

REVIEW

Metabolomics, a step towards understanding environmental stress tolerance of major African cereals

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Abstract

Secondary metabolites isolated from plants are usually complex mixtures consisting of varieties of active ingredients which need to be characterized. Environmental stresses, including but not limited to drought and salinity, cause significant challenges to crop growth and development. These stresses can disrupt various physiological and biochemical processes within plants, leading to reduced yields and compromised quality of agricultural products and producing different secondary metabolites. Scientific agronomists can utilize environmental stresses to optimize crop traits and improve the quality of resilient crop products. Metabolomics investigations play an important role in identifying the chemical composition of natural products. This technique is a useful tool in agrochemistry and biocontrol for crop protection via biostimulation. Metabolomics plays an essential role in decoding mechanisms of action employed by biostimulants under environmental stresses. It can also assist in understanding the plant-microorganism interaction and lead to exploring the biocontrol products under biotic and abiotic stresses in the crop industry. Lipidomics, sensomics, hormonomics and some other functional metabolomic-based techniques can assist in improving the quality of stressed crops. This review discusses a metabolomics analysis of three vital African cereals (maize, rice and wheat) to demonstrate the potential value of metabolomic investigation in enhancing the nutritional quality and quantity of these cereals under environmental stresses.

Keywords: African cereals, environmental stresses, hormonomics, metabolomics, sensomics

Introduction

It has been estimated that there are between 200,000 and 1,000,000 metabolites in the plant kingdom each with different fundamental characters and polarities (Bueno and Lopes 2020). Micro-molecules of primary and secondary metabolites can be transformed into macromolecules through reaction inhibition or phytohormones which regulate cellular signaling regarding environmental stresses, such as salinity, drought, extreme temperature and nutrient deficiency (Dawid and Hille 2018; Salvi *et al.* 2021). According to Dixon *et al.* (2006), metabolomics investigation can integrate and monitor different functional statuses of a living organism and its whole metabolome which needs different techniques and tools (Dawid and Hille 2018). Agricultural production is crucial for improving nutrition and is

the primary source of income for many communities and countries. Increased crop production is necessary for ending hunger and malnutrition, and promoting economic and social development. Worldwide, there has been an increase in the diversity of diets (Ritchie *et al.* 2023). Agriculture has significant environmental impacts and the environment affects agricultural production. Currently, the world's population is growing, and food and nutritional scarcity are becoming more prevalent. Climate change and variability pose a significant threat to global food and nutritional security, leading to reductions in crop productivity, particularly in tropical and subtropical regions (Ritchie *et al.* 2023).

In recent years, metabolomics has emerged as a powerful tool for investigating the responses of plants

to abiotic stresses. Metabolites play an important role in the regulation of various metabolic pathways that enable plants to cope with stress conditions. The development of metabolomic technologies holds the potential to significantly improve diagnosis, unravel more appropriate therapeutic targets and enable more precise prognosis of disease development.

Effect of environmental stresses on crop products

Global climate change poses a significant threat to the survival of natural and agricultural ecosystems. The environment is a complex and dynamic system that can affect both non-living (abiotic) and living (biotic) components of the world. Changes in environmental conditions, such as temperature, CO₂ concentration, heat waves, and rainfall intensity, can lead to the emergence of new pests, weeds, and pathogens. These changes can ultimately reduce crop yield and sustainability, as highlighted by Chaudhry and Sidhu (2022). Plants are often subjected to unfavorable or adverse environmental pressures known as abiotic stresses, such as salinity, drought, heat, cold, flooding, heavy metals, ozone, ultraviolet radiation, and nutrient deficiencies. These stresses can have a significant impact on the growth and yield of crops, leading to reduced productivity (Wang and Frei 2011; Shafique *et al.* 2014; Haggag *et al.* 2015; Mekonnen *et al.* 2022). Abiotic stress can have a negative impact on the growth and yield of plants and crops, which can reduce their overall sustainability and production. Plants can exhibit both temporary and permanent responses to various types of stress (Cramer *et al.* 2011). Environmental stresses can reduce crop yield depending on the crop type, intensity of stress, and stress duration. The combinations of different stresses, timing of plant growth stages and intensity of stresses have severely affected plant growth and biomass production. In many semi-arid and arid regions of the world, crop yield is limited due to an increased rate of different abiotic stresses. (Haggag *et al.* 2015).

Plants exhibit various defense mechanisms of action to combat environmental stresses. The responses can differ from species to species depending on the type of stress and its intensity (Dawid and Hille 2018). The diverse stress factors that plants must face often activate similar cell signaling pathways and cellular responses, such as the production of stress proteins, up-regulation of the antioxidant machinery, and accumulation of compatible solutes (Ma *et al.* 2020). Wang and Frei (2011) have classified the physiological responses to abiotic stresses into six categories: i) altered gene expression and enzyme activity, ii) oxidative stress, iii) accelerated senescence, iv) reduced water content, v) altered mineral uptake and translocation and vi) re-

duced biomass. These physiological responses lead to the synthesis of primary and secondary metabolites, which help to regulate osmotic pressure in cells, preventing oxidation of cell components, and protecting the plant from herbivores, infection elements, and pathogenic microorganisms (Dawid and Hille 2018). Stresses can increase signaling compounds such as abscisic acid and ethylene in plant tissues. As a result, stomatal conductance is decreased by producing corresponding compounds such as glycine, betaines, proline, sugar osmolytes and compounds with strong sugar antioxidative properties (Piasecka *et al.* 2019). This physiological response is categorized as reducing water content.

According to a review study by Wang and Frei (2011), while the effects of environmental stresses on crop yields are almost always negative, they have shown that the picture is much more complex when it comes to crop quality, where both positive and negative effects occur. While starch concentration, lipids, feed value, and physical/sensory traits tend to be decreased, positive effects dominate in terms of protein and antioxidant concentration, while no clear trend can be detected in sugar and mineral concentration. In crop research, scientists are dedicated to creating superior characteristics and genetic makeups for various crops, to ensure that they possess strong resistance and meet the highest quality standards. However, changes in crop quality due to environmental stresses have received less attention than yield losses, due to the difficulty of detection. Exploiting the positive effects of stresses on crop quality without compromising yield can be a proposed strategy towards improving the quality of crops grown in stressful environments.

In the agricultural sector, the central focus remains on mitigating crop yield reductions from biotic and abiotic stressors. However, certain significant advancements in new strategies and techniques can effectively utilize stresses to induce elicitor and phytoalexins, resulting in enhanced nutritional quality and flavor of crops (Wüst 2018; Dawid and Hille 2018). For example, if stress improves the antioxidant level of a crop, mild and monitored stress could be tolerated to an extent that does not affect yields. For instance, in a study by Sgherri *et al.* (2007) tomatoes irrigated with saline water did not exhibit visible damage but had enhanced antioxidant concentrations. Although, the focus of this review paper is based on the three main African crops, in some instances due to a lack of resources, other plants have also been utilized.

The value of crop products in Africa

The highly populated developing countries in tropical and sub-tropical regions mostly in Africa and Asia are at a particularly high risk of food shortage trig-

gered by stress factors (Wang and Frei 2011). According to the Food and Agriculture Organization of the United Nations (FAO 2023a), cereals are the most common group of crops worldwide, with a production of 3.1 billion tons in 2022. It is followed by sugar crops with 2.2 billion tons, vegetables with 1.2 billion tons, oil crops with 1.1 billion tons, fruit with 0.9 billion tons, and roots and tubers with 0.9 billion tons. Global primary crop production reached 9.6 billion tons in 2022, a 56% increase since 2000 and a 0.7% increase from 2021. Maize (*Zea mays* L.), wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) collectively accounted for 90% of total cereals production in 2022 (FAO 2023a).

Among all agricultural products, cereals are the most cultivated and traded crop in Africa. The production value of primary crops for each group in US\$ million (2021) in Africa is as follows; cereals (US\$61,390 million), vegetables (US\$32,022 million), fruit (US\$45,186 million), oil crops (US\$14,092 million), roots and tubers (\$78,423 USD million) and sugar crops (US\$5,325 million) (FAO Statistical Yearbook 2023). According to the Statistical Yearbook (2023) of the FAOSTAT, the production of the three main cereals in 2021 (thousand tons) of the African continent were maize (96,637), rice (37,189) and wheat (29,219) (FAO 2023b).

Maize is a major food crop (with the highest production) that is grown in different agroecological zones and farming systems across sub-Saharan Africa (SSA). It is consumed by people from different socioeconomic backgrounds with varying food preferences. In terms of its importance as a staple food, maize is comparable to rice or wheat in Asia. Its highest rate of consumption is in eastern and southern Africa (Badu-Apraku *et al.* 2017). Rice, on the other hand, has become an essential and high-priority commodity for ensuring food security in Africa. Its consumption rate is increasing faster than any other major staple food on the continent due to rapid population growth, urbanization, and changes in dietary preferences (Diagne *et al.* 2013). Rice is the most significant source of dietary energy in West Africa and ranks second in importance across the continent. Wheat is a crucial staple crop for many countries and an imported commodity for all African nations. Over the past two decades, wheat consumption has steadily grown in all African countries due to population growth, shifting food preferences, and socioeconomic changes linked to urbanization (Silva *et al.* 2023).

Metabolomics application to investigate the metabolite patterns of crops under environmental stresses

In the post-genomic era, comprehensive analyses using systematic approaches or omics have increased the

understanding of the complex molecular regulatory networks associated with stress adaptation and tolerance. The rapidly growing technology, 'omics' has become a valuable tool for advancing our understanding of primary and secondary metabolites in plants (Tugizimana *et al.* 2013). Metabolomics is a well-known technique for the study of all types of organisms. It was developed from metabolic profiling and is the most recent of the '-omics' techniques that have emerged and is very different from the other '-omics' technologies. Metabolomics application can help to develop biological control of the adverse effects of environmental stresses via different objectives such as biomass characterization, identification of active constituents, characterization of complex mixtures and characterization of biomarkers and their related mechanisms of action and estimate the increase or decrease of different compounds or biomarkers. This technique is generally defined as a holistic qualitative and quantitative analysis of all metabolites present within a biological system under specific conditions. For example, according to metabolomics investigations, the content of organic acids generally increases when plants are under stress. So, it would give some idea about managing the crops under certain environmental stresses (Yang *et al.* 2019; Bertrand *et al.* 2021). Metabolomic application can help to develop the biological control of the adverse effects of environmental stresses via different objectives such as biomass characterization, identification of active constituents, characterization of complex mixtures and characterization of biomarkers and their related mechanisms of action and estimate the increase or decrease of different compounds or biomarkers. For example, according to metabolomics investigations, the content of organic acids generally increases when plants are under stress. So, it would give some idea about managing crops under certain environmental stresses (Yang *et al.* 2019; Bertrand *et al.* 2021). In this regard, high throughput analytical techniques such as nuclear magnetic resonance spectroscopy (NMR), mass spectrometry (MS), gas/liquid chromatography-mass spectrometry (GC/LC-MS), ultra-performance liquid chromatography (UPLC-MS), and more sophisticated bioinformatics and analytical methods can provide a high degree of sensitivity to identify and characterize the compounds' structure and quantify changes of the primary and secondary metabolites of plants under environmental stresses (Zhang *et al.* 2015; Piasecka *et al.* 2019).

The link between metabolomics, environmental stresses and crops makes an interesting triangle with a complex multilayer of investigations. Metabolomic investigation as a powerful analytical tool, on crops under single or multiple abiotic stresses gives valuable insight into the metabolic responses of crops under environmental pressure and it can give valuable knowl-

edge regarding the underlying crops' biochemical and physiological mechanisms of actions.

Applying metabolomic analysis provides a unique opportunity to investigate metabolomic patterns based on NMR spectroscopy techniques to identify the effects of different abiotic and biotic stresses. This technique has been used to evaluate environmental stress in several plants, including citrus, barley, and *Arabidopsis thaliana*. Kusano *et al.* (2011) conducted a time-series experiment on the effects of UV-B light on *Arabidopsis* using metabolomics analyses. They found that plants responded in two phases with an upregulation of primary metabolites in the first phase and the induction of protective secondary metabolites, especially phenolics, in the second phase.

In this review, some examples and shreds of evidence are provided which shed light on the importance of metabolomic application to understand the effects and mechanisms of actions of environmental stresses so that it can help to improve crop production, especially in Africa which needs more secure and reliable nutritional sources for its population.

Metabolomics application in the study of crops under stress

A metabolomics approach to detect stress tolerance in crops

Metabolomics technologies provide a better understanding of the defense mechanisms of plants under stress conditions. This technique uses different mul-

tivariate data analyses, generated from various high throughput screening of chromatographic systems, such as GC/LC-MS, or NMR-based methods. Global climate change as a dynamic multifaceted system of alterations in environmental conditions is a major threat to the survival of natural and agricultural ecosystems since it affects the abiotic and biotic components of the world. It results in alterations in environmental conditions such as heat waves, intensity of rainfall, CO₂ concentration and temperature that lead to a rise in new pests, weeds and pathogens (Chaudhry and Sidhu 2022). Therefore, plants are frequently exposed to a plethora of unfavorable, or even adverse, environmental conditions, termed abiotic stresses. These stresses pose serious threats to the sustainability of crop yield (Cramer *et al.* 2011; Kopecká *et al.* 2023).

The following review reports on the investigation of three African main cereals under abiotic stresses. According to the literature, the most extensively examined abiotic stresses were salinity, drought and temperature. Figure 1 illustrates a metabolomics workflow to identify the cereals' tolerance under abiotic stresses.

Metabolomics investigation of maize production under abiotic stresses

Salt stress restricts the entire growth processes of plants. Seedlings are most sensitive to salt in the early stages of growth. Salinity stress inhibits water uptake and transport in plants, and consequently toxic concentrations of Na⁺ and Cl⁻ are often stored in the cytosol (Jiang *et al.* 2019). According to Zezulka *et al.* (2019), seedlings are the most sensitive phase to salt in the early stages of growth, though the entire growth process

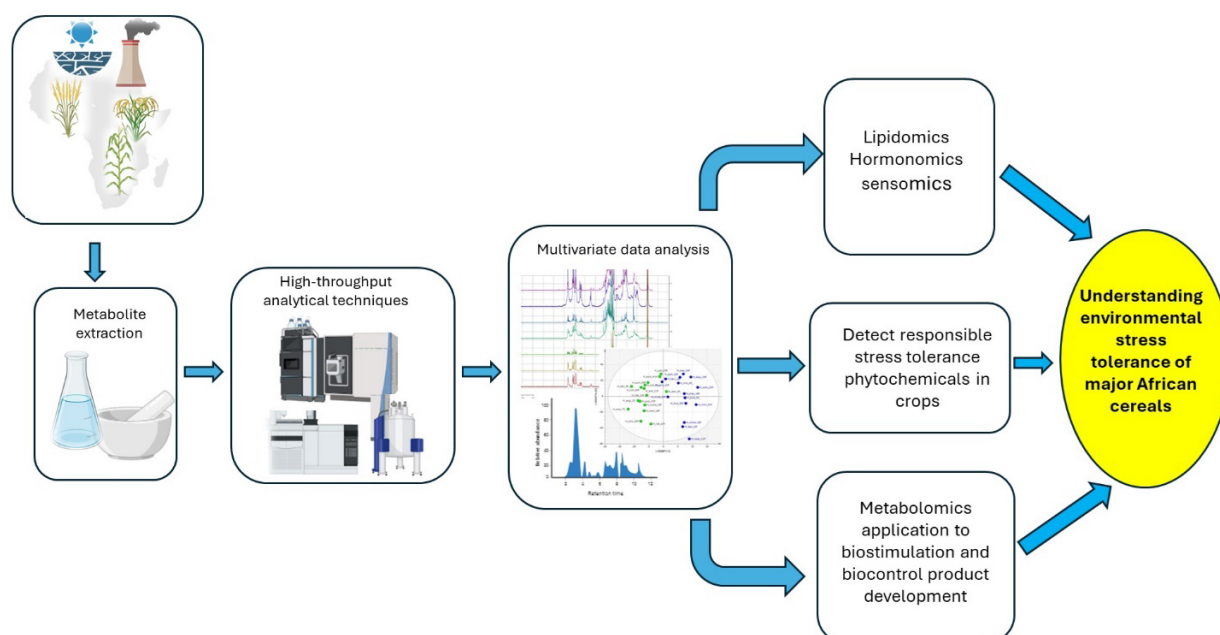


Fig. 1. The diagram represents the workflow of a metabolomics investigation to understand the environmental stress tolerance of African cereals

of plants is limited due to the salt stress. Maize crops are sensitive to NaCl stress. An NMR-based metabolomic study conducted by Gavaghan *et al.* (2011) on maize showed that the primary damages of salt stress are related to osmotic elements. This study illustrated that the osmotic effects were stronger in shoots and leaves than in the roots of maize plants (Gavaghan *et al.* 2011). This experiment showed a clear dose-dependent effect of saline treatment on the growth of shoots and roots. In this case, metabolomics found that the levels of alanine, glutamate, glycine-betaine, sucrose and asparagine were increased while the levels of malic acid, trans-aconitic acid and glucose were decreased in the shoots. According to Chen *et al.* (2022), alanine, glutamate, asparagine, glycine, betaine, and sucrose as osmotic regulators are synthesized in large quantities under salt stress conditions. The balance of intracellular and extracellular osmotic pressure is maintained by these components.

According to the literature, there are several reports on metabolomics investigation of the biochemical mechanisms involved in the complex responses of maize plants to environmental stresses. Yue *et al.* (2020) conducted a metabolomics and physiological analysis to understand the reaction of salt tolerant (PH6WC) and sensitive (PH4CV) cultivars of maize to gain further insights into the differential metabolic responses to salinity stress. According to Yue *et al.* (2020), two different examined cultivars responded differently to NaCl stress. The obtained results showed that salt stress had several adverse effects in both the tolerant and sensitive genotypes compared to the control, such as a significant root growth reduction, lower root numbers, softened roots, leaf etiolation, inhibition of leaf formation, and decreased shoot height and stem width (Yue *et al.* 2020). The study revealed that increasing levels of the salinity concentration had a direct relation to the mentioned morphological characteristics, which were, however, less prominent in the salt-tolerant genotype. The results of Evans blue staining (a common marker for measuring plasma volume and for the study of microvascular leakage in animal models) to determine the survival of plant cells demonstrated that salinity stress induced root cell death, although the exposure to salinity stress increased the Evans blue level more significantly in sensitive than in salt tolerant seedlings. Furthermore, after 9 days of NaCl stress, the sensitive cultivar seedlings turned blue indicating that the root cells were no longer viable. Staining was increased during exposure to salinity. No stains were observed in the control roots that were not treated with NaCl. LC-MS metabolomic analysis of both cultivars under treatment with 100 mM NaCl, revealed or identified 79 compounds of sensitive and 85 compounds of salt-tolerant maize cultivars as sig-

nificant metabolites in the roots. Among the identified metabolites in both cultivars, about 30 different metabolites of basic compounds such as cis-9-palmitoleic acid, L-pyroglutamic acid, galactinol, deoxyadenosine, and adenine were found in both maize cultivars as a response to salinity stress. Yue *et al.* (2020) showed that glucose metabolism was exclusively induced by NaCl in the sensitive cultivar seedlings while nucleic acid metabolism was more significant in the salt-tolerant cultivar seedlings in response to salinity stress (Yue *et al.* 2020). In 2021, Liang *et al.* conducted a study using metabolomics investigation and gene mining to improve the tolerance of a maize cultivar to salt-induced osmotic stress (SIOS). In this research, they used an LC-MS-based untargeted metabolomics method to profile the metabolomes of 266 maize inbred lines under both control and SIOS conditions. The study identified 37 metabolite biomarkers of SIOS tolerance, categorized as METO1-37 (Liang *et al.* 2021).

Another LC-MS metabolomic analysis illustrated higher levels of proline, malate, p-coumarate, and caffeate for maize xylem sap under drought stress. However, reduction of ferulate was observed under adverse environmental conditions (Alvarez *et al.* 2008). The metabolomics study conducted by Witt *et al.* (2012) found that drought stress decreased the volume of quinic and pyruvic acid and increased the levels of histidine, putrescine, proline, and phenylalanine in maize hybrids grown under glasshouse conditions. The generated principal component analysis (PCA) of data separated all tested tissue regarding metabolite composition, independently from genotype or treatment, signifying that major differences exist in metabolite composition within the different tissues. Interestingly, under well-watered conditions, the metabolomics of different tested hybrids showed a very similar metabolic pattern. However, with drought, these hybrids had a more diverse metabolic composition concerning their genetic background (Witt *et al.* 2012).

Drought is a major threat to grain production, especially maize crops. Water deficiency leads to sterility and reduced grain filling rates. Several studies have explored the role of sugar and enzymes during drought stress (Nephali *et al.* 2021). Pelleschi *et al.* (2006) explored the genetic basis of maize photosynthetic-related traits under water stress at the molecular level. They analyzed the relationships between growth, photosynthesis and carbohydrate metabolism of young maize plants using quantitative trait loci analysis [QTLs: a statistical method that links two types of information, phenotypic data (trait measurements) and genotypic data (usually molecular markers), to explain the genetic basis of variation in complex traits (Lynch and Walsh 1998)] when subjected to water deficiency. This study showed mapping near the *Ivr2* gene, an inver-

tase-encoding gene. Moreover, co-location between the sucrose-P synthase and ADP-glucose pyrophosphorylase has been reported in young maize plants under drought stress. These studies revealed the key role of metabolites and proteins in the development of stress-tolerant crops (Pelleschi *et al.* 2006).

Recently, the importance of root adaptations to environmental stresses has received increasing attention. A stimulating study was conducted by Li *et al.* (2021) to identify the metabolic responses to combined drought and salinity stress in maize primary root development and its metabolite profiles. The obtained results showed that a single stress (drought or salt) and the combined stresses (drought-salt) reduced the length of the primary root, and the growth rate and that the treatment time had a reverse relationship. However, combined stresses had stronger adverse effects than single ones. The primary roots of a maize plant were analyzed using GC-MS to identify metabolites present under various stresses such as drought, salt, and their combination. The analysis revealed 86 metabolites, including 29 amines and amino acids, 21 organic acids, 10 polyols, 10 sugars, six phosphoric acids, four fatty acids, and six other types of compounds. From the 86 identified metabolites, 53 metabolites with significant changes under different stresses were identified in the primary root, and the content of most metabolites showed down-accumulation. The volume of sugars and polyols was increased to help maintain the osmotic balance. Also, the levels of metabolites involved in the tricarboxylic acid (TCA) cycle, such as ketoglutaric acid, citric acid, fumaric acid, and malic acid were decreased in the primary root (Li *et al.* 2021). In a similar study conducted by Sun *et al.* (2015), the metabolic response of maize plants to combined drought and salt stress illustrated that the combined stresses severely affected the development of aerial tissues and the photosynthetic rate in maize.

In another study, Joshi *et al.* (2021) investigated a metabolome response of maize leaves subjected to long periods of drought, salt, or heat stresses. They reported a stress metabolome, raffinose, as a corresponding substance linked to drought stress tolerance in maize. Also, it was revealed that some amino acids including proline, arginine, and aminobutyrate combined with a reduction of key glycolysis and tricarboxylic acid cycle intermediates are responsible for the balance between carbon and nitrogen metabolism in stressed leaves. Although convergent metabolome shifts were correlated with gene expression changes in affected pathways, patterns of differential gene regulation induced by the three stresses indicated distinct signaling mechanisms highlighting the plasticity of plant metabolic responses to abiotic stress.

Metabolomics investigation of rice production under abiotic stresses

Fumagalli *et al.* (2009) analyzed the metabolic content of two different cultivars of rice using NMR techniques coupled with multivariate statistical analysis under abiotic stress conditions. In this study, the metabolite profiling of rice cultivars under salinity showed enhanced sugar contents during salinity stress in both cultivars. The obtained results also demonstrated that salt stress reformed the accumulation of various metabolites in rice such as amino and organic acids, sugars and aromatics. Also, a small number of unassigned aromatic resonances were detected, which have a vital role in salt tolerance. They also recommended that the PCA based on NMR analysis is a remarkable tool for characterizing rice varieties under different variations of stress conditions (Fumagalli *et al.* 2009).

A GC-MS-based analysis metabolomics investigation on rice under salinity stress was conducted to understand the metabolomic responses of two salt-sensitive seedlings (Sujala and MTU 7029) and two tolerant varieties (Bhutnath, and Nonabokra) of indica rice (Gupta and De 2017). Different tested varieties exhibited different responses to NaCl stress. The four varieties responded differently to NaCl treatment of the leaves of rice seedlings. It must be taken into consideration that the primary metabolites namely sugars, polyols, amino acids, organic acids and certain purine derivatives, were conserved. In both salt-tolerant varieties, the serotonin level was increased in response to NaCl stress. The signaling molecule gentisic acid was elevated in both salt-tolerant varieties in response to salinity treatment. Also, levels of ferulic acid and vanillic acid were increased in salt-tolerant varieties. However, cinnamic acid derivatives, 4-hydroxycinnamic acid (in Sujala) and 4-hydroxybenzoic acid (in MTU 7029) were increased in the leaves of the salt-sensitive varieties. Therefore, increased production of serotonin and gentisic acid as signaling molecules may be characterized as two important biomarker compounds produced in tolerant varieties against salinity tolerance (Gupta and De 2017).

Metabolic profile analysis and identification of key metabolites during rice seed germination were investigated under low-temperature stress by Yang *et al.* (2019). In their study, two different varieties of rice, 02428 (japonica) and YZX (indica), were subjected to experiments which included low temperature, normal temperature and a transition from low to normal temperatures. LC-MS/MS-based metabolite analysis identified 730 metabolites, of which 35 different metabolites were identified as responding to low-temperature stress among the 730 metabolites. It was found that seven out of the 35 metabolites responded significantly to low-temperature stress with a fold change < 0.5 or

variable importance in projection (VIP) score > 1 at the transition point and were defined as key metabolites. These seven key metabolites, N-acetyl-L-glutamic acid (Tri208), L-ascorbate (Tri890), anthranilic acid (Tri524), inositol (Tri845), Lysine butyrate (Tri142), LysoPE 18:0 (2n isomer) (Tri760), and Ncaffeoyl putrescine (Tri251), participate in the biosynthesis of amino acids and phenylpropanoids and the metabolism of glutathione and inositol phosphate (Yang *et al.* 2019).

In another comparative metabolomic investigation of rice under cold temperature stress, a reactive oxygen species-dominated dynamic model underlying chilling environment adaptation and tolerance in rice was revealed (Zhang *et al.* 2016). More than 200 known metabolites were detected. During cold treatment, significant biochemical changes in such biochemicals as glutathione, putrescine, asparagine, β -alanine, γ -glutamylleucine, oxalate, mannose-6-phosphate were observed in antioxidation. Interestingly, unlike other types of environmental stresses, chilling produces phenotypic changes in plants, not during exposure to low temperature, but rather in the later recovery growth stage. Therefore, there are differences in the metabolic pattern during cold treatment and the recovery stage, and some important anti-stress compounds are produced in the recovery growth stage rather than during chilling treatment. During cold stress treatment, significant metabolic changes occur in antioxidation-related compounds. During recovery growth, large-scale accumulation of amino acids was observed due to an imbalance of protein metabolism (Zhang *et al.* 2016).

In a recent study conducted by Xie *et al.* (2020), the GC-MS-based metabolites related to rice salt tolerance exhibited that amino acids were enriched more in three salt-tolerant lines (G58, G1710, and IR64) than in salt-sensitive lines (G45 and G52) under control conditions. It revealed the presence of fundamental metabolite differences between the tolerant and sensitive lines. In this case, the PCA was used to separate biological samples based on the contribution of a set of metabolites. Metabolomics analysis was successful in separating the metabolites in the leaves of five rice lines under control, salt stress and 3 days after salt treatment.

Toxic environmental pollutants are readily absorbed by crops and grains and pose serious threats to human health. The selection and breeding of different varieties of crops with low toxic pollutant accumulation is one of the most economical and ecological methods to reduce toxic exposure to humans. In a study conducted by Zeng *et al.* (2021), two different indica rice grains were subjected to a mass spectrometry-based metabolomics investigation under cadmium stress. With increased cadmium concentration in rice grains, most carbohydrates and amino acids

were down-regulated. It was also observed that myo-inositol was up-regulated to prevent cadmium toxicity. The other compounds that were amplified with increased cadmium concentration were D-Mannitol and L-cysteine in low-cadmium-accumulating rice. Also, some organic acids such as 13-(S)-hydroperoxy-9(Z),11(E),15(Z)-octadecatrienoic acid were activated which is related to the α -linolenic acid metabolism and jasmonic acid production.

Metabolomics investigation of wheat production under abiotic stresses

Metabolomics research in wheat production under abiotic stress is scarce. Saia *et al.* (2019) provided a review of a metabolomics investigation of the durum wheat plant. Guo *et al.* (2015) compared wheat plant metabolomics responses and adaptive strategies to salt and alkali stresses. A brief review of the results of this study indicated that salt stress and alkali stress are two distinct types of stress and revealed that the adverse effects of alkali stress on wheat are more severe than the harmful effects of salt stress. According to this study, salt stress has a more injurious effect caused by low-water potential and ion toxicity; on the other hand, alkali stress not only involves the two stress factors mentioned but also can cause high-pH stress. Metabolomics analysis showed that the sugar content of wheat seedlings increased in response to salt stress. However, a dramatic decrease in sugar levels was found under alkali stress. Also, it was shown that alkali stress induced the production of high amounts of phosphate and metal ion precipitate, except Na and K (Guo *et al.* 2015).

Utilizing metabolomics to identify health-promoting metabolites in crops under stress

The agricultural industry is currently challenged with developing improved crops with higher yields, increased nutrition, and resilience to environmental stresses to support a global population of around 10 billion people while reducing the use of pesticides and insecticides. In addition, as chronic diseases such as cancer, cardiovascular disease, and diabetes (type 2) become more prevalent and are directly related to diet, there is growing interest in plant-based foods that contain bioactive compounds to assist in reducing the risk of chronic diseases (Hickey *et al.* 2019; Ranilla 2020). Therefore, understanding plant molecular networks' metabolites and biochemical pathways under environmental stresses is crucial for the agricultural industry.

Metabolomics research revealed that analyzing carbohydrate metabolism in stressed plants is important since primary metabolites of plants exhibited major changes in response to environmental stresses. Also, during environmental stresses, plants increase their usage of starch and fructans as energy supplies in comparison to glucose (Dawid and Hille 2018). Another class of primary metabolites in plants that are affected by abiotic stresses are lipidomes. According to Tenenboim *et al.* (2016), the biosynthesis, regulation, function, role and interaction of lipids in plants are modified under various environmental stresses. The membrane of lipid plant cells is altered based on the response to biotic and abiotic pressures (Tenenboim *et al.* 2016; Dawid and Hille 2018). Lipidomics is one of the metabolomics fields of study which investigates large-scale cellular lipids using analytical chemistry principles and technological tools such as mass spectrometry (Yang and Han 2016). Lipidomics become a decisive tool in the identification and quantification of all lipid conversions during environmental stresses such as analyzing the oxidation reaction of polyunsaturated fatty acids which can change phytohormone precursor formation and/or lead to rancidity (Dawid and Hille 2018). Plants produce low-molecular-weight compounds as part of their defense systems in response to various environmental stresses, especially microorganisms exhibiting antimicrobial and health-beneficial properties such as anti-inflammatory, antifungal, anti-oxidant, anti-cholesterol and anti-cancer (Jeandet *et al.* 2014).

Although there are several reports on the mechanisms of modifying the primary metabolites of plants under biotic and abiotic stresses (Nakabayashi and Saito 2015; Okazaki and Saito 2016), there is a lack of information on the mechanisms of alteration of secondary metabolites of plants under abiotic stressors particularly in crops. Therefore, investigation of mild and in-control environmental stresses can help increase the amount of bioactive secondary metabolites of plants, increase the nutritional value of crops, and turn threats into positive opportunities.

Sensomics and hormonomics

Sensomics and hormonomics are subgroups of metabolomics. Sensomics or flavoromics are useful tools in the food industry as they investigate compounds that influence sensory perception in agricultural products. These sensory compounds are related to nutrition, food safety, and the quality of agricultural products. Sensomic analysis aims to define the sensory properties of nutrition at a molecular level (Vrzal and

Olšovská 2019). According to Dawid and Hille (2018), the flavor and aroma of food products greatly influence the purchasing decisions of more than 80% of customers. To enhance crop product flavor, it is vital to identify the right combination of odors and taste-active compounds at specific concentrations to create new and improved chemosensory traits and unique flavor profiles. Even though environmental stresses can negatively affect crop products during growth and post-harvest storage resulting in adverse, off-flavoring effects in crops, mild stress factors can have a positive impact. This can increase the presence of flavor-active compounds and result in the desired aroma and taste in the crops (Wüst 2018).

Another sub-metabolomics field of study is hormonomics. Hormonomics investigates the quality and quantity of hormones in plant samples and identifies plant cellular components by studying their hormone metabolites (Vrobel and Tarkowski 2023). Another class of bioactive compounds in plants consists of phytohormones with diverse low molecular weight structures. They act as chemical messengers and regulate all known biological phenomena and physiological processes during cell growth and development in plants, both under normal conditions and in response to environmental stress (Novák *et al.* 2017; David and Hille 2018). Phytohormones such as auxins, gibberellins, cytokinins, jasmonates, brassinosteroids, and strigolactones play crucial roles in creating abiotic stress-tolerant crops in metabolic engineering. In the quest to identify stress-tolerant crops, metabolomic investigation can assist in producing balanced phytohormones and reducing potential adverse effects on growth and development in crops (Wani *et al.* 2016). The study of hormonomics is beneficial for the management and enhancement of crop products. It involves genetic manipulation of specific genes and alleles in crop breeding. This sub-metabolomics technique facilitates the discovery and extraction of genes and alleles by mapping intermediate phenotypes and leads to the identification of complex agronomic traits.

Hirayama and Mochida (2022) demonstrated that employing reverse engineering to design stress-resistant crops by decoding the interaction of genotype and environment can enhance agronomic traits of crops. On the other hand, phenotype mapping based on hormones and environmental fitness causal loci in genotype-to-phenotype modelling in crops displays genetic factors. Therefore, improvement of resilience in plants is largely based on the engineering of appropriately selected target genes.

Regarding sensomic analysis of crops, in a study by Duggan *et al.* (2022), researchers conducted a sensomic investigation on crops to identify, quantify, and provide sensory elucidation of off-taste compounds in wheat bran. The study's results illustrated the suc-

cess of the sensomic approach in identifying the key off-taste compounds in this crop. Targeted and untargeted analytical techniques such as LC-MS/MS, LC-TOF-MS and 1D/2D-NMR spectroscopy were utilized to characterize the off-taste compounds in wheat bran. According to the results, the major compounds responsible for the bitter taste in wheat bran are saturated analogues, alkyl resorcinols such as (Z)-5-nonadec-12/14-enylresorcinol and (Z)-5-heneicos-12/14/16-enylresorcinol and off-taste fatty acids and fatty acid oxidation compounds. Although this study was not conducted under any specific environmental circumstances, it demonstrates the ability of metabolomics to identify what is responsible for off-flavor and the taste of wheat (Duggan *et al.* 2022).

Castro-Alves *et al.* (2020) applied an untargeted sensomic analysis to investigate the quality of dill (*Anethum graveolens* L.) under standard greenhouse conditions in the presence or absence of supplementary UV, using GC-MS/MS. It was found that dill exposed to UV produced metabolites similar to 'gold standard' samples with higher quality. They emphasized that this modification in the metabolite profile of dill was induced by UV light (Castro-Alves *et al.* 2020).

Belgis *et al.* (2023) reported a study on a combination of metabolomic and sensomic approaches to investigate the aromatic constituents and sensory profiles of three cultivars of mangoes (*Mangifera indica* L.) from Indonesia. The PCA classified cultivars into different groups and showed that dominant volatile compounds are the major secondary metabolites in each cultivar. The volatile compounds were extracted using headspace solid-phase microextraction (HS-SPME) and GC-MS. The sensory and aroma profiling was described using the Rate All That Apply (RATA) method and hedonic tests.

As mentioned earlier, a significant challenge to global rice production is heat stress which reduces yield and grain quality. Mishra *et al.* (2024) investigated the effect of high temperatures on the aromatic metabolites in grains of 15 rice genotypes. GC-MS-based metabolomics discovered a significant increase in proline levels as a discernible response to heat stress. Furthermore, volatile compounds, such as 2-acetyl-1-pyrroline (2-AP), a pivotal aroma-contributing constituent, exhibited reduced levels during the grain-filling stage under high-temperature stress. Furthermore, it illustrated the link between aroma variations and inactive BADH2 gene expression under high-temperature stress. These findings can assist in resolving the proline and 2-AP pathways to identify metabolites triggering aroma loss in aromatic rice and develop a stable aromatic rice variety under heat stress (Mishra *et al.* 2024).

Šimura *et al.* (2018) conducted a targeted hormonal analysis to profile the phytohormones in *Arabi-*

dopsis seedlings under salinity stress and control conditions. This study quantified about 43 endogenous compounds and main phytohormones in root and shoot samples such as cytokinins, auxins, salicylates, brassinosteroids, gibberellins, jasmonates and abscisates. It was shown that the integration of multivariate data analysis and cross-validation with transcriptomic data exhibited that the main hormone metabolites were involved in *Arabidopsis* adoption to salt stress. Therefore, agronomists can enhance crop yields by using hormonomics to study the physiological effects of biostimulants. Although sensomics and hormonomics are capable of sub-metabolomic analyses in crop production, in comparison to other omics there is still a lack of knowledge, thus preventing them from reaching their full potential.

Metabolomics applied to biostimulation and biocontrol product development

Biostimulants are organic and inorganic bioactive substances and microorganisms which are used as fertilizers and plant growth regulators. These products improve plant growth and produce more resistant plants under environmental stresses by inducing plants' physiological processes. On the other hand, biostimulants improve the absorption and assimilation of productivity of nutrients, therefore leading to increased crop yields (Franzoni *et al.* 2022; Martínez-Lorente *et al.* 2024).

Yakhin *et al.* (2018) demonstrated that the use of biostimulant substances resulted in an improvement in plant growth, stress resistance, and productivity in the agricultural industry, although, the mechanism of action is still enigmatic. The interest in applying biostimulants in crop industry is constantly increasing due to the need for more efficient and effective organic materials for soil health sustainability and to reduce adverse environmental conditions because of climate change leading to negatively affecting crop growth and productivity (Rouphael *et al.* 2020).

Nephali *et al.* (2021) characterized microbial biostimulant-induced mechanisms for growth promotion and improved drought tolerance in maize plants using metabolomics. In this study, five *Bacillus* strains were used as growth-promoting rhizobacteria (PGPR). The PGPR-induced metabolic alterations spanned a wide spectrum of metabolite classes including phenolic compounds, lipids, organic acids, hormones and amino acids. Bioinformatics tools and chemometric profiles disclosed PGPR treatment-related changes in metabolome extracted from maize leaves. Principal component analysis (PCA) revealed key characteris-

tics of the data regarding drought- and PGPR-related sample grouping. Metabolite classes including phenolic compounds, lipids, organic acids, hormones and amino acids are a wide spectrum displayed in PGPR-induced metabolic alterations (Nephali *et al.* 2021). These authors further reported decreased levels of primary metabolism such as alanine, serine, aspartic acid, cysteine, proline and threonine in non-stressed maize plants treated with PGPR-based biostimulants. They concluded that PGPR-based biostimulants significantly impacted phenolic compounds and lipid spanning pathways as key mechanisms facilitating drought tolerance. However, caffeoyl-shikimic acid content was not detected in all drought-treated maize and PGPR treatment did not have any distinguishable effects under drought stress (Nephali *et al.* 2021).

In another study, an untargeted metabolite profiling was conducted to evaluate leaf metabolome changes in wheat cultivars treated with PGPRs, *Bacillus subtilis* and *Paenibacillus alvei* (T22). The approach of this study was to profile the rhizosphere exo-metabolome of wheat generated from seed inoculated with *P. alvei* and *B. subtilis* strains and to explain the effects of PGPR treatment on the metabolism of above-ground tissues. A PLS-DA generated model showed the differential clustering and separation of rhizosphere PGPR-treated and untreated wheat leaf samples. Also, treatment of the rhizosphere with varying strains of PGPR revealed the differential regulation of the wheat leaf metabolome as shown by the separation between Gariep cultivar *B. sub* and Gariep cultivar *P. alvei*. The same result was obtained with the treatment of the Koonap cultivar with *B. sub* and *P. alvei*. A heatmap revealed treatment-associated metabolite up/down-regulations, thus giving insight into the effects of each type of rhizosphere treatment on the measured metabolome of the plants (Mashabela *et al.* 2022).

Bernardo *et al.* (2019) researched the modulation of the tripartite interaction plant-AMF (arbuscular mycorrhizal fungi)-environmental stress. In this study, metabolomic responses to enhance tolerance by AMF to water stress in two wheat cultivars (*Triticum turgidum* ssp. *durum* and *T. aestivum* L.) were analyzed. Metabolomics showed that the water deficit regime had a similar regulation of secondary metabolism in wheat cultivars. More representative of metabolic classes from VIP analysis were lipids, flavonoids, carbohydrates, terpenoids, amino acids and hormones. It was reported that the most intensely modulated class of compounds in response to mycorrhization under water stress was lipids, while carbohydrates were in second place. The obtained results illustrated that sugars and lipid type compounds characterize discriminant biomarkers, both being positively modulated by AMF colonization under water stress. Regulation of metabolites related to oxidative stress and tuning of

crosstalk between phytohormones were also observed (Bernardo *et al.* 2019).

Conclusions

Metabolomics has been recognized as a powerful tool for analyzing the impact of abiotic stresses on the biology and biochemistry of plants. However, further research is needed to integrate this analysis method with other omics. An extensive variety of metabolites and chemical substances can be identified and analyzed by metabolomic investigation. These metabolites include sugars, organic acids, amino acids, and secondary metabolites with a holistic view of the metabolic status of plants. This approach holds immense potential for unravelling the metabolic responses of crops to environmental stresses, offering valuable insights into the reprogramming of metabolic pathways and the accumulation of stress-related metabolites. Employing advanced analytical techniques such as GC/LC-MS and NMR spectroscopy makes metabolomic investigation a powerful tool to identify and quantify metabolites present in plants, which leads to a comprehensive understanding of the metabolic dynamics in crops under stress conditions.

Metabolomics study on crop responses to environmental stresses can develop scientific knowledge and help to better understand plant stress physiology. The integration of metabolomic approaches in studying crop responses to environmental stresses has revolutionized our understanding of plant stress physiology. By employing metabolomic techniques, researchers can elucidate the metabolic pathways and biochemical processes that are altered in response to specific environmental stresses. For instance, metabolomic studies have revealed the accumulation of compatible solutes such as sugar, polyols, amino acids proline and glycine betaine in plants subjected to osmotic stress, serving as osmoprotectants to maintain cellular turgor and mitigate the adverse effects of stress. Furthermore, metabolomic investigations revealed the ability to modulate primary and secondary metabolic pathways in crops under stress, highlighting the dynamic reprogramming of metabolic networks to cope with environmental stresses. The integration of metabolomics in studying crop responses to environmental stresses not only enhances our fundamental knowledge of plant stress physiology but also holds immense potential for identifying metabolic markers associated with stress tolerance and developing stress-resistant crop varieties (Rodrigues Neto *et al.* 2023; Mehta and Vyas 2023).

According to the reviewed articles, the most extensively detected and studied environmental stresses in the mentioned crops were drought and salinity. A com-

mon response to salt and drought stresses is growth inhibition in the shoots and roots which consequently decreases crop yields (Li *et al.* 2021). The combination of drought and salinity stress affects more than 50% of the world's agricultural and arable lands (Guo *et al.* 2015; Abdelraheem *et al.* 2019). The effect of two or more environmental stresses causes more damage and yield loss than a single stress. Therefore, understanding how environmental stresses affect crops, their responses and tolerant mechanisms of plants against each of the stresses and combinations of them is a great opportunity for improvement of stress tolerance in plants especially in crops. Moreover, the determination of biomarkers and characterization of metabolic pathways are helpful for the selection of resistant varieties of crops with low environmental toxic accumulation. In general, metabolomic analysis suggests a comparable metabolic regulation in different crops under environmental stresses, for most identified metabolites. Metabolomics can give valuable information about the metabolic reaction and a plant's mechanism of action under environmental stresses considering geographical climatic, and species-associated factors by analyzing changes in the content of small-molecule substances (Umair *et al.* 2019).

Moreover, to achieve a comprehensive understanding of the link between crops and environmental stresses and the molecular mechanisms underlying stress responses in crops, the integration of multi-omics approaches, including genomics, transcriptomics, and proteomics plays a powerful role. Incorporating data from multiple omics can provide a holistic view of the complex regulatory networks governing stress tolerance in crop plants. Different varieties of environmental stresses on plants can activate or inhibit enzymes and accordingly influence the regulation of certain metabolic pathways in plants. Therefore, subjecting plants to controlled and regulated abiotic stresses may improve the quality and nutritional value of crops containing phytoalexins and antimicrobial substances (Dawid and Hille 2018).

Therefore, plant metabolomics is a worthwhile tool in agrochemistry and biocontrol to develop an alternative biobased solution for modification of the environment to stimulate existing micro-organisms capable of bioremediation in the crop industry. Metabolomic studies can reveal the system for targeted manipulation of metabolic pathways to enhance stress resilience by deciphering and recognizing metabolomic patterns and metabolic mechanisms of action of stress tolerance in crops. Metabolomic-based techniques such as lipidomics, sensomics or hormonomics using high throughput analytical methods such as LC-MS, GC-MS and NMR have led to the discovery of altered metabolomes produced during biotic and/or abiotic stress circumstances.

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