The Crop Journal xxx (xxxx) xxx

Contents lists available at ScienceDirect

The Crop Journal

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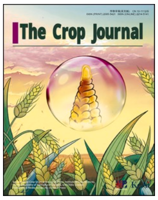

Abiotic stress tolerance: Genetics, genomics, and breeding

1. Tenth anniversary of The Crop Journal

The Crop Journal will be 10 years old in October 2023. The journal is sponsored by the Crop Science Society of China, the Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, and China Science Publishing & Media Group Ltd. (Science Press). It is published by Science Press and KeAi (founded by China Science Publishing & Media Ltd. and Elsevier). As a bi-monthly, international, peer-reviewed research journal, The Crop Journal covers all aspects of crop sciences, including crop germplasm conservation, enhancement and utilization, crop genetics and breeding, crop physiology and metabolism, crop management practices, crop ecology and production, plant–microbe interaction and crop resistance, health-beneficial and nutritionally enhanced plants, grain chemistry, crop biotechnology, and biomathematics. The journal is now indexed in the international index systems SCIE, Scopus, DOAJ, AGRIS (FAO), CAB Abstracts, Food Science and Technology Abstracts, Japan Science & Technology Corporation, Chinese Science Citation Database, EBSCO Essentials, USDA-PubAg, and Cabells Journalytics.

The Crop Journal has been supported by the global crop science community. It is currently directed by the Editorial Board, consisting of 116 experts from 16 countries. During the past 10 years, more than 1500 worldwide experts have provided anonymous reviews for the journal. The number of articles published annually has increased from 46 (2014) to 190 (2023, anticipated) (Fig. 1). The three institutions (excluding those from China) that have contributed the most articles are United States Department of Agriculture - Agricultural Research Service (USDA-ARS), International Maize and Wheat Improvement Center (CIMMYT) and Indian Council of Agricultural Research (ICAR).

In the past 10 years, the journal has published 10 special issues and three special sections on various topics. The journal will continue to publish special issues with focus on contemporary topics in the field of crop science. As of January 30, 2023, ScienceDirect has recorded 3,456,459 downloads from 126 countries. Citations continue to grow and the impact factor has increased from 2.658 (2017) to 6.6 (2022) (Fig. 1). The journal ranks in the top 4.5% in “Agronomy” and 8.4% in “Plant Sciences”.

Our goal for the journal’s future development is to continue serving the global crop science community with high impact. Development faces the challenges of continuing to increase both volume and impact factor.

2. The special issue on abiotic stresses

Abiotic stresses incur severe yield losses in crop production. Several approaches can be used to develop crop cultivars that better tolerate stressful environments. To celebrate the 10th anniversary of The Crop Journal, this special issue focuses on the topic “Abiotic stress tolerance: Genetics, genomics, and breeding” to address abiotic stresses that affect crop production. The issue features 10 reviews, 16 research articles, and one short communication, contributed by 217 authors from 13 countries. We hope this special issue will advance our understanding of abiotic stress tolerance and development of improved cultivars for sustainable and environment-friendly crop production.

Abiotic stressors including water (drought and flooding), extreme temperatures (heat and cold), salt and salinity, acidic soil, nitrogen and phosphorus deficiencies, micronutrient deficiencies, and heavy-metal pollution, impair crop plant growth and development [1]. Recently, great progress has been achieved in identifying key genes underlying crop responses to environmental adversity with the rapid advance of sequencing technology, combined multi-omics studies, and genetic analyses (see reviews [2–9]). Key stress resistance genes have been identified in multiple crop species including maize, rice, soybean, wheat, foxtail millet, cotton, and alfalfa, some of which are described in this special issue. They encode either stress-signaling factors, metabolic enzymes, or regulators of biological processes in stress adaptation. With the development of transgenic technology, more and more direct gene functional validations in crops are available and permit translating lab-based studies to field tests. The accumulating studies will enable us to identify genes conferring high breeding value that may serve as molecular targets for genetic enhancement of crop-stress tolerance. These genes likely differ from species to species, owing to inherent differences in plant development, agronomic practices, and the plant part of economic value.

Modern agriculture relies heavily on application of chemical fertilizers. Their excessive application not only increases production cost, but causes severe environmental problems. The macronutrients nitrogen (N), phosphorus (P), and potassium (K) are the most essential nutrients for crop yield. Some other elements including silicon (Si), iron (Fe), and zinc (Zn), are also critical for crop yield and human health. In contrast, cadmium (Cd), a non-essential and toxic metal, impairs or prevents plant growth. Plants employ various strategies to overcome Cd toxicity. Breeding cultivars with increased nutrient-use efficiency (NUE) and reduced Cd toxicity aims to improve both crop yield and quality. In the last two decades, efforts to dissect variation in NUE-associated traits and identify their underlying genetic basis in crops including rice and soybean have borne fruit (see reviews [10–12]).

2.1. Water stress: drought

Crops have evolved extensive morphological, physiological, and molecular mechanisms to combat drought stress. Comprehensive

https://doi.org/10.1016/j.cj.2023.07.002

Please cite this article as: Yunbi Xu et al., *The Crop Journal*, https://doi.org/10.1016/j.cj.2023.07.002

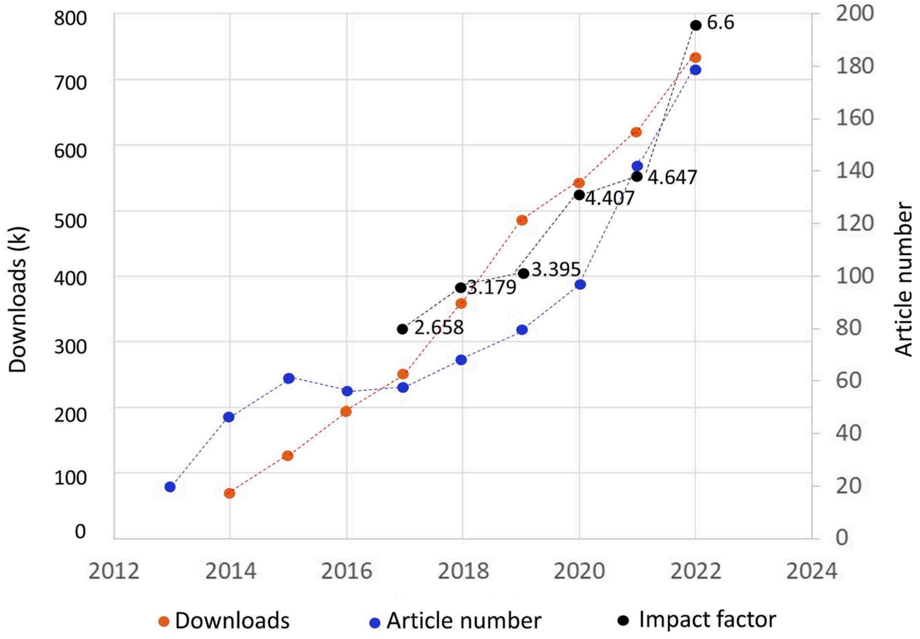

Fig. 1. Three statistics: number of downloads, number of published articles, and impact factor, for The Crop Journal, founded in 2013.

linkage- and association-mapping studies have been conducted to dissect the genetic mechanisms underlying drought resistance [6]. Exploitation of associated genetic loci and genes can be achieved by marker-assisted selection, genomic selection, gene transfer, and genome editing to develop stress-resistant crops. In this special issue, Liu et al. [13] summarize recent progress in elucidating the genetic basis of crop drought resistance and applying currently available molecular-breeding technologies to develop drought-resistant germplasm.

In this special issue, Wu et al. [14] describe the genetic dissection of yield-associated traits affected by drought stress in common bean, using a panel of 210 bean accessions with large variation in 11 agronomic traits at the adult stage under two watering conditions. A set of candidate genes were found that encode MYBs, AREBs, WKRYs, and protein kinases. In maize, Xia et al. [15] reported that a sulfite oxidase (*ZmSO*) was associated with drought tolerance in seedlings. A 14-bp insertion variation, containing two ABA-responsive elements, in the promoter region of *ZmSO* conferred ABA-inducible expression, leading to increased drought tolerance. In another study, Li et al. [16] found by cross-species comparison of 514 stress-treated transcriptomic libraries that ms33-6038, a genic male-sterile mutant deficient in the *ZmMs33/ZmGPAT6* gene, triggered a transcriptional reprogramming similar to that in plants exposed to drought stress. They concluded that jasmonic acid-mediated stress responses share the molecular mechanism underlying male sterility induced by deficiency of *ZmMs33* in maize.

In cotton, Ma et al. [17] reported that mitochondrial protein acetylation was mediated by a new client protein of GhHSP24.7, cotton lysine deacetylase (GhHDA14). The regulation circuit represents a post-translational mechanism in plant abiotic-stress response that integrates the regulation of ROS and ATP. Liu et al. [18] reported that overexpression of ZxABCG11 from *Zygophyllum xanthoxylum* increased tolerance to drought and heat in alfalfa owing to increased cuticular wax deposition, suggesting a promising avenue for developing forage cultivars suitable for planting in hot, arid, and marginal lands. GmPUB21 (an E3 ubiquitin ligase) was previously reported to negatively regulate drought and salinity response in soybean. As reported by Yang et al. [19] in this special issue, its interaction with one of the drought-induced proteins revealed that the interacting proteins regulated drought and salinity tolerance via an ABA-dependent pathway.

2.2. *Water stress: waterlogging*

In common wheat, this special issue contains a report [20] of QTL mapping for waterlogging tolerance using a doubled-haploid population developed from Yangmai 16 (waterlogging-tolerant) and Zhongmai 895 (waterlogging-sensitive) and genotyped with a 660K SNP array. The authors describe QTL, associated candidate genes, and KASP markers developed and validated for molecular breeding for waterlogging tolerance.

2.3. *Extreme temperatures: heat and cold or chilling*

The rate of plant growth and development depends on the temperatures surrounding the plant. Extreme temperature events are projected to become more intense, frequent, and longer-lasting. Climate change-mediated heat stress depends on vapor-pressure deficit at maximum temperature. In this special issue, Zaidi et al. [21] review the CIMMYT maize program in Asia, which is implementing an initiative for developing and deploying heat-tolerant maize by integrating genomics-assisted breeding, doubled haploidy, field-based precision phenotyping, and trait-based selection. Twenty high-yielding heat-tolerant maize hybrids have been developed and released. Even when grown under unstressed conditions, these hybrids yielded as well as or better than the best commercial checks. In a rice study [22], yellow-green leaf was induced by high-temperature and high-light stress. The mutation in *green-revertible yellow leaf 3* in rice disrupts the geranylgeranyl diphosphate balance in cells with excessive ROS accumulation and cell death and damages photosystem proteins and chloroplasts.

Low temperature is another harmful environmental stress of increasing frequency with climate change. Plants employ differing enrichment pathways in differing periods of cold stress, such as the amino sugar and nucleotide sugar metabolism, and alanine and protein export. Using a previously generated *MeMYB2*-RNAi transgenic cassava, Guo et al. [23] found that down-regulation of MeMYB2 led to anthocyanin accumulation and increased chilling tolerance. In wheat, by imposing two-year treatments at the terminal spikelet stage under two temperatures (2 and −2 °C) and durations (1, 2, and 3 days), Lin et al. [24] compared the effects of late spring cold on grain number and yield in two cultivars, Yannong 19 (cold-tolerant) and Xinmai 26 (cold-sensitive). Late spring cold reduced total dry matter accumulation and dry matter partitioning to spikes, resulting in poor spikelet development and thus high losses of grain yield.

2.4. Light stress: shade tolerance and high light response

Plant growth and development are regulated by light quality, light intensity, and photoperiod. Cryptochromes are blue/ultraviolet-A light receptors involved in stem elongation, shade tolerance, and photoperiodic flowering. In this special issue, Fan et al. [25] report that overexpression of cryptochrome 1 (CRY1) from maize (*ZmCRY1a*) promoted seedling de-etiolation under blue and white light in *Arabidopsis* and reduced the lengths of mesocotyls and first leaf sheaths in maize. *ZmCRY1a* genes were insensitive to low blue light-induced shade avoidance syndrome in *Arabidopsis* and maize. As a response to high light in rice, as reported by Jiang et al. [22], excessive ROS accumulation and cell apoptosis were exacerbated under high-temperature and high-light stress.

2.5. Soil stress: saline and alkaline

Plant roots are frequently exposed to adverse soil conditions that limit growth and production such as acidity, salinity, and alkalinity. As a major global constraint on crop productivity, salinity causes water stress, cytotoxicity, and nutritional imbalance due to high ion intake [26]. Oxidative stress often accompanies salinity, owing to ROS generation. Plants respond to high-salt stress with an array of tactics including osmotic regulation, ion-selective uptake, and detoxification. Cao et al. [27] discuss, in this special issue, the urgent need to dissect salt-tolerance mechanisms to facilitate the breeding of salt-tolerant maize. They review current progress in characterizing genetic variation in maize salt tolerance, including variation associated with Na^+, K^+ and Cl^- regulation and challenges and prospects for the development of salt-tolerant maize cultivars. Wu et al. [28] summarize the physiological, biochemical, and molecular processes underlying the tolerance of foxtail millet to salt stress, including physiological reactions, sensing, signaling, and control at the transcriptional, post-transcriptional, and epigenetic levels. Tao et al. [29] report that mutagenesis generated by cluster editing of *OsPIP1* revealed an osmotic regulatory role of the *OsPIP1* genes in increasing rice salt tolerance. Functional loss of the *OsPIP1* genes prevented their expression and increased influxes of Na^+ and effluxes of K^+ and H^+ in roots, thereby accumulating more Na^+ in rice mutants under salt stress. To investigate the potential mechanisms by which alfalfa responds to saline–alkaline stress, Zhang et al. [30] cloned a saline-alkaline-induced flavonol synthase gene (*MsFLS13*). Plant tolerance to saline-alkaline stress was promoted by overexpression of MsFLS13 in alfalfa. Their findings indicate the crucial role of MsFLS13 in response to saline–alkaline stress and provide a novel genetic resource for creating saline–alkaline stress-resistant alfalfa by genetic engineering.

DnaJA proteins are present in many plant species and can function as molecular chaperones in response to various environmental stressors. As reported in this special issue, Zhang et al. [31] identified soybean *GmDnaJA* family genes. Whole-genome analyses of soybean *DnaJA* family genes and functional characterization of *GmDnaJA6* indicated that *GmDnaJAs* are regulators of soybean growth and development, and *GmDnaJA6* is a key candidate regulator of saline and alkaline stress resistance.

2.6. Soil stress: acid soils and Al tolerance

Acid soils occupy approximately 50% of potentially arable lands. Increasing crop productivity in acid soils will be crucial for ensuring food security and agricultural sustainability. High soil acidity often coexists with P deficiency and aluminum (Al) toxicity, a combination that severely impairs crop growth and yield across wide areas. As roots explore soil for the nutrients and water required for plant growth and development, they also sense and respond to underground stresses. In this special issue, Li et al. [32], focusing on legumes, especially soybean, review recent advances in our understanding of root-based mechanisms linked with root architecture modification, exudation, and symbiosis, together with associated genetic and molecular strategies used by plants to adapt to individual and/or combined P and Al stresses in acid soils.

2.7. Soil stress: nutrient availability and use efficiency

Low NUE not only increases the input cost of fertilizers but causes environmental problems such as soil degradation, water eutrophication, and air pollution. Increasing the nutrient uptake capacity of the root is the first step toward increasing NUE. As reviewed in this special issue by Hao et al. [33], the root nutrient absorption system is composed mainly of members of a specific ion transporter or channel family. Under nutrient-starvation conditions, protein phosphorylation-based regulation increases ion transporter- or channel-mediated nutrient uptake capacity, whereas under excessive-nutrient conditions, it suppresses nutrient uptake by activating the opposite processes to prevent nutrient-induced toxicity. Using maize as an example, Zhang et al. [34] discuss potassium nutrition efficiency determined by K^+ uptake, transport, and remobilization. They review basic information about K^+ channels and transporters in maize, their functions and regulation, and the roles of K^+ in N transport, sugar transport, and salt tolerance. Also in maize, Liu et al. [35] used recombinant inbred line and advanced-backcross populations and their testcross populations to evaluate midparent heterosis for N-use efficiency. Heterosis for the trait was regulated by non-additive and non-dominant loci. A major QTL explained 27% of genetic variation, with *Gln1*-3 identified as a candidate gene. Genomic prediction using genome-wide molecular markers for N-use efficiency traits in the testcross populations yielded 14%–51% accuracy.

Plants have evolved multiple strategies for coordinately acquiring and utilizing N and P. As reported in this special issue, Zhou et al. [36] investigated the interactions of N and P in soybean as reflected by increases of phosphate (Pi) concentration in both leaves and roots with N deficiency under Pi-sufficient conditions. Four members of *nitrogen limitation adaptation* (*NLA*), encoding RING-type E3 ubiquitin ligase, were identified in the soybean genome. The results suggested that redundant and diverse functions are present in *GmNLA* members for coordinating responses to the availability of N and P despite their functions in mediating P homeostasis.

2.8. Soil stress: hazardous (toxic and heavy) metals

With urbanization and industrialization, there has been an increase in solid-waste generation that has become a global concern. Effective management of solid waste, including toxic metals (Cr, Mn, Cu, As) and heavy metals (Cd, Ba, Hg, Pb) in soil and water, is increasingly required owing to their adverse effects on human health and the environment. When rice is grown in soils contaminated with Cd, the metal is accumulated into the grain. In this special issue, Sun et al. [37] outline progress in elucidating the physiological mechanisms and the genetics of Cd accumulation in rice, and summarize the strategies and outcomes of low-Cd rice breeding over the past decade. They discuss the phenotypic plasticity and subspecies divergence in Cd accumulation by rice grain and offer genetic explanations for these two features. Gong et al. [38] investigated the effects of silicon treatment on lead toxicity and accumulation in two rice mutants defective in silicon uptake and in their wild types. Silicon accumulation in rice shoots was required to reduce lead uptake and the effect was achieved via silicon-induced suppression of genes encoding proteins involved in lead uptake and/or transport.

2.9. Abiotic stress regulators: ABA and hormones

Abscisic acid (ABA) as a stress hormone can act either to inhibit or to activate root growth and development under normal and stress conditions including salt, drought, and cold stress, by positively regulating root architecture development. In this special issue, Teng et al. [39] review the molecular, cellular, and organismal basis of ABA homeostasis in the root and ABA signaling that affects root architecture development as an inhibitor and activator. They discuss how to use ABA signaling components to design crop plants for improved root systems and stress resistance.

2.10. Germplasm diversity and abiotic stresses

To meet future global food demand, there is an urgent need to increase annual genetic gain by capturing more genetic diversity in breeding for crop tolerance of stressful environments caused by climate change. As reviewed by Katamadze et al. [40] in this special issue, wheat ancestors and modern varieties may contain novel traits that have been undervalued or overlooked, but may contribute to future food security. They propose that mining natural variation among wheat ancestors offers a means of enhancing wheat agronomic performance, ear architecture, canopy and organ-level photosynthetic capacity, and responses to abiotic stress, as well as developing new wheat hybrids.

3. Future perspectives

Several aspects of abiotic stress tolerance demand further research and exploration. It is desirable to strengthen the study of stress response at reproductive in addition to vegetative growth stages. The predictive value of plant survival rate under severe stress conditions as an index of seedling-stage tolerance and of yield should be investigated. Can a single gene confer plant tolerance to multiple stressors? With global climate change, several environmental stresses may occur simultaneously: drought and heat, high salinity and alkalinity, flooding and lodging. The key regulators functioning under different stresses should be identified. Can the tradeoff between stress tolerance or resilience and plant growth be disrupted? Can high productivity be achieved with yield stability? New technologies, such as high-throughput phenotyping, artificial intelligence, and gene and base editing and genomic selection, will facilitate research and its translation to breeding practice by molecular design [41,42].

NUE is a complex trait that is determined by multiple physiological processes and developmental events. Genetic variants associated with NU have been identified by reverse genetics, mutant screening and characterization, QTL mapping, and genome-wide association study (GWAS). However, traits directly favoring nutrient acquisition, such as root architecture, are rarely used for crop phenotyping and characterization. In view of the difficulty of phenotyping underground organs, approaches such as computed tomography-based high-throughput imaging for capturing root architecture under varying nutrient conditions would be helpful for characterizing NUE-associated genetic variation. Very recently, it was shown [43] that root microbiota diverge among rice subspecies and that root microbiota and N utilization are tightly associated. GWAS toward understanding the N-use efficiency traits related with root microbiota might identify plant loci that influence plant–microbe interaction and thereby plant NUE variation.

The vast body of reports on marker–trait association and gene discovery in plant abiotic-stress research, and on the functional analysis of abiotic stresses, driven largely by genotyping, phenotyping, and envirotyping, poses the challenge of transforming research progress into genetic gain in crop breeding (Fig. 2). Precision phenotypic evaluation of abiotic stress tolerance should be coupled with precision envirotyping [42,44]. Although molecular breeding has been making large contributions to crop improvement in multinational seed companies, many gaps in the breeding pipeline remain to be closed [41,45]. First, a conventional breeding pipeline, from which many improved base and founder varieties can be developed and used for molecular breeding, should be well established. Second, an integrated breeding platform (IBP, Fig. 2) should be developed and equipped with advanced breeding technologies [42], including marker-assisted selection, genomic selection, integrated genomic–enviromic prediction, speed and doubled-haploid (DH) breeding, gene transfer, and genome editing to improve crop plant abiotic-tress tolerance. Third, an open breeding network

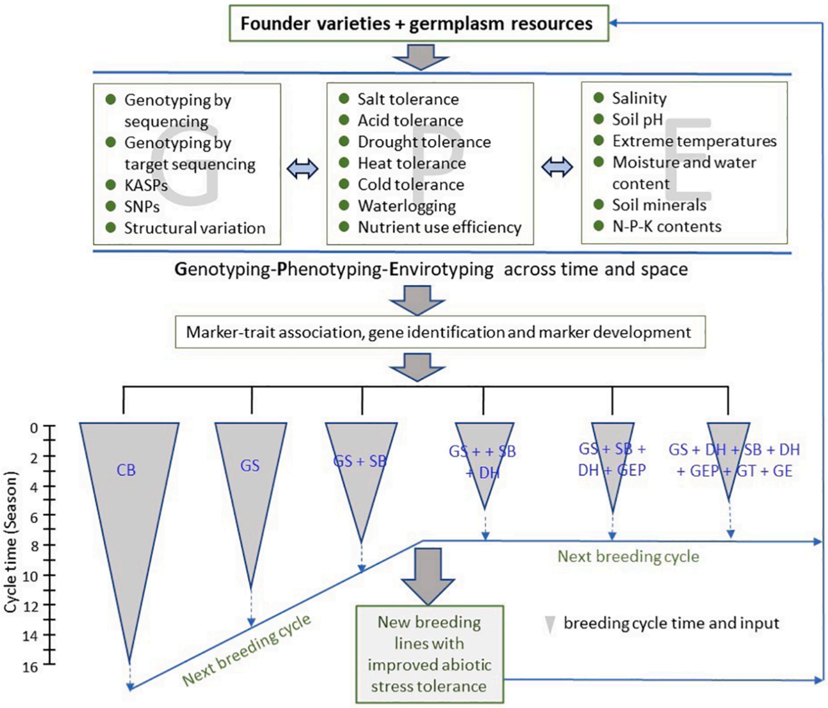

Fig. 2. Integrated genetics, genomics, and breeding approaches for abiotic stress tolerance. Several integrative breeding strategies are compared for their breeding cycle time and resource inputs (time, land, and lab, etc.). CB, conventional breeding; DH, doubled haploid; GE, genome editing; GEP, genomic-enviromic prediction; GS, genomic selection; GT, gene transfer; SB, speed breeding.

should be established for sharing all available breeding facilities and resources, given that an IBP can be established only through collaboration and coordination across regions, countries, and continents [46,47].

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank all authors for their contributions and reviewers for their comments and suggestions for improving the manuscripts published in this special issue. We thank the editorial office staff of The Crop Journal for their efficient handling and processing of the submitted manuscripts.

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