Research Progress in Tomato Responses to Abiotic Stress

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Abstract Tomato is a kind of vegetable with high economic benefits in protected farmland. Accounting for 30% of vegetable planting area in the entire protected farmland, tomato plays an essential role in cultivation of protected vegetable. Different abiotic stresses have different degrees of influence on growth and development, yield, and fruit quality of tomatoes. Therefore, finding out life activity rules of tomatoes under different abiotic stresses will be of great significance to breeding for stress tolerance and increasing tomato yield and income. This paper made an overview of research progress in tomato responses to abiotic stress in growth and development, physiology and biochemistry, and gene regulation.

Key words Tomato, Abiotic stress, Response mechanism

1 Introduction

Tomato is the edible, often red berry-type fruit of the nightshade *Solanum lycopersicum*, it is annual or perennial plant, and distributed in more than 160 countries or regions in 45°S to 65°N[1]. All wild species of tomato are distributed in narrow strips of Andes Mountains in the west of South America[2]. Tomato was introduced to Italy from Peru in the 16th century, and introduced to China from Italy in the 17th century, and introduced to England, France, North America, and Japan in the 18th century, and later was widely planted in all parts of the world as a world-wide vegetable[1]. In recent years, tomato, as a kind of vegetable with high economic benefits in protected farmland, accounts for 30% of vegetable planting area in the entire protected farmland, tomato plays an essential role in cultivation of protected vegetable[2]. Tomato contains sugar, protein, fat, organic acid, cellulose, and rich vitamins and trace elements, so it has high nutritional value; besides, tomato has certain medicinal value, for example, lycopene in tomato has function of anti-oxidation and anti-tumor[4–6]. Abiotic stress is defined as the negative impact of non-living factors on the living organisms in a specific environment. Abiotic stress is the most harmful factor concerning the growth and productivity of crops worldwide. Tomato belongs to moderate salt sensitive species. Treatment through certain concentration of salt can adjust flavor, color, and soluble matters of tomato, is favorable for increasing acid-sugar ratio of tomato, and thus improving tomato quality; however, too high salt concentration will lead to slow growth of tomato, and degradation of quality and yield[7,8]. In addition, drought, high temperature, and heavy metal stress will exert different degrees of influence on growth, development, yield, and fruit quality of tomato. Thus, finding out life activity rules of tomatoes under such abiotic stresses as saline and alkaline conditions, drought, temperature, and heavy metals will be of great significance to breeding for stress tolerance and increasing tomato yield and income. In this study, we made an overview of research progress in tomato responses to abiotic stress in growth and development, physiology and biochemistry, and gene regulation.

2 Influence of abiotic stress on growth and development of tomato

2.1 Influence of abiotic stress on growth and development of tomato leaves Drought stress will hinder growth of growth of tomato leaves and reduce stomatal conductance. Some researches have shown that length, width, area, water content and stomatal conductance of tomato leaves will drop with decrease of soil moisture, and the decline rate of abiotic stress will increase after 4 days[9]. Also, the drought stress will lead to decrease of thickness of leaf palisade tissue and spongy tissue[10]. Chlorophyll content is an essential physiological indicator reflecting photosynthetic intensity. When tomato is suffered from salt damage, nitrogen content in leaves will decline, while nitrogen is composition of chlorophyll molecule, so the tomato plant will have light color leaves and chlorophyll content will decrease[11]. In certain Pb stress condition, old leaves of tomato will show yellow mesophyll, while leaf vein still keep green and have chlorosis; with extension of treatment time, chlorosis will deteriorate[12].

2.2 Influence of abiotic stress on growth and development of tomato fruits Different water treatment has different influence on tomato yield: under mild stress, tomato fruit weight and yield have no great changes; under moderate and severe stress, tomato fruit weight and yield are obviously lower[13]. Huang Lihua *et al.*[14] found that different degrees of soda saline-alkali stress will reduce single fruit weight and organic acid of tomato, but increase the soluble sugar and the sugar-acid ratio; mild soda saline-alkali stress can increase vitamin C in tomato, while severe soda saline-alkali stress is not favorable for accumulation of vitamin C in toma-

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to fruit[14]. Li Hongyan *et al.* [15] found that different concentration of Na_2SO_4 stress has insignificant influence on tomato fruit. Sugar content in tomato is an essential indicator determining tomato quality. At 25 – 29℃, with temperature rise, sucrose gradually increases in dissepiment, while sucrose gradually decreases in pulp and pectinic[16]. Coloring of tomato fruit is greatly influenced from temperature. Lycopene formation is inhibited in high temperature, so the sustained temperature will make tomato show yellow color. In flowering period or early fruiting period, if the temperature is too high, puffy fruits will increase; when the temperature exceeds 35℃ and it lasts for a long time, fruit growth and development speed will be not coordinated and consequently generate puffy fruit[16].

2.3 Influence of abiotic stress on growth and development of tomato roots High salt concentration exerts significant influence on tomato seed sprouting or seedling growth, as well as micronuclei frequency in root-tip cells[17]. Mild drought stress will promote root system growth of tomato seedlings; under mild drought stress, length, surface, and volume of root system take on increasing trend[10].

3 Influence of abiotic stress on growth and development of tomato photosynthesis

Under drought stress, tomato leaves will generate large volume of reactive oxygen, which will damage cell membrane, reduce activity of photosystem II, and reduce generation of photosynthetic products[18]. Drought stress may also lead to drop of stomatal density and size, chloroplast becomes round and larger, granum lamella arrangement is disorderly, and starch grain decreases or disappear[19]. Compared with normal temperature, during the temperature stress, stomatal conductance and photosynthetic intensity take on the trend of first decline then rise, and gradually decline with extension of stress time[20]. Lu Shaowei *et al.* found that salt stress may damage photosynthetic functions of tomato leaves, reduce efficiency of photosynthesis, change direction of sugar metabolism in tomato leaves, promote decomposition of starch and sucrose, and increase fructose and glucose content of tomato leaves[21].

4 Influence of abiotic stress on physiological and biochemical indicators of tomato

Malondialdehyde (MDA) is the product of membrane lipid peroxidation, and its content reflects the degree of membrane lipid peroxidation. MDA content in plant tissue generally increases with the degree of stress. Yang Zaiqiang *et al.* found that with aggravation of drought stress, membrane lipid peroxidation of tomato leaves will gradually increase[22]. Song Qinfei *et al* found that MDA content in tomato leaves rises with increase of Pb concentration[12]. According to findings of Ding Haidong *et al.*, with increase of Cd^{2+} and Zn^{2+} concentration, MDA content in tomato root system and levels also increases[23]. The relative electrical conductivity (EC) is an essential indicator reflecting cell membrane permeability. Meng Changjun *et al* found that with increase of salt stress concentration, EC value of tomato plants takes on rising trend[24]. The dynamic balance between generation and clearance mechanism of reactive oxygen in plant body keeps normal growth of plants, while the adversity stress will break such balance, lead to accumulation of reactive oxygen in plant body and bring about various physiological and biochemical changes in plant body[25]. Anti-oxidant enzymes participating in enzymatic mechanism of reactive oxygen in plant body include superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and peroxidase (POD). As reactive oxygen scavenging agent, SOD plays certain role in protecting cell membrane system. Under low salt stress, SOD activity in tomato increases with rise of salt concentration; under high salt stress, SOD activity declines with rise of salt concentration[26]. Under the salt stress, high active SOD can effectively eliminate reactive oxygen in cells, to make tomato keep certain salt resistance[15]. Besides, researches have indicated that under certain drought stress, SOD and POD activity first rise and then decline, while CAT activity rises continuously[27, 28]. Under the Pb ion stress, POD activity in tomato leaves first rises then declines with increase of Pb concentration[12]. Ding Haideng *et al* found that with increase of Cd^{2+} and Zn^{2+} stress concentration, APX, POD, and CAT activity of tomato plants rises, and rise of superoxide dismutase can improve adaptation of seedlings and resistance to heavy metal stress[23].

5 Progress in researches of tomato stress tolerance genes

In nature, plants are subject to various abiotic stresses of external environment. In the long time of evolution process, plants have generated corresponding adjustment mechanism, namely adjusting the expression of related resistant genes, so as to survive once the environment is changed. Liu Hui cloned two different types of cold-resistant genes from low temperature resistant S. habrochaites. According to chip analysis results, we found that over-expression of shDHN can increase cold resistance and drought resistance of tomato plants and promote growth and development of tomato plants; over-expression of shCHLP increases chlorophyll content of tomato leaves[29]. Mitogen activated protein kinase (MAPK) cascade reaction is an essential approach for eukaryote signal transmission network and plays an important role in stress resistance. Through researches of SpMPK1 /SlMPK1, SpMPK2 / SlMPK2, and SpMPK3 /SlMPK3 gene expression methods under the drought, salt, and low temperature stress, Li *et al.* found that drought, salt, and low temperature stress can induce SpMPK1 / SlMPK1, SpMPK2 /SlMPK2, and SpMPK3 /SlMPK3 gene expression[30]. Jia *et al.* found that Betainealdehyde dehdyoregn (BADH) gene can strengthen salt resistance of tomato plants, mainly manifested in root system growth and development under the salt stress. In addition, it will lead to rise of POD and SOD to a certain extent, raise anti-oxidation ability, and keep relative balance and stability within cells[31].

6 Regulation mechanism of transcription factor to stress response

The transcription factor is also called trans-acting factor and its major function is to activate or inhibit transcription effect of genes. As a member of complex signal network, transcription factor plays an essential role in regulating stress of environment factors. WRKY is stress resistant transcription regulation factor unique to a certain type of plant and it forms a huge protein family in higher plants. According to findings of Liu Chang *et al*., over-expression of SlWRKY53 gene can strengthen salt stress resistance of tomato plants[32]. Liu Shujun found that the same MYB transcription factor of tomato has different expression amount in different conditions: under different adverse and hormone stress, the expression amount of MYB transcription factor has significant changes and the inductive intensity is high, indicating that tomato MYB transcription factor participates in plant resisting environmental stress[33]. NAC transcription factor is unique to plants. NAC family gene plays extremely important role in plant growth and development and resisting biotic and abiotic stress. SISRN1, located in cell nucleus, is negative regulator of tomato resisting drought stress. After silencing, this gene can strengthen drought resistance ability of tomato[34]. Liu Hui cloned an NAC transcription factor from tomato LA1777, named it ShNAC, and low temperature, drought, and high salt stress can induce expression of this gene. Over-expression of ShNAC transgenic plants is more sensitive to low temperature and drought. ShNAC may be a negative regulator of plant growth and development and abiotic stress response[29]. Ma *et al* cloned an NAC transcription factor SlNAC1 from tomato leaves and found that over-expression of this gene strengthens low temperature resistance of tomato plants[35]. Many tests indicate that SlNAC1 may activate cold response gene and improve low temperature resistance through CBF1 expression[35]. Inducer of CBF expression 1 (ICE1) transcription factor may respond to low temperature signal, activate downstream COR (cold-regulated) gene expression through regulating CBF / DREB1 transcription factor, so as to regulate low temperature resistance ability of plants. Feng *et al* cloned a new ICE1 gene from tomato leaves, and found that over-expression of ICE1 and CBF transcription factor can improve low temperature resistance ability of transgenic plants, thus genes in regulating network in tomato CBF downstream may be a decisive factor leading to tomato sensitive to low temperature[36]. Zinc finger protein (ZIP) is a type of transcription factor richest in plants and studied most deeply and it plays a role of regulation in growth and development and adverse stress of all periods of plants. Some researches have indicated that over-expression of ZIP family SlZF6 can improve salt resistance and drought resistance of tomato[37].

7 Prospects

In sum, abiotic stress plays an extremely important role in influencing growth and development and various physiological indicators of tomato. Under different stress conditions, MDA and EC content in tomato tissue is correlated with stress degrees, while the change of anti-oxidant enzymes activity is different in different stress conditions. In recent years, exploration and researches of tomato stress tolerance genes have made certain achievements, but the responses of plant body to stress are quantity traits controlled by many genes. Thus, the exploration of single gene function is not able to clarify molecular mechanism of tomato stress response. At present, with issue of tomato genome-wide data[38], researches of tomato has formally entered times of Genomics. Therefore, the study on changes in expression of transcription group, protein group and metabolism group in tomato gene group and stress group using new generation high-throughput sequencing technology will be helpful for expounding molecular mechanism of tomato to abiotic stress response, to provide theoretical basis for stress tolerance breeding of tomato.

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regions should scientifically plan and strictly control new orchard development in accordance with ecological, climatic, soil, slope and water conditions, actively use slope farmland, high drainage field, and dry land to develop fruit industry, resolutely eliminate fruit planting in unsuitable areas, adjust and reduce planting in non-advantageous regions, and exit fruit planting in capital farmland, to provide sufficient place for grain production. (ii) Actively developing intercropping of fruit trees with grain crops and cash crops, and conducting vertical orchard planting. Suitable areas should develop vertical agriculture, full explore and use various resources, and increase agricultural resource utilization efficiency, land output rate, to realize harmonious coexistence of fruits with other crops. (iii) Promoting optimization of fruit tree structure. Under the condition of total fruit planting area not changed, it is recommended to properly reduce planting area of staple fruits, adjust planting area of apple, orange and pear to 50%, expand planting area of pineapple, mango, litchi, and longan, to satisfy diversified demands of consumers for fruits. (iv) Encouraging local skillful fruit farmers, leading enterprises and cooperatives to contract orchards, implement relatively centralized large scale production, specialized operation, and market-oriented operation. It is recommended to strengthen socialized services for process before the production, in the production and after the production, improve organizational level of fruit production, and actively popularize and develop mechanized operation in suitable regions, to reduce worker demands of orchard production.

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