Triticeae Genomics and Genetics, 2025, Vol.16, No.4, 166-174
http://cropscipublisher.com/index.php/tgg

Research Insight Open Access

Strategies to Improve Wheat's Drought and Heat Resistance

Zhen Li
Hainan Institute of Biotechnology, Haikou, 570206, Hainan, China
Corresponding email: zhen.li@hibio.org

Triticeae Genomics and Genetics, 2025, Vol.16, No.4 doi: 10.5376/tgg.2025.16.0018
Received: 11 Jun., 2025
Accepted: 24 Jul., 2025
Published: 11 Aug., 2025

Preferred citation for this article:
Li Z., 2025, Strategies to improve wheat's drought and heat resistance, Triticeae Genomics and Genetics, 16(4): 166-174 (doi: 10.5376/tgg.2025.16.0018)

Abstract Wheat (*Triticum aestivum* L.) is a globally important staple crop whose productivity is increasingly threatened by climate stressors, particularly drought and heat. This study comprehensively reviews the physiological and molecular responses of wheat to drought and high temperature conditions, elaborates on the effects on plant growth and yield components, explores genetic strategies aimed at enhancing wheat stress resistance, including conventional breeding, molecular marker-assisted selection and gene editing technology, evaluates the role of agronomic and management measures such as optimized irrigation, nutrient management and crop adjustment in alleviating the effects of stress, and also focuses on the application of biotechnology and omics approaches (including transcriptomics, proteomics and microbiome engineering) in improving wheat adaptability. The effectiveness of the integrated strategy is evaluated through case studies in the Indo-Gangetic Plain, the Australian Wheat Belt and the Mediterranean region. This study highlights the importance of integrating multidisciplinary innovations for developing climate-resilient wheat systems, points out current knowledge gaps, and proposes directions for future research and development.

Keywords Wheat; Drought tolerance; Heat stress; Genetic improvement; Climate-resilient agriculture

1 Introduction

Wheat is the most widely grown crop in the world. It is a staple food for many people every day and is very important for human nutrition. It can be said that wheat is one of the core of global food security (Langridge and Reynolds, 2021; Bapela et al., 2022). Because of its strong adaptability, wheat can be grown in various climates. But this also makes it more vulnerable to environmental problems (Kulkarni et al., 2017).

Drought and high temperature are the two main problems affecting wheat yields. These two problems often occur together, especially at important stages of wheat growth, which can greatly reduce yields (Farooq et al., 2017; Azmat et al., 2022). As the climate warms, drought and high temperature will occur more frequently and more severely. This is a big challenge for wheat cultivation (Tricker et al., 2018). When drought and high temperature occur together, the situation is particularly bad, not only will the number and weight of wheat grains decrease, but it will also affect its physiological and genetic performance (Omar et al., 2023).

The goal of this study is to review what methods are currently available to help wheat better cope with drought and heat. We will look at some traditional methods, such as breeding improvements and agronomic measures, and also introduce some new technologies, such as nanomaterials and plant extracts. We will compare the advantages and disadvantages of these methods, share the latest research results, and propose directions for future research and improvement, hoping to help wheat maintain stable yields in the context of intensified climate change.

2 Physiological and Molecular Responses of Wheat to Drought and Heat

2.1 Key physiological responses

When wheat is exposed to drought and high temperatures, it will respond to stress through some physical changes. For example, it will have less water in its body, less chlorophyll and carotenoids in its leaves, and slower photosynthesis (Sattar et al., 2020). Wheat often closes its stomata to reduce water evaporation, and the water relationship in its body will also change, such as changes in osmotic pressure and turgor pressure (Marček et al., 2019). Although these practices can help wheat save water, they will also affect its growth. In addition, wheat will accumulate some substances to adapt to drought, such as proline, sugar and protein. These are called "osmotic regulators" that can help cells maintain stability. It will also activate some antioxidant enzymes, such as SOD, POD, CAT and GR, to reduce oxidative damage (Ahmad et al., 2018). When drought and high temperature occur together, these reactions are usually more intense, and sometimes the combined effects of the two stresses are more serious than either alone (Ru et al., 2022).

2.2 Molecular mechanisms involved

At the molecular level, wheat activates some stress-related genes. These genes allow it to synthesize some special proteins, such as dehydrins (DHNs) and heat shock factors (TaHSF1a), as well as some transcription factors (such as TaWRKY-33, TaNAC2L) and genes related to abscisic acid signaling (Rampino et al., 2006). Dehydrins are activated when wheat is short of water, which can help plants retain water and protect tissues (Vukovic et al., 2022). In addition, wheat also strengthens antioxidant pathways, such as the ascorbic acid-glutathione cycle, to remove harmful reactive oxygen species in the body (Itam et al., 2020). These genes and pathways are more obviously expressed in wheat varieties with strong drought and heat resistance, indicating that they have genetic advantages in stress resistance. In wheat, some metabolites will also change, such as proline, GABA, sugars and organic acids, and their increase also helps to improve the ability to resist stress.

2.3 Impact on growth and yield components

Sometimes, wheat grows short, does not tiller much, and has a small flag leaf area. This is not necessarily due to improper management. Drought and high temperature are often the "masterminds" behind the scenes. These stresses are bad enough when they occur alone. When they occur together, the impact is even more obvious - short spikes, fewer grains, and reduced thousand-grain weight (Alsamadany et al., 2023). Especially if the stress happens to occur during the reproductive period of wheat, it will be even more troublesome. The grains will not be fully filled, and the yield will naturally fall (Qaseem et al., 2019). However, not all varieties will "fall down". Some wheat can mature early or allocate resources better in the face of adversity. In this case, their performance is usually okay. On the other hand, those varieties that are sensitive to adversity often cannot resist, and their growth and yield will be greatly affected (Sareen et al., 2023b). Of course, the final result also depends on how long the stress lasts and how severe it is, and it cannot be generalized.

3 Genetic Strategies for Enhancing Stress Resistance

3.1 Conventional breeding and landrace utilization

Traditional breeding has been used for many years. Breeders select drought-resistant or heat-resistant individuals from existing germplasm resources and local varieties, and then crossbreed and improve them (Trono and Pecchioni, 2022). However, because many modern wheat varieties have undergone long-term repeated selection, their genetic diversity has decreased. This also makes the number of stress resistance genes available for breeding even smaller (Mao et al., 2023). To increase the source of stress resistance genes, researchers will introduce some wild relatives or traditional local varieties. For example, *Haynaldia villosa* is a very useful resource (Xing et al., 2017). In addition, synthetic hexaploid wheat and diversified germplasm banks can also help expand the genetic base, allowing wheat to have multiple resistances at the same time.

3.2 Marker-assisted and genomic selection

In the past, we relied on experience, but now many breeding works have been promoted by "looking at genes". Technologies such as MAS, MABC, and GS actually use molecular information to pick out genes or QTLs related to drought and heat resistance, and then introduce them into new varieties. It is not to say that every QTL is reliable, but some "meta-QTL" (MQTL) have repeatedly appeared in different experiments, indicating that they are still quite stable (Tanin et al., 2022). Some have been verified by GWAS studies and can be used. However, it is interesting that in addition to these phenotype-related genes, breeders are now paying more and more attention to the integration of traits such as root structure, antioxidant function, and even osmotic regulation. Putting these favorable factors together is indeed helpful to accelerate variety improvement (Pn and Patil, 2024). Research on synthetic hexaploid wheat has also found many potential stress resistance genes, which can be regarded as a foundation for subsequent improvement work (Bhatta et al., 2019).

3.3 Gene editing and transgenic approaches

Of course, breeding is not the only way to think about this. Now there are more and more direct methods, especially transgenic and gene editing technologies (Figure 1), such as CRISPR/Cas9, which are used quite a lot. This kind of method does not need to wait for so long for intergenerational hybridization, and genes can be directly "taken action". Some experiments have achieved good results. For example, transferring ERF1-V of wild wheat or SNAC1 of rice into wheat not only improves drought and salt tolerance, but also does not affect yield (Saad et al., 2013). More interestingly, some research teams simply changed the regulatory pathway, such as modifying the TaGW2-TaARR12 pathway, and the result was that drought resistance and yield were improved together (Li et al., 2023). In addition, transcriptome analysis has also given us a lot of hints. Some genes and transcription factors that are active under stress have been regarded as objects that can be used in the future (Saidi et al., 2022). These new technologies are not intended to replace traditional methods, but can be used in conjunction with them, providing us with more tools to respond to climate change quickly and accurately.

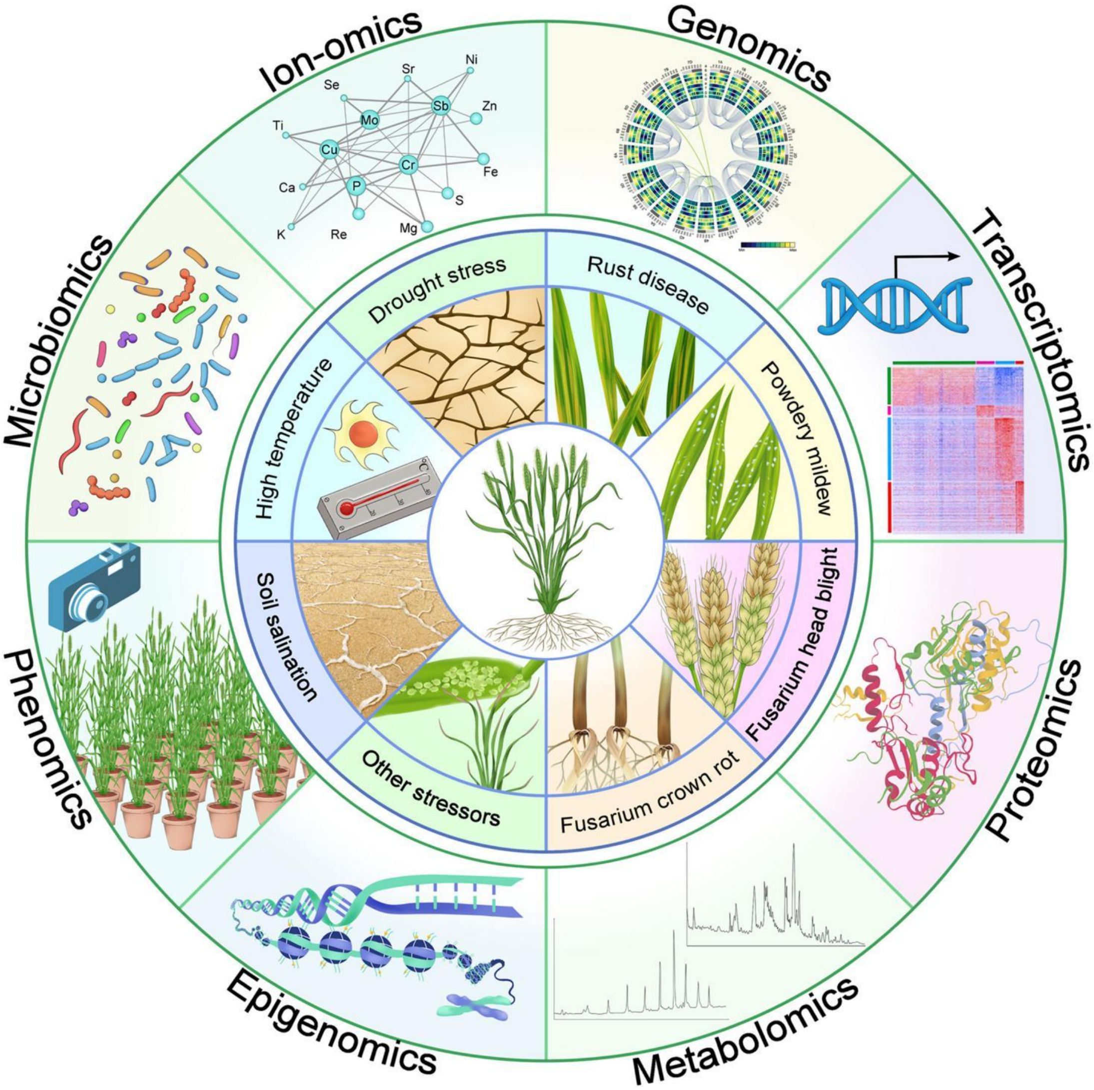

Figure 1 Genetic dissection of abiotic and biotic stress using muti-omics techniques (Adopted from Mao et al., 2023)

4 Agronomic and Management Practices

4.1 Optimized irrigation and water conservation

When it comes to irrigation, it is not just about more water. If the method is wrong, no matter how much water you use, it may be wasted. For example, at the critical time of wheat filling, if the moisture in the soil cannot keep up, wheat yields can easily decrease (Hunt et al., 2018). But on the other hand, if irrigation is done accurately and when it is necessary, the effect will be different, and the impact of high temperatures can be much smaller. However, sometimes irrigation alone is not enough. Crop rotation is another method worth considering. Although it is "changing the land for planting", there are many benefits behind it, such as improving soil structure and making the land more water-retaining. Some other farming methods, such as reducing tillage or planting grass cover, have also been proven to be very helpful in saving water (Kathuria et al., 2024).

4.2 Soil and nutrient management

The state of the soil is crucial to whether wheat can withstand stress. This may sound a bit cliché, but it is true. If the soil is soft and has sufficient organic matter, it not only has a strong water retention capacity, but also nutrients are more easily absorbed (Zahra et al., 2021). At this time, even if there is a little drought or heat, wheat will not easily have problems. Of course, there are many ways to improve the soil. Crop rotation is one way, and adding some soil conditioners is another. Now many places are using precision agriculture tools, such as smart fertilization systems. It is not to say that this type of technology can completely solve the problem of drought and high temperature, but at least it can manage fertilizers more scientifically, use them economically and accurately, and the pressure reduction effect is more obvious.

4.3 Planting time and density adjustments

Avoiding the worst weather periods is the intuitive approach of many farmers. For example, early sowing, especially with early-maturing wheat varieties, can effectively avoid the embarrassment of encountering high temperatures during the filling period (Li et al., 2024). However, it does not mean that the earlier the better. In some places, early sowing is more likely to encounter late frosts. This depends on the specific local climate. Planting density is not a constant. If the planting is too dense, the plants will compete for water, shade, and easily accumulate heat; but if it is too sparse, the land will be wasted and the water utilization rate will be low. How to adjust the reasonable density? In fact, the key lies in whether the canopy structure is reasonable, that is, whether the leaves can "stand open and get sun" (Deihimfard et al., 2023). As long as this point can be mastered, the heat load can be reduced a lot and water can be used more efficiently.

5 Biotechnological and Omics Approaches

5.1 Transcriptomics and proteomics for stress response

Now, we can use transcriptomic and proteomic techniques to more clearly see how wheat responds to drought and heat. Transcriptomic analysis can find genes that change under stress (also called differentially expressed genes, DEGs), and can also discover key transcription factors such as TaWRKY33, which are important for wheat to adapt to stress (Ullah et al., 2024). Proteomic studies can see changes in proteins, such as how much they are and whether they are modified (post-translational modifications). These changes are critical for wheat to regulate its own response (Komatsu et al., 2014). These two methods combined can help us find some useful candidate genes and provide references for future breeding and genetic modification (Shah et al., 2018).

5.2 Metabolomics and systems biology

Metabolomics studies can tell us what substances wheat accumulates under stress, such as water-retaining substances (called osmoprotectants) and antioxidants that remove harmful substances (Da Ros et al., 2023). Systems biology integrates the data of genome, transcriptome, proteome and metabolome to see how they interact with each other (Sehgal et al., 2023). For example, by analyzing the co-expression relationship between genes, we can find some "key genes" or "regulatory hubs", which can sometimes be combined to improve wheat's stress resistance.

5.3 Microbiome engineering for stress tolerance

Although not much has been said before, the microbiome is also a very promising direction. Adjusting the microbial environment around wheat, such as beneficial bacteria in the soil, can help wheat absorb nutrients better and regulate its response to drought and high temperatures (Jeyasri et al., 2021). This is actually a supplement to traditional breeding and genetic methods. If we can combine microbiome data with other omics data, we may be able to find more ways to improve wheat's resistance to stress.

6 Case Study

6.1 Drought-tolerant wheat in the Indo-Gangetic plains

In the Indo-Gangetic Plain, local researchers tested multiple wheat varieties in the field. They found several lines that can maintain high yields in drought and high temperature environments (Sareen et al., 2023b). These wheats usually have high biomass, high harvest index, and high thousand-grain weight, which are closely related to yield. Wheat with early heading and high tillering also performs well in adverse conditions (Figure 2) (Sareen et al., 2023a). For example, WS 2016-4 and WS 2016-12 can produce stable yields under normal, drought and high temperature conditions. This shows that in this environment, it is very valuable to carry out targeted breeding and variety selection.

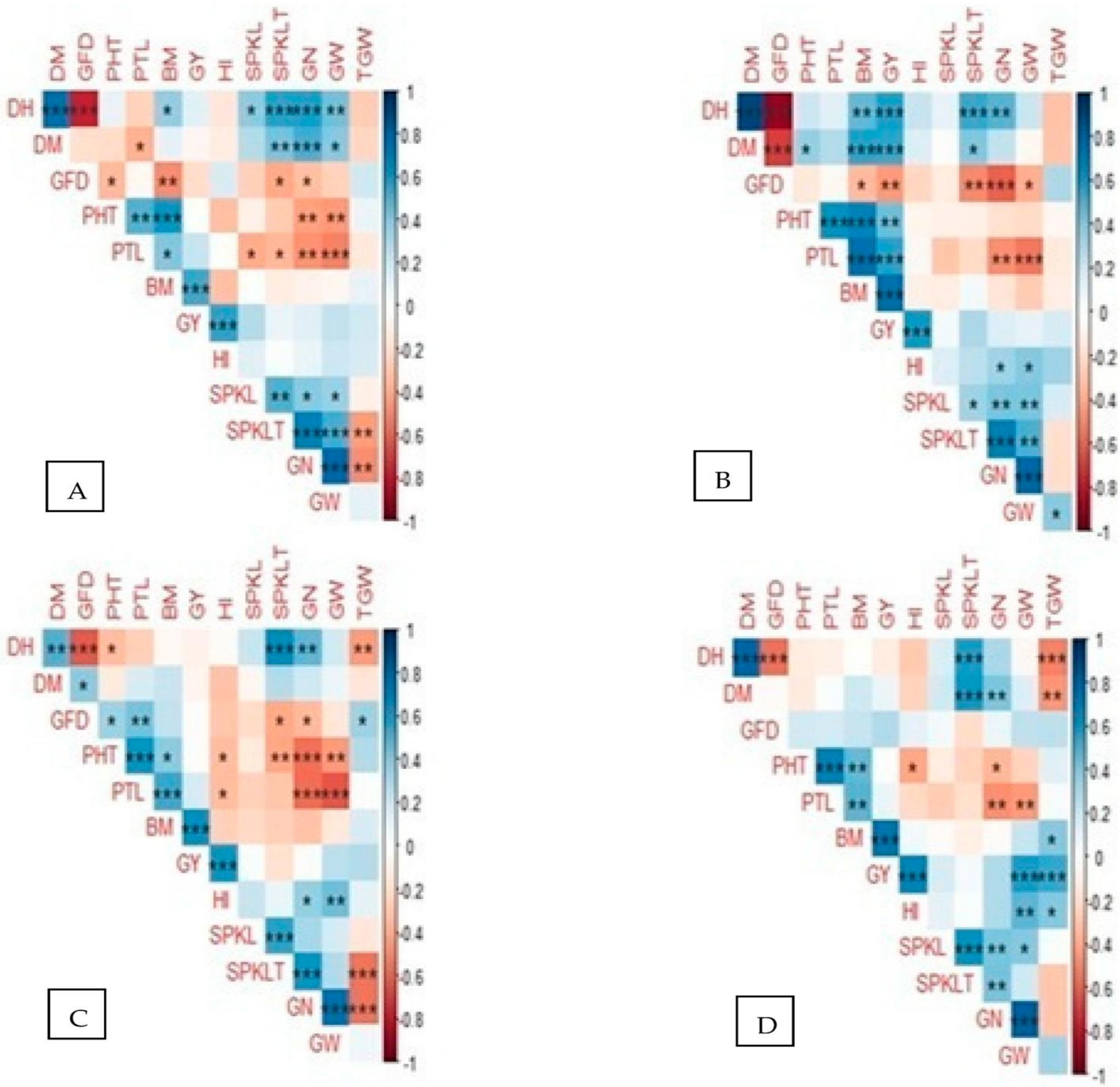

Figure 2 Correlation coefficients among various traits under TSIR-NS (A), TSRF-DR (B), LSIR-HT (C) and LSRF-DHT (D). Grain yield (GY) had a significant positive correlation with biomass (BM) under all conditions and BM had a significant positive correlation with plant height (PHT) and productive tillers (PTL). DH: Days to heading, DM: Days to maturity, GFD: Grain-filling duration, PHT: plant height, PTL: productive tillers, BM: biomass, GY: grain yield, HI: harvest index, SPKL: spike length, SPKLT: spikelets/spike, GN: grain number/spike, GW: grain weight/spike, TGW: 1000-grain weight. *, **, *** Significant at $p < 0.05$, 0.01, 0.001 respectively; empty cells represent non-significant correlation (Adopted from Sareen et al., 2023a)

6.2 Heat stress adaptation in Australian wheat belt

In Australia's main wheat-producing areas, the main goal of breeding is to ensure that wheat has stable yields in both normal and hot seasons (Langridge and Reynolds, 2021). Their methods include genetic analysis, selection of key physiological traits, and direct screening under different stress conditions. At the same time, these studies also use advanced phenotyping techniques and genomic data support. Although the process is not easy and progress has been fast and slow, these practices have helped everyone better understand the changes in wheat yield under high temperature and drought. This also explains why it is necessary to continue to innovate and integrate a variety of effective methods.

6.3 Integrated management in Mediterranean Regions

In Mediterranean countries such as Morocco and Oman, local integrated management measures are used and local wheat varieties are used to cope with drought and heat (Aberkane et al., 2021). Some varieties are obtained by distant hybridization, such as the local variety "Cooley" in Oman. These wheats accumulate more antioxidant enzymes and water-retaining substances in the body when the temperature is high and drought, so the yield loss is smaller (Farooq, 2023). They also combine multiple methods, such as looking at canopy temperature, NDVI (vegetation index) and other adversity indicators, to select varieties that are more suitable for these areas. These methods improve the efficiency of screening and make wheat more adaptable to the Mediterranean climate conditions.

7 Future Perspectives and Recommendations

It is not just one way. If wheat wants to withstand drought and high temperature, it has to take many approaches. Breeding alone is not enough. Agronomic measures, soil management, climate models, and even how farmers plant and whether it is cost-effective are all unavoidable. Sometimes, a stronger root structure or some resistance in the genes can really come in handy; but if the soil management can't keep up, the water that should be lost will still flow, and it can't withstand the heat. Of course, the problem is not so serious in some places, but once faced with complex climate change, it is necessary to analyze specific problems specifically. Not all regions are suitable for the same strategy. Take climate simulation as an example. It is not omnipotent, but there is a reliable model that can at least help us judge where the risk of growing wheat is greater and where there are more opportunities, which is very helpful for formulating local planting plans. Simply put, what should be combined should be combined, and what should be distinguished should not be mixed.

Changing varieties or adjusting fertilizers will not solve all problems. The climate is becoming increasingly unpredictable, and wheat needs to change technology and management to keep up. Some places have tried some ways, such as improving soil, making nutrition more reasonable, and combining them with varieties that are inherently more drought-resistant and heat-resistant. The effect is indeed much better than before. Wheat that grows fast in the early stage and blooms later still has potential in the face of future climates with good management methods. However, not all measures work. Adjustments to planting structures, such as crop rotation and changing sowing periods, sound simple, but they really depend on the land and people. Not every piece of land is suitable for wheat, so doing a suitability analysis in the early stage is also very important and can avoid many detours.

The problem is that the temperature is rising faster than expected. To be honest, our current breeding speed and management methods may not keep up with this pace of change. Even if technology is improving, it will be useless if we don't update data and change ideas. Therefore, in addition to technical efforts, we need to make breeding more flexible and data updates more timely, and at the same time, farmers need to understand and afford it. To promote some tools and methods, scientific research alone is not enough; policy incentives and training are also essential.

Acknowledgments

I am grateful to Dr. Huang and Dr.Qi for their assistance with the helpful discussions during the course of this research.

Conflict of Interest Disclosure

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

References

Aberkane H., Belkadi B., Kehel Z., Filali-Maltouf A., Tahir I., Meheesi S., and Amri A., 2021, Assessment of drought and heat tolerance of durum wheat lines derived from interspecific crosses using physiological parameters and stress indices, Agronomy, 11(4): 695.
https://doi.org/10.3390/AGRONOMY11040695

Ahmad Z., Waraich E., Akhtar S., Anjum S., Ahmad T., Mahboob W., Hafeez O., Tapera T., Labuschagne M., and Rizwan M., 2018, Physiological responses of wheat to drought stress and its mitigation approaches, Acta Physiologiae Plantarum, 40: 1-13.
https://doi.org/10.1007/s11738-018-2651-6

Alsamadany H., Alzahrani Y., and Shah Z., 2023, Physiomorphic and molecular-based evaluation of wheat germplasm under drought and heat stress, Frontiers in Plant Science, 14: 1107945.
https://doi.org/10.3389/fpls.2023.1107945

Azmat A., Tanveer Y., Yasmin H., Hassan M., Shahzad A., Reddy M., and Ahmad A., 2022, Coactive role of zinc oxide nanoparticles and plant growth promoting rhizobacteria for mitigation of Synchronized effects of heat and drought stress in wheat plants, Chemosphere, 297: 133982.
https://doi.org/10.1016/j.chemosphere.2022.133982

Bapela T., Shimelis H., Tsilo T., and Mathew I., 2022, Genetic improvement of wheat for drought tolerance: progress, challenges and opportunities, Plants, 11(10): 1331.
https://doi.org/10.3390/plants11101331

Bhatta M., Morgounov A., Belamkar V., Wegulo S., Dababat A., Erginbas-Orakci G., Bouhssini M., Gautam P., Poland J., Akci N., Demir L., Wanyera R., and Baenziger P., 2019, Genome-wide association study for multiple biotic stress resistance in synthetic hexaploid wheat, International Journal of Molecular Sciences, 20(15): 3667.
https://doi.org/10.3390/ijms20153667

Da Ros L., Bollina V., Soolanayakanahally R., Pahari S., Elferjani R., Kulkarni M., Vaid N., Risseuw E., Cram D., Pasha A., Esteban E., Konkin D., Provart N., Nambara E., and Kagale S., 2023, Multi-omics atlas of combinatorial abiotic stress responses in wheat, The Plant Journal, 116(4): 1118-1135.
https://doi.org/10.1111/tpj.16332

Deihimfard R., Rahimi-Moghaddam S., Eyni-Nargeseh H., and Collins B., 2023, An optimal combination of sowing date and cultivar could mitigate the impact of simultaneous heat and drought on rainfed wheat in arid regions, European Journal of Agronomy, 147: 126848.
https://doi.org/10.1016/j.eja.2023.126848

Farooq M., 2023, Tolerance against combined drought and heat stresses in wheat landraces of omani origin: morphological, physiological, biochemical, and grain yield assessment, Journal of Soil Science and Plant Nutrition, 23: 6034-6047.
https://doi.org/10.1007/s42729-023-01462-6

Farooq M., Rizwan M., Nawaz A., Rehman A., and Ahmad R., 2017, Application of natural plant extracts improves the tolerance against combined terminal heat and drought stresses in bread wheat, Journal of Agronomy and Crop Science, 203: 528-538.
https://doi.org/10.1111/JAC.12214

Hunt J., Hayman P., Richards R., and Passioura J., 2018, Opportunities to reduce heat damage in rain-fed wheat crops based on plant breeding and agronomic management, Field Crops Research, 224: 126-138.
https://doi.org/10.1016/J.FCR.2018.05.012

Itam M., Mega R., Tadano S., Abdelrahman M., Matsunaga S., Yamasaki Y., Akashi K., and Tsujimoto H., 2020, Metabolic and physiological responses to progressive drought stress in bread wheat, Scientific Reports, 10: 17189.
https://doi.org/10.1038/s41598-020-74303-6

Jeyasri R., Muthuramalingam P., Satish L., Pandian S., Chen J., Ahmar S., Wang X., Mora-Poblete F., and Ramesh M., 2021, An overview of abiotic stress in cereal crops: negative impacts, regulation, biotechnology and integrated omics, Plants, 10(7): 1472.
https://doi.org/10.3390/plants10071472

Kathuria D., Singh N., Thakur S., Awasthi T., and Mudgal S., 2024, Nurturing wheat resilience: an overview of unravelling the detrimental effects of drought and heat stress (HS) on plant growth and grain quality and mitigation approaches for sustainable agriculture, Environment Conservation Journal, 25(4): 1238-1251.
https://doi.org/10.36953/ecj.30560424

Komatsu S., Kamal A., and Hossain Z., 2014, Wheat proteomics: proteome modulation and abiotic stress acclimation, Frontiers in Plant Science, 5: 684.
https://doi.org/10.3389/fpls.2014.00684

Kulkarni M., Soolanayakanahally R., Ogawa S., Uga Y., Selvaraj M., and Kagale S., 2017, Drought response in wheat: key genes and regulatory mechanisms controlling root system architecture and transpiration efficiency, Frontiers in Chemistry, 5: 106.
https://doi.org/10.3389/fchem.2017.00106

Langridge P., and Reynolds M., 2021, Breeding for drought and heat tolerance in wheat, Theoretical and Applied Genetics, 134: 1753-1769.
https://doi.org/10.1007/s00122-021-03795-1

Li S., Wang B., Liu D., Chen C., Feng P., Huang M., Wang X., Shi L., Waters C., Huete A., and Yu Q., 2024, Can agronomic options alleviate the risk of compound drought-heat events during the wheat flowering period in southeastern Australia? European Journal of Agronomy, 153: 127030. https://doi.org/10.1016/j.eja.2023.127030

Li S., Zhang Y., Liu Y., Zhang P., Wang X., Chen B., Ding L., Nie Y., Li F., Ma Z., Kang Z., and Mao H., 2023, The E3 ligase TaGW2 mediates transcription factor TaARR12 degradation to promote drought resistance in wheat, The Plant Cell, 36(3): 605-625. https://doi.org/10.1093/plcell/koad307

Mao H., Jiang C., Tang C., Nie X., Du L., Liu Y., Cheng P., Wu Y., Liu H., Kang Z., and Wang X., 2023, Wheat adaptation to environmental stresses under climate change: Molecular basis and genetic improvement, Molecular Plant, 16(10): 1564-1589. https://doi.org/10.1016/j.molp.2023.09.001

Marček T., Hamow K., Végh B., Janda T., and Darko E., 2019, Metabolic response to drought in six winter wheat genotypes, PLoS ONE, 14(2): e0212411. https://doi.org/10.1371/journal.pone.0212411

Omar A., Heikal Y., Zayed E., Shamseldin S., Salama Y., Amer K., Basuoni M., Ellatif S., and Mohamed A., 2023, Conferring of drought and heat stress tolerance in wheat (*Triticum aestivum* L.) genotypes and their response to selenium nanoparticles application, Nanomaterials, 13(6): 998. https://doi.org/10.3390/nano13060998

Pn V., and Patil S., 2024, Integrating genetic tools for enhancing abiotic stress resilience in wheat, International Journal of Advanced Biochemistry Research, 8(8): 1114-1122. https://doi.org/10.33545/26174693.2024.v8.i8n.2498

Qaseem M., Qureshi R., and Shaheen H., 2019, Effects of pre-anthesis drought, heat and their combination on the growth, yield and physiology of diverse wheat (*Triticum aestivum* L.) genotypes varying in sensitivity to heat and drought stress, Scientific Reports, 9: 6955. https://doi.org/10.1038/s41598-019-43477-z

Rampino P., Pataleo S., Gerardi C., Mita G., and Perrotta C., 2006, Drought stress response in wheat: physiological and molecular analysis of resistant and sensitive genotypes, Plant, Cell & Environment, 29(12): 2143-2152. https://doi.org/10.1111/J.1365-3040.2006.01588.X

Ru C., Hu X., Chen D., Wang W., and Zhen J., 2022, Photosynthetic, antioxidant activities, and osmoregulatory responses in winter wheat differ during the stress and recovery periods under heat, drought, and combined stress, Plant Science, 327: 111557. https://doi.org/10.1016/j.plantsci.2022.111557

Saad A., Li X., Li H., Huang T., Gao C., Guo M., Cheng W., Zhao G., and Liao Y., 2013, A rice stress-responsive NAC gene enhances tolerance of transgenic wheat to drought and salt stresses, Plant Science, 203-204: 33-40. https://doi.org/10.1016/j.plantsci.2012.12.016

Saidi M., Mahjoubi H., and Yacoubi I., 2022, Transcriptome meta-analysis of abiotic stresses-responsive genes and identification of candidate transcription factors for broad stress tolerance in wheat, Protoplasma, 260: 707-721. https://doi.org/10.1007/s00709-022-01807-5

Sareen S., Budhlakoti N., Mishra K., Bharad S., Potdukhe N., Tyagi B., and Singh G., 2023a, Resilience to terminal drought, heat, and their combination stress in wheat genotypes, Agronomy, 13(3): 891. https://doi.org/10.3390/agronomy13030891

Sareen S., Meena B., Sarial A., and Kumar S., 2023b, Dissecting physiological traits for drought and heat tolerance in wheat, Cereal Research Communications, 52: 1373-1384. https://doi.org/10.1007/s42976-023-00463-6

Sattar A., Sher A., Ijaz M., Ul-Allah S., Rizwan M., Hussain M., Jabran K., and Cheema M., 2020, Terminal drought and heat stress alter physiological and biochemical attributes in flag leaf of bread wheat, PLoS ONE, 18(4): e0284070. https://doi.org/10.1371/journal.pone.0232974

Sehgal D., Dhakate P., Ambreen H., Shaik K., Rathan N., Anusha N., Deshmukh R., and Vikram P., 2023, Wheat omics: advancements and opportunities, Plants, 12(3): 426. https://doi.org/10.3390/plants12030426

Shah T., Xu J., Zou X., Cheng Y., Nasir M., and Zhang X., 2018, Omics approaches for engineering wheat production under abiotic stresses, International Journal of Molecular Sciences, 19(8): 2390. https://doi.org/10.3390/ijms19082390

Tanin M., Saini D., Sandhu K., Pal N., Gudi S., Chaudhary J., and Sharma A., 2022, Consensus genomic regions associated with multiple abiotic stress tolerance in wheat and implications for wheat breeding, Scientific Reports, 12: 13680. https://doi.org/10.1038/s41598-022-18149-0

Tricker P., ElHabti A., Schmidt J., and Fleury D., 2018, The physiological and genetic basis of combined drought and heat tolerance in wheat, Journal of Experimental Botany, 69: 3195-3210. https://doi.org/10.1093/jxb/ery081

Trono D., and Pecchioni N., 2022, Candidate genes associated with abiotic stress response in plants as tools to engineer tolerance to drought, salinity and extreme temperatures in wheat: an overview, Plants, 11(23): 3358. https://doi.org/10.3390/plants11233358

Ullah I., Majeed H., Batool R., Farooq S., Gulab R., and Habiba S., 2024, A review: exploring genetic variation and regulatory networks in wheat heat stress tolerance, Biological and Clinical Sciences Research Journal, 1(1): 1342.
https://doi.org/10.54112/bcsrj.v2024i1.1342

Vukovic R., Čamagajevac I., Vukovic A., Šunić K., Begović L., Mlinarić S., Sekulić R., Sabo N., and Španić V., 2022, Physiological, biochemical and molecular response of different winter wheat varieties under drought stress at germination and seedling growth stage, Antioxidants, 11(4): 693.
https://doi.org/10.3390/antiox11040693

Xing L., Di Z., Yang W., Liu J., Li M., Wang X., Cui C., Wang X., Wang X., Zhang R., Xiao J., and Cao A., 2017, Overexpression of ERF1-V from *Haynaldia villosa* can enhance the resistance of wheat to powdery mildew and increase the tolerance to salt and drought stresses, Frontiers in Plant Science, 8: 1948.
https://doi.org/10.3389/fpls.2017.01948

Zahra N., Wahid A., Hafeez M., Ullah A., Siddique K., and Farooq M., 2021, Grain development in wheat under combined heat and drought stress: plant responses and management, Environmental and Experimental Botany, 188: 104517.
https://doi.org/10.1016/J.ENVEXPBOT.2021.104517