MYB and NAC are like command centers, busy coordinating the emergency response of downstream genes. However, there are also "hindrance" ones, such as BnA.JAZ5 (Figure 4) (Cao et al., 2022). By interfering with ABA and JA hormone signals, it not only causes dysregulation of stomatal density but also reduces the seed germination rate. These findings indicate that the drought resistance of rapeseed cannot be resolved by just one or two genes, but is the result of the combined effect of the entire gene network-some genes charge ahead while others secretly create obstacles. This complex interaction ultimately determines the drought tolerance of the plant.

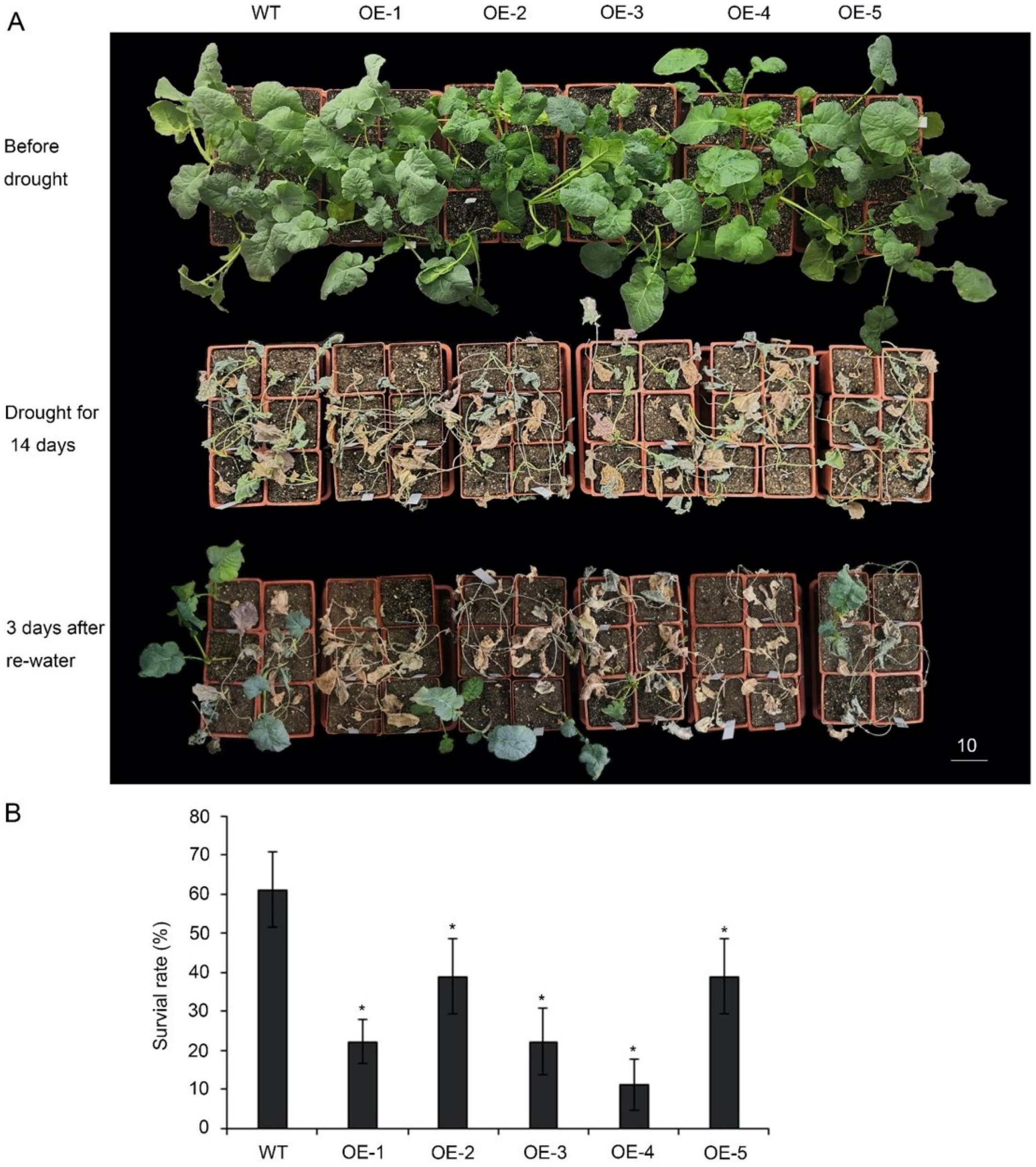

Figure 4 Drought resistance testing of p35S::BnA.JAZ5 plants at the five-leaf stage. (A) Drought resistance assay of five overexpressing lines. (B) Survival rates of five overexpressing lines after 3-day recovery from drought stress treatment. WT, accession K407. OE-1, OE-2, OE-3, OE-4 and OE-5, p35S::BnA.JAZ5 plants. Asterisks indicate significant differences between wild-type and p35S::BnA.JAZ5 lines ($p < 0.05$, Student’s *t*-test). Scale bar, 10 cm (Adopted from Cao et al., 2022)

8.3 Potential breeding and genetic engineering solutions

To cultivate drought-resistant rapeseed varieties, researchers have found several breakthroughs. That disruptive BnA.JAZ5 gene has instead become an important clue-regulating its expression may improve the stomatal response of rapeseed. More interestingly, lncrnas that are abnormally active during drought; In 2020, they act as the driving forces behind the genome, influencing drought resistance by regulating mRNA. The current breeding strategy is relatively clear: on the one hand, traditional methods are used to screen for superior stress-resistant traits; on the other hand, gene editing is employed to precisely regulate key transcription factors and lncrnas. However, in actual operation, it should be noted that the genetic background of different varieties varies greatly, and the same genetic modification may have completely different effects. Translating these molecular discoveries into field manifestations still requires a large number of experiments, but at least it provides new ideas for dealing with increasingly frequent droughts.

9 Current Advances in Genetic Engineering for Transcriptional Modulation

9.1 CRISPR-Cas9 applications in transcription factor editing

The CRISPR-Cas9 gene editing technology is revolutionizing the way rapeseed varieties are improved. Taking glyphosate resistance as an example (Wang et al., 2021), researchers used a twin virus system to deliver CRISPR components and precisely modify the EPSPS gene to cultivate herbicide-resistant rapeseed seedlings. The most remarkable aspect of this technology lies in its ability to simultaneously handle multiple similar genes in the tetraploid genome of rapeseed (Li et al., 2018b), which is difficult to achieve with ordinary methods. Nowadays, this system is often used to edit the transcription factors that regulate stress resistance (Jaganathan et al., 2018), compared with traditional breeding, the target traits are obtained more quickly. However, in actual operation, it was also found that although CRISPR has high efficiency, the editing effects of different targets vary greatly (Tian et al., 2022), which reminds that multiple target schemes should be prepared when designing experiments. Overall, this technology has brought the improvement of rapeseed varieties into a new stage of precise regulation. From disease and drought resistance to increasing yields, the improvement of various agronomic traits has become easier to achieve.

9.2 Overexpression and knockdown approaches in stress tolerance

In the research on the stress resistance of rapeseed, scientists often play the "addition and subtraction game"-either increasing the expression levels of key transcription factors or knocking out the genes that hold them back. For example, the bZIP transcription factor BnaABF2 (Zhao et al., 2016), when several copies are stuffed into *Arabidopsis thaliana*, the plants immediately become drought-tolerant and salt-tolerant because it can activate drought-resistant genes such as RD29B. Recently, it has become more popular to use CRISPR for "subtraction" (Sathee et al., 2022), directly knocking out the "brake pad" gene in the nutrient signaling pathway to enable crops to absorb nutrients more efficiently. However, it has been found in practice that regulating these genes requires moderation-overexpression of certain transcription factors can actually inhibit growth (Debbarma et al., 2019), just as overstepping the accelerator can cause problems. With the continuous emergence of new technologies (Nascimento et al., 2023), it is now possible to adjust these "switches" more precisely, allowing rapeseed to maintain good growth in harsh environments. The principle is simple, yet it offers unlimited possibilities for cultivating stress-resistant varieties.

9.3 Future directions for genetic modulation in rapeseed

There are several particularly notable directions for future research on enhancing the stress resistance of rapeseed. There are more and more new applications of CRISPR technology-now not only gene knockout can be performed, but also the expression level of genes can be precisely regulated by CRISPRa and CRISPRi, just like installing adjustable knobs on genes. Even more remarksable is the multi-editing technology (Debbarma et al., 2019), which can adjust multiple genes at one time, enabling rapeseed to possess multiple abilities such as drought resistance and salt-alkali tolerance simultaneously. However, what is most anticipated are still those new transcription factors that have not yet been discovered (Jain, 2015), and each one found may bring about new breeding ideas. Combine these technologies (Bortesi and Fischer, 2015), it is possible to cultivate more "hardy" rapeseed varieties, which not only have stable yields but also can cope with increasingly extreme climates. Of course, ultimately these studies must return to the fields and truly help farmers solve practical problems. This is where the value of agricultural research lies.

10 Conclusion and Future Perspectives

Rapeseed, as a globally important oil crop, its growth is like a precise molecular symphony. When exposed to low temperatures, plants will quickly activate complex emergency mechanisms-hormone signals and reactive oxygen species clearance systems take turns to work, ensuring that seeds can germinate smoothly in the severe cold. Research shows that transcription factors such as ERF and bZIP can be called "all-rounders of stress resistance", being able to handle drought, salinity and alkalinity, as well as cold with ease. Interestingly, lncrnas, which were once overlooked, are abnormally active under drought conditions and regulate various metabolic pathways by interacting with mrnas. Recently, it has also been discovered that the ATG8 protein family is equally busy, dealing with salt stress while regulating nitrogen metabolism. These findings, when pieced together, gradually outline a molecular roadmap for rapeseed to address environmental challenges. Although there are still many details to be refined, they have already provided a clear direction for cultivating more resilient rapeseed varieties.

Studying the transcriptional regulatory network of rape feels like piecing together a super complex jigsaw puzzle, and each piece looks almost the same. When exposed to environmental stress, the expression levels of thousands of genes will undergo earth-shaking changes. To identify the true "core regulatory factors" from them is like looking for a needle in a haystack. What's more troublesome is that transcription factors and lncrnas often compete with each other for work, with their functions overlapping significantly. Several people can do the same thing, making it hard to tell who is in charge. The responses of different rapeseed varieties to the same stress vary greatly, which makes it more difficult to identify universally applicable stress resistance strategies. Although there are now high-precision and cutting-edge data such as transcriptomics and metabolomics, how to integrate and analyze them and clarify the complex relationships among molecules remains a new topic, which requires more intelligent algorithms to overcome. Every difficult problem is like a checkpoint, waiting for researchers to solve one by one.

Future research to crack the genetic code of rapeseed's stress resistance can focus on several key directions. First of all, it is necessary to apply CRISPR gene editing technology more proficiently and precisely modify those potential "resilience commanders"-key transcription factors-to verify which genes play a core role in the resilience process. Secondly, to achieve the joint operation of multi-omics data, integrating and analyzing information such as gene expression, protein interaction, and metabolic networks is like assembling a complex jigsaw puzzle, which is expected to reveal unknown regulatory patterns. At the breeding level, high-throughput methods such as TWAS can be utilized to conduct "genetic check-ups" on rapeseed and identify molecular markers highly associated with stress resistance traits. In addition, the natural stress-resistant gene resources of wild relatives also have great potential. These genes, which have undergone long-term natural selection, often contain unexpected advantages. Through the organic combination of these strategies, we can gradually build stronger rapeseed varieties, enabling them to maintain stable and high yields even under extreme climatic conditions. Despite numerous challenges, each regulatory puzzle solved brings us one step closer to the goal of cultivating highly resilient rapeseed.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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