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Computational Modeling of Metabolic Networks in Rice Under Salt Stress

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Abstract Salt stress is one of the main abiotic stresses affecting the growth and yield of rice, and it can significantly disrupt the ionic homeostasis and metabolic activities within cells. A thorough understanding of the metabolic regulation mechanism of rice under salt stress is of great significance for enhancing the salt tolerance of crops and achieving precise breeding. This study reviews the typical physiological and metabolic responses of rice to salt stress, including osmotic regulation, ion balance mechanisms, antioxidant metabolism, and dynamic reprogramming of primary and secondary metabolism. Based on metabolic network modeling methods such as flux balance analysis (FBA), combined with transcriptome and metabolome data, a specific metabolic model under salt stress conditions was constructed. And network mapping and throughput estimation are carried out by using databases such as KEGG and MetaCyc, as well as tools like COBRA and CellDesigner. In the case analysis, this study focused on the simulation and functional verification of central carbon metabolism and amino acid metabolism (such as proline and GABA), revealing the modular reconstruction process of the metabolic network under stress, identifying key nodes and restricted pathways, and predicting possible metabolic engineering modification strategies. This study provides a systems biology perspective for analyzing the metabolic regulation of rice under adverse conditions, and at the same time offers theoretical basis and computational support for the molecular design of salt-tolerant varieties.

Keywords Rice; Salt stress; Metabolic network; Computational modeling; Flux balance analysis

1 Introduction

Not all abiotic stresses are as troublesome as salt stress, especially for rice (*Oryza sativa* L.). The high-salt environment in coastal and saline-alkali areas often leads to a sharp decline in yield. Ion imbalance is just the beginning; the subsequent changes in osmotic pressure and oxidative pressure are even more difficult to deal with. Sometimes, a sudden drop in photosynthetic efficiency or a slower absorption of nutrients by the root system may also be related to these factors (Luo et al., 2024). Inside the cells, the metabolic network also has to be adjusted accordingly. Amino acids, sugars, organic acids, and even some secondary metabolites start to be redistributed, most of which come into play to combat water loss or eliminate free radicals. In fact, there is a considerable difference in the accumulation of such metabolites between salt-tolerant varieties and sensitive varieties, and the gene expression patterns are also different. All these indicate from the side that metabolic regulation is indeed involved in the salt-tolerant process (Kong et al., 2019; Rajkumari et al., 2023; Deng et al., 2025).

However, when looking at the data, sometimes it can be quite confusing. The transcriptome and metabolome can each be seen in parts, but they tell fragmented stories. To "piece together" all this information, relying solely on data from a single dimension is often insufficient. This is also why people are increasingly beginning to use metabolic network models to string together these scattered pieces of information. By simulating the flux distribution and tracking how molecules "move", you can see which pathways become particularly active under salt stress, such as photosynthesis, the respiratory chain, antioxidant pathways, and sometimes even hormone metabolism. Such modeling results repeatedly remind us that some metabolic nodes are frequent "alerts", indicating that they play a key role in salt responses (Wanichthanarak et al., 2020).

This study will construct and apply a metabolic network model of rice under salt stress to reveal its systematic metabolic adaptation mechanism, identify potential targets for improving salt tolerance, review the relevant background and modeling methods, introduce model construction and validation, analyze metabolic responses, and finally discuss the research significance and future directions. By integrating multi-omics datasets and computer-simulated metabolic flow analysis, this study aims to deepen the understanding of rice metabolic reprogramming and its regulatory mechanisms, which is expected to provide information for breeding and biotechnology intervention, thereby promoting crop improvement.

2 Physiological and Metabolic Responses of Rice to Salt Stress

2.1 Osmoregulation and ion homeostasis mechanisms

Not all rice varieties can remain unscathed in high-salt environments. Generally speaking, salt-tolerant varieties have a lower Na^+/K^+ ratio than sensitive types. This difference is related to their absorption, transport and isolation of sodium and potassium ions. When rice responds to salt stress, it often initiates a series of osmotic regulatory mechanisms first to maintain the balance of water and ions in cells. The expression of Na^+/H^+ reverse transporters like NHX will increase, and Na^+ will be isolated into the vacuole or simply expelled from the cell. During this process, small molecules such as proline, stachyose and raffinose also accumulate quietly, playing a role in regulating blood pressure and protecting cell structure (Figure 1). If these mechanisms operate smoothly, photosynthesis will not be greatly affected and oxidative damage can also be reduced (Gerona et al., 2019; Liu et al., 2022; Lelekami et al., 2025).

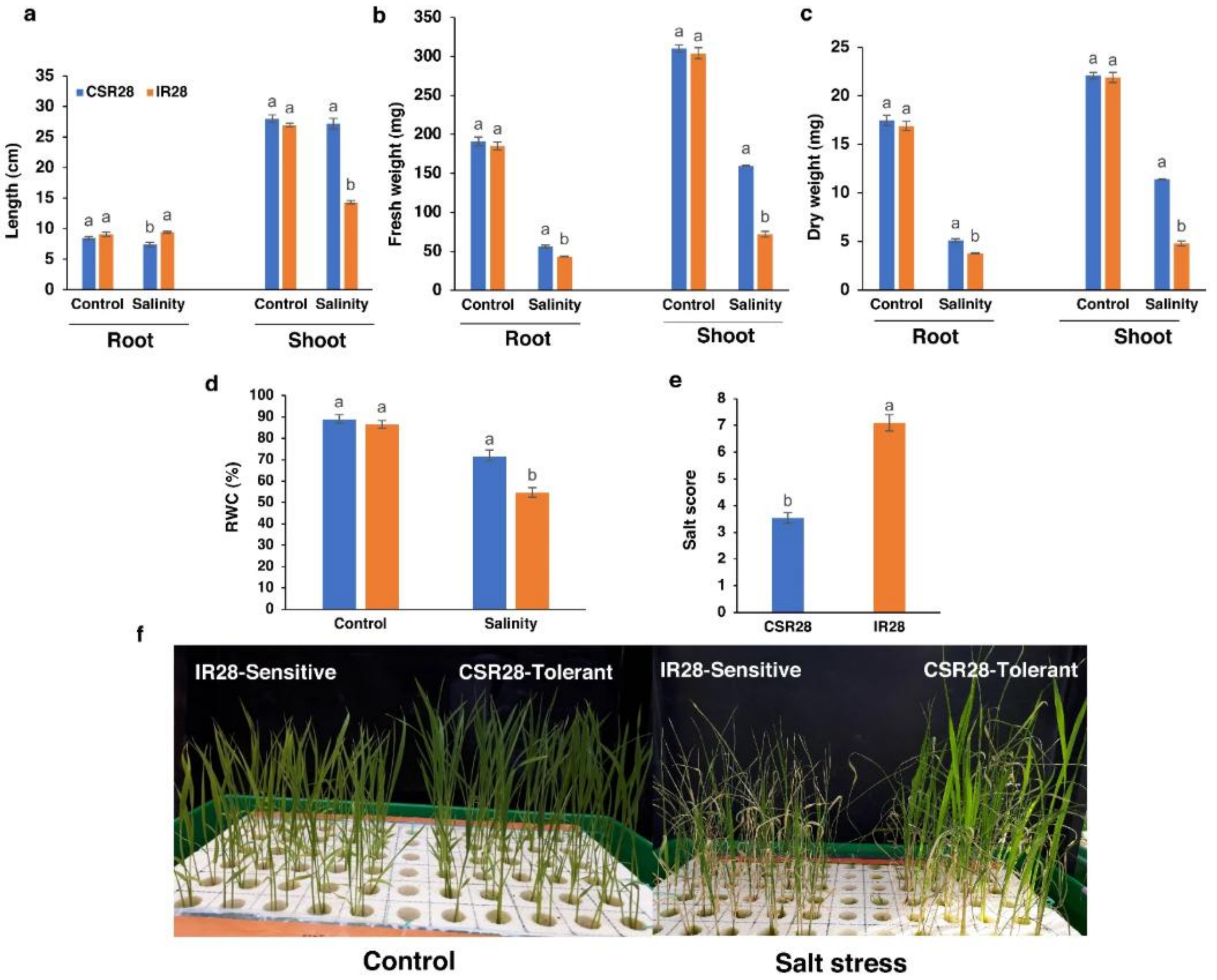

Figure 1 Phenotypic assessment of the salt sensitive (IR28) and tolerant (CSR28) rice genotypes after 1 week of 150 mM salt stress. (a) Length, (b) Fresh weight, (c) Dry weight, (d) Leaf RWC, (e) Salt score, including 1, 3, 5, 7 and 9 as very tolerant (normal growth), tolerant (relatively normal growth), relatively tolerant (delayed growth), sensitive (completely stopped growth) and very sensitive (death of all plants), respectively. (f) Phenotype of the seedlings under control and salt stress conditions. Different letters indicate significant difference between the genotypes based on Student's t-test (*P* value ≤ 0.05) (Adopted from Lelekami et al., 2025)

2.2 Accumulation of secondary metabolites and antioxidants

When confronted with salt stress, some responses are rapid and instinctive, such as the activation of the antioxidant system. However, apart from those well-known enzymes (SOD, CAT, POD, APX), there is another category of "marginal roles" that should not be overlooked - such as polyamines, phenolic amides, salicylic acid and serotonin, which are signaling molecules and also have the function of clearing ROS. The accumulation differences of these substances among different varieties often indicate their actual role in salt tolerance regulation. In some salt-tolerant strains, the levels of these metabolites are significantly higher, and it is not difficult to understand what role they play in the defense line against stress (Du et al., 2025).

2.3 Overview of key metabolic pathways involved in stress responses

The impact of salt stress is not a disturbance through a single path; rather, it is more like a systematic metabolic "major dispatch". A reduction in chlorophyll content, inhibition of starch synthase expression, and restricted photosynthesis are common phenomena, and energy supply will also be restricted. Meanwhile, the main energy pathways such as glycolysis and the TCA cycle need to adjust their rhythms to meet the survival demands of cells. Rice also activates the synthesis of branched-chain amino acids and sugar alcohol metabolism, which are crucial for alleviating osmotic pressure changes. At the cell membrane stage, lipid metabolism cannot fail either - the change in the ratio of PE to PC is precisely helping cells stabilize their membrane structure. These seemingly independent pathways are actually a kind of coordination mechanism formed by rice under "forced" conditions (Liu et al., 2025; Praphasanobol et al., 2025).

3 Computational Approaches for Metabolic Network Modeling

3.1 Fundamentals of static and dynamic modeling (e.g., GSMM, FBA)

Not all metabolic models focus on changes over time. Some, such as Flux equilibrium analysis (FBA), do not deal with the "time" dimension at all - it operates based on steady-state assumptions, does not pursue dynamic simulation, but uses an objective function (often maximizing biomass) to identify possible flux distributions. Relatively speaking, dynamic modeling follows a different path. Methods like set dynamics attempt to incorporate time and regulatory changes. Even if some parameters may not be measurable at all, they can still run and barely provide the behavioral trend of the system. However, before modeling, most people still build a static framework first, such as a genome-scale metabolic model (GSMM). After all, such models can systematically organize metabolic reactions and related genes, laying the foundation for subsequent modeling (Vlassis et al., 2013).

3.2 Network construction and definition of nodes/reactions

The construction of a metabolic network may sound like building with blocks, but in fact, it is a process of data blending. Each metabolite in the network is like a node, and each reaction is facilitated by enzymes. However, these reactions are not randomly selected. It depends on which reactions are actually operating under specific conditions. So many times, it is more practical to first pick out a set of core reactions and then gradually build a simplified but reasonable sub-network structure. In order to make these pathways fit the biological system as closely as possible, the modeling process often requires repeated optimization with the aid of algorithms, such as whether the fluxes are consistent and whether they meet the basic metabolic requirements, etc. (Pandey, 2025).

3.3 Visualization and flux estimation tools (e.g., COBRA, CellDesigner)

After having the model, without good tools to support it, it's basically impossible to move forward even an inch. The COBRA toolbox is almost the "starting point package" for many people's modeling. It can run FBA, conduct flux analysis, and also support modeling with specific conditions, making it highly versatile. In contrast, CellDesigner does not do much numerical calculation. It is more like a "drawing expert", capable of visualizing complex metabolic pathways and helping you understand reaction structures and molecular interactions at a glance. As for flux estimation, many people will use methods such as Monte Carlo sampling or linear programming. They can outline the flux distribution range under different conditions and also identify the bottleneck points that are "choke points" in the network. Although these tools each have their own strengths, when used together, they can basically cover the entire process from metabolic network modeling to verification (Fallahi et al., 2020).

4 Data Integration and Model Reconstruction

4.1 Strategies for integrating multi-omics data (transcriptomics, metabolomics, proteomics)

Take the case of salt stress for example. Looking at just one piece of data is very likely to fall into the trap of one-sided interpretation. For instance, in the transcriptome, it seems that the gene expression has increased, but sometimes the corresponding enzyme shows no significant movement. However, the changes in metabolites provided by the metabolome do not always indicate which pathway has truly been activated. This kind of misalignment is not uncommon. After all, gene expression, protein abundance and metabolic levels do not always align in rhythm. It is precisely for this reason that data from multiple omics must be uploaded simultaneously in order to piece together a reliable metabolic panorama.

Methods like Flux Balance analysis (FBA) can be regarded as a common integration approach. Although it relies on a static model, different reactions can be weighted in the model, and the transcriptome can be used to "indirectly" regulate the reaction intensity. As for the metabolome, some people simply use reverse modeling to study the covariance between metabolites and, in turn, infer the strength of reactions and the direction of networks. In this way, it's not just about seeing who appears on the Internet, but also estimating who has actually moved and how much they have moved.

Of course, these methods are not perfect. Sometimes, it also depends on the quality of the data. But the benefits are obvious - especially under salt stress, the dynamic adjustment of metabolism is the key point, and the fusion of multi-omics just helps us grasp the rhythm of these changes (Blazier and Papin, 2012; Töpfer et al., 2015).

4.2 Mapping metabolic pathways using public databases (KEGG, MetaCyc)

Sometimes, building a model doesn't start from an "open space". Databases like KEGG and MetaCyc are like architectural drawings. They not only provide structural information such as pathways and enzyme functions, but also help us match the annotated genes with the corresponding metabolic reactions one by one. With the help of tools like RAVEN 2.0, these data can be quickly transformed into a preliminary metabolic network sketch. Of course, these paths may not be fully applicable to every species, but they remain the fundamental framework for integrating omics data. For those who want to simulate the metabolic response of rice under salt stress, without this step, it is basically impossible to move forward (Karlsen et al., 2018; Wang et al., 2018).

4.3 Extraction and optimization of salt stress-specific metabolic networks

Although genome-wide metabolic models are good, under specific stress conditions, full acceptance seems too "heavy". In fact, what is more crucial is to screen out those reactions that are truly active under salt stress. Algorithms like fastcore are designed for this purpose - they can extract a core sub-network from a large model that only retains high-throughput responses, eliminate edge paths, and reduce the complexity of the model. Then, if the model prediction does not match the experimental observation, the reaction flow can still be adjusted through optimization methods to make the overall performance more in line with the real physiological data. This approach is not omnipotent, but it is a very practical entry point in studying salt stress responses and identifying regulatory nodes (Li et al., 2023).

5 Simulation and Analysis of Salt Stress Scenarios

5.1 Comparative analysis of metabolic flux under normal and stress conditions

When rice is exposed to salt stress, the metabolic system's response is not ambiguous (Figure 2). When the simulation results were compared, the differences became apparent - especially in photosynthesis, respiration, and the synthesis of antioxidant substances, the fluxes of several key pathways all changed. In fact, once salt gets involved, the utilization of hexose is easily disturbed, while the process of breathing alone "works overtime" instead, with a significant increase in flow. This kind of phenomenon has long been reflected in the equilibrium analysis combining transcriptome and metabolome data. These changes do not seem accidental and are quite consistent with the physiological phenomena observed in the experiment. Ultimately, behind these adjustments, it might be that rice is redistributing energy and resources to cope with the pressure brought by stress.

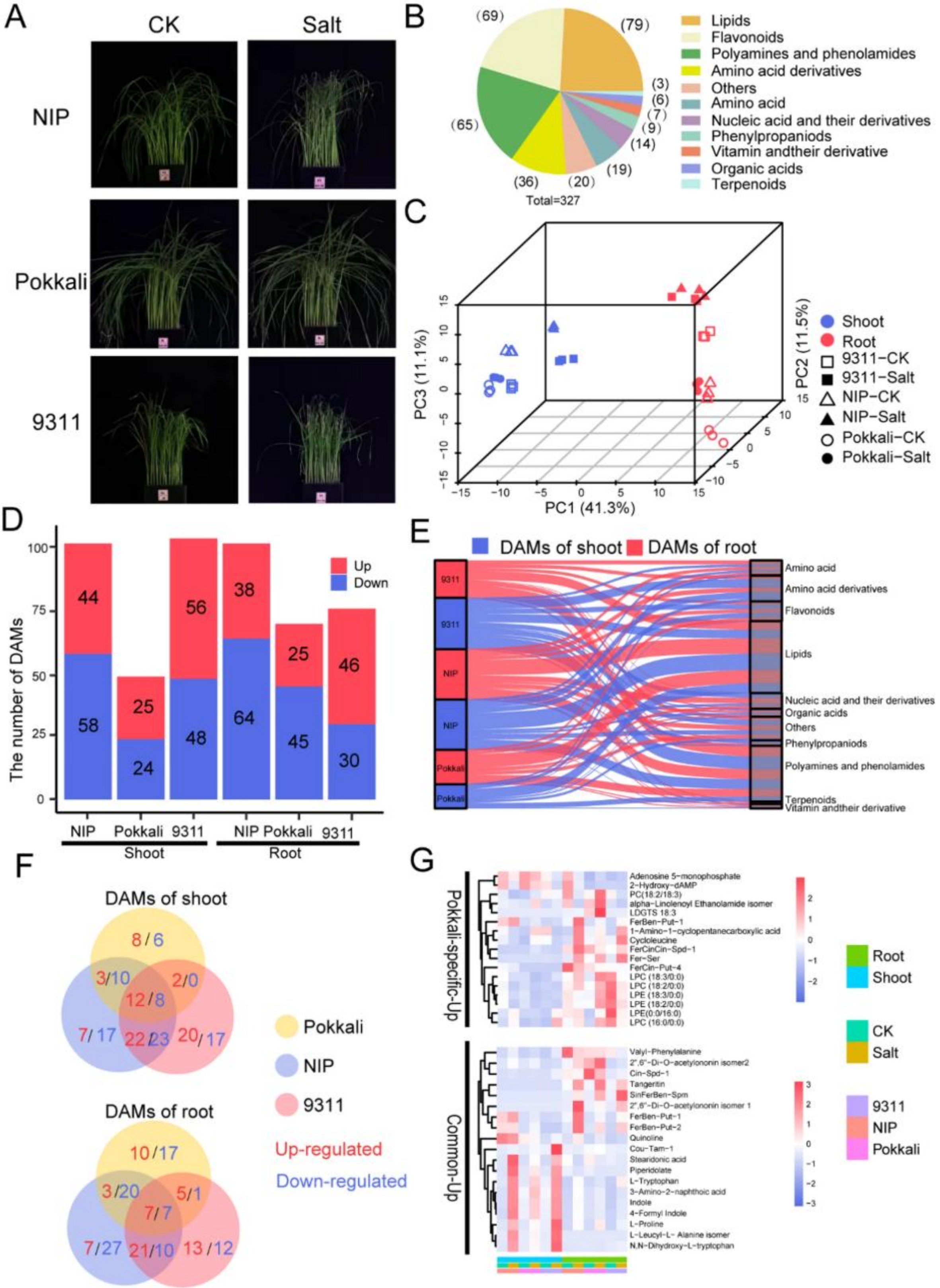

Figure 2 Metabolite profiles of rice from different varieties and tissues under salt stress. A Phenotypic characteristics of the NIP, Pokkali, and 9311 under salt stress. B Composition and proportion of different metabolites in rice. C PCA of the metabolites in different tissues and varieties under salt stress in rice. D The number of DAMs in different samples under salt stress. E Sankey diagram of identified DAMs in six comparative groups. F Venn diagram analysis of identified DAMs in the shoots and roots of different rice varieties after salt treatment. G Heatmap of DAMs that are specifically up-regulated in Pokkali and common (Adopted from Tong et al., 2025)

5.2 Identification of key nodes and bottleneck pathways

When some pathways malfunction, the entire metabolic chain is prone to getting stuck. In the simulation analysis, several nodes involved in antioxidant synthesis, hormone generation, and energy regulation were particularly "sensitive", and these areas are very likely to be the metabolic bottlenecks. Once these links are restricted, resources may accumulate or run out. But this is not a bad thing either - precisely because they control the direction of flux, they instead provide a "clue point" for understanding the metabolic adaptation mechanism under salt stress. Of course, these bottlenecks also imply potential vulnerable areas or regulatory Windows, which could be both restrictions and adjustable entry points (Krasensky and Jonak, 2012).

5.3 Prediction of potential metabolic engineering targets and in silico mutant simulations

Not all targets are worth taking, but some pathways do hold potential breakthroughs. By simulating the knockout or overexpression of certain key genes, researchers attempt to identify those "lever positions" that can enhance salt tolerance. Several main lines such as photorespiration, antioxidant biosynthesis, and carbohydrate metabolism have been repeatedly proven to be closely related to stress responses (Tong et al., 2025). The targets selected in this way are not only the data in the model, but also the "seed list" for subsequent experimental verification and engineering improvement. The model cannot directly produce salt-tolerant varieties, but it can help us choose the right direction first and avoid detours.

6 Case Study: Modeling of Central Carbon and Amino Acid Metabolism Under Salt Stress

6.1 Experimental validation of metabolic pathways (e.g., GC-MS data support)

Not all computational predictions hold water, so experimental verification is particularly crucial. Tools like GC-MS can directly demonstrate the changes in metabolites within plants under salt stress conditions - and these changes often confirm the "reprogrammed" metabolic pathways predicted by the model. For instance, the accumulation of sugars, organic acids and amino acids under stress conditions has been observed in various crops, and barley is no exception (Zhang et al., 2017; Derakhshani et al., 2020). And these changes actually involve the "reconstruction" of core metabolic pathways such as glycolysis and the tricarboxylic acid cycle. By comparing experiments with simulations, researchers gradually clarified which fluxes were regulated and which paths were deflected under stress.

6.2 Network-based analysis of amino acid accumulation (e.g., proline, GABA)

Not all amino acids are activated on a large scale under salt stress; some show almost no activity. However, proline and GABA are always indispensable in metabolic analysis and almost consistently rank among the top high-frequency substances. Their roles are far more than just helping to maintain osmotic pressure; they are more like the pivotal nodes in the entire stress response network. Especially the GABA pathway, when the tricarboxylic acid cycle function is compromised, it can always provide a safety net and output energy, and also stabilize the REDOX state within the cell. Interestingly, once there is a problem with the GABA pathway, not only is energy metabolism impaired, but the structure of the cell wall may also have problems (Renault et al., 2013; Che-Othman et al., 2019). Many studies, through network module analysis, have also found that the abnormal accumulation of this amino acid is not a solo effort but is closely linked to the coordinated regulation of the entire metabolic system.

6.3 Simulating the impact of central carbon metabolism adjustment on energy balance and stress adaptation

In the face of high salt, plants do not just sit and wait to die. Carbon metabolism is often the first to take action. In the simulated data, a clear trend is evident: glycolysis is enhanced the fastest, while some less conspicuous pathways, such as the GABA bypass and the glyoxylic acid cycle, are rapidly activated. It is not difficult to understand that when the key enzymes of the TCA cycle start to "strike" under high-salt conditions, alternative detour routes become the main force for emergency rescue (Arense et al., 2010; Sharma and Kapoor, 2023). Through these dynamic simulations, it can be seen how plants redistribute carbon flows to ensure the normal supply of ATP. Moreover, the synergy between carbon metabolism and amino acid metabolism is no coincidence.

When they work together, they not only stabilize the basic functions of cells but also provide energy and material support for salt resistance. The existence of these "alternative plans", in the final analysis, is actually an orderly self-rescue mechanism. It is not a stopgap measure but part of a systematic response.

7 Challenges and Future Perspectives

To be honest, it's not that easy to build a reliable rice metabolism model under salt stress. First of all, no matter how beautifully the model framework is set up, as long as the parameters are not up to standard, such as the kinetic values of those enzymes or the post-translational modification information being scattered, the model may get stuck halfway. Either it cannot simulate anything or the results are ridiculously poor. What's more troublesome is that some variables cannot be taken into account at the very beginning, such as fluctuations in salt concentration and in which compartment metabolic reactions occur in the tissue - these may seem like "details", but once added, the complexity of the model rises sharply. Even if you really want to add it, it's hard to have data to support it. Many people have attempted to solve dynamic simulation problems with more complex formulas, but the result is often that as more formulas are added, the uncertainty also soars. To take it a step further, even if a certain team does have a complete set of data, if the format, naming, and annotation standards are inconsistent, they would have to redo everything on a different platform. This is not an isolated case but a long-standing problem that cannot be avoided in the field of modeling at present - models "don't get along", data cannot be used, and results cannot be reproduced. It is precisely for this reason that an increasing number of researchers have begun to call for model development not to rely solely on individual efforts, and it is really time for community-led standard construction to catch up.

However, to be fair, although models are difficult to make, they are indeed very useful. Even though it is not yet perfect, genome-scale metabolic network models can already help us identify potential bottleneck links and even lock onto certain metabolic pathways that can regulate salt tolerance. In this way, it is expected that the metabolic impacts brought about by genetic modification can be simulated in the model in advance, and the laboratory can avoid many detours. For breeding, this approach of directly guiding from genotypes to salt-tolerant phenotypes has accelerated the pace of selection and breeding, and also made the goal of precision agriculture no longer so distant.

What is even more worth mentioning is that the integration of artificial intelligence and machine learning is changing the game. The past approach that relied on assumptions and explicit modeling is gradually being replaced by AI tools that can "learn" patterns from omics big data. These algorithms not only fill the "loopholes" in model parameters, but sometimes can also discover some metabolic linkage mechanisms that are simply unimaginable in traditional paths. When these methods mature, the predictive power of the metabolic network will be stronger and its adaptability higher, and it can even be directly used to guide the synthetic biological design and metabolic engineering development of rice. This kind of cross-border integration might be the key for the model to truly "come alive" in the next step.

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Conflict of Interest Disclosure

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

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