

Research Progress on Waterlogging Tolerance of *Cucurbit* Crops

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Abstract As one of the most frequent natural disasters in China, flooding seriously affected the plant growth and development, decreased the yield and quality of *Cucurbit* crops seriously, and thus led to huge economic losses. Here, we reviewed the effects of waterlogging stress on root growth, respiration, leaf photosynthesis and reactive oxygen species metabolism in *Cucurbit* crops. In order to response to waterlogging, the plants promote the formation of adventitious roots mediated by ethylene, lower the aerobic respiration, and induce the activity of antioxidant enzymes and the synthesis of antioxidant substances. Moreover, we summarized the identification indexes of waterlogging tolerance such as the loss rate of chlorophyll. In addition, we reviewed the progress of genetic breeding for waterlogging tolerant cultivars from three aspects, including traditional breeding, molecular marker-assisted breeding and genetic engineering breeding. Besides, we highlighted the future research direction. The purpose of this review was to understand the mechanism of waterlogging tolerance and to provide a theoretical basis for the breeding of waterlogging resistant cultivars in *Cucurbit* plants.

Keywords *Cucurbit* crops; Waterlogging tolerance; Waterlogging stress

Global climate change causes frequent floods all over the world, which seriously affects the growth of crops. According to the report of the Food and Agriculture Organization of the United Nations (FAO) in 2007 (Setter et al., 2009), there were about 3×10^7 hm² of cultivated land damaged by waterlogging, and the crop yield was reduced by about 20%. About 2/3 of China's land area and 80% of cultivated land suffered from waterlogging, which increased year by year (Li, 2011). In the first three quarters of 2017, there were 39 regional rainstorms across China. Floods and geological disasters caused by floods led to a total of 4.78×10^6 hm² of crops affected across China, of which the crop failures were 7.37×10^5 hm², and direct economic loss of 1.74×10^{11} yuan (Liu and Ding, 2017). *Cucurbit* crops are important cash crops in China, which have a wide cultivation area and remarkable economic benefits. FAO report showed (<http://www.fao.org>) that the area of *Cucurbit* crops in China reached 2.91×10^7 hm² in 2018, mainly including cucumber, watermelon and muskmelon. In recent years, rotten melons and crop failures caused by rain and waterlogging has occurred from time to time, so waterlogging has become an important factor affecting the production of *Cucurbit* crops. At present, the waterlogging tolerance of rice, cotton, wheat and other field crops has been deeply studied, but the research on *Cucurbit* crops is still relatively weak. Therefore, deeply understanding of the waterlogging tolerance of *Cucurbit* crops and revealing its adaptation mechanism can provide a theoretical basis for the sustainable production of *Cucurbit* crops.

1 Effect of Waterlogging on Roots of *Cucurbit* Crops

1.1 Primary roots

Root system is the most direct and initial flooded part of plant. In the hypoxic environment, the respiration of roots is inhibited. With the extension of waterlogging time, some roots experience programmed cell death (PCD) and form ventilating tissue to adapt to the stress environment (He et al., 1996). Long-term hypoxia will lead to rust color of roots and eventually rot and die. Mi et al. (2018) conducted waterlogging experiments on waterlogging tolerant white gourd 'RW101' and sensitive white gourd 'SW15', and found that the original root system of 'SW15' was browning, easy to break and gradually lost its function after 72 h; After 96 h, about 50.0% of the plants decayed in the rhizosphere.

1.2 Adventitious roots

In order to adapt to the waterlogging environment, plants have evolved the mechanism of forming adventitious roots. In most species, adventitious roots induced by waterlogging have highly developed ventilating tissue, which can effectively reduce the resistance of oxygen transport from the shoot to the waterlogged roots and improve the ability of plants to tolerate hypoxia stress. Xu et al. (2018) conducted waterlogging experiments on the seedlings of waterlogging tolerant cucumber 'Zaoer-N' and sensitive cucumber 'Pepino', and found that after 7 day's waterlogging, a large number of adventitious roots appeared in the hypocotyl of 'Zaoer-N' and almost no adventitious roots were formed in the hypocotyl of 'Pepino'. Fang (2015) identified the waterlogging tolerance of 20 kinds of watermelon, screened out the waterlogging tolerant watermelon 'HD26' and the sensitive watermelon 'XFM', and found that the number of adventitious roots of 'HD26' was about 4 times than that of 'XFM'.

The participation of ethylene in hypoxia response is a key factor in the production of adventitious roots and formation of ventilating tissue. After 24 hours' waterlogging treatment, the content of ethylene in the hypocotyls of 'HD26' and 'XFM' was significantly higher than that in their respective control groups; When treated for 72 h, the ethylene release of waterlogging tolerant watermelon 'HD26' was significantly higher than that of 'XFM' (Fang, 2015). ACC synthase (ACS) in roots is activated under waterlogging conditions (Xu et al., 2014). The precursor of ethylene synthesis, 1-aminocyclopropane 1-carboxylic acid (ACC), is massively synthesized through ACS and concentrated in the hypocotyl. Under the joint action of O₂ and ACC oxidase (ACO), ethylene is generated and accumulated at the node, resulting in the death of epidermal cells covering the top of primordium and the formation of adventitious roots (Mergenmann and Sauter, 2000). In addition, after waterlogging treatment, the gene expression of *ACS* and *ACO* in waterlogging tolerant cucumber 'Zaoer-N' was up-regulated, the synthesis speed was accelerated, the synthesis and release of ethylene were promoted, and the damage to plants was reduced (Xu et al., 2017a).

Before waterlogging, most hypocotyls of dicotyledons do not have specific cells to form adventitious roots (Zhang et al., 2015). The formation of adventitious roots usually requires four key steps, namely cell dedifferentiation, cell division, adventitious root primordium growth and adventitious root elongation (Ahsan et al., 2007). Transcriptome analysis of *Solanum dulcamara* L. found that waterlogging affected multiple hormone signaling pathways such as auxin and activated dormant adventitious root primordia, such as the expression of root primordium auxin response genes *LBD16*, *LBD18*, *LBD29* and *PUCHI* (Dawood et al., 2016). The interaction between auxin and ethylene is an important factor in inducing the formation of adventitious root. After waterlogging, ethylene synthesis and response as well as auxin (IAA) transport and response in hypocotyl of waterlogging tolerant watermelon 'HD26' were stronger than those of sensitive watermelon 'XFM'; Exogenous IAA treatment with appropriate concentration can promote the synthesis of ethylene and formation of adventitious roots (Fang, 2015).

In addition, a large number of studies have shown that the expression of many genes related to the formation of adventitious roots is up-regulated after waterlogging. It was found that the cucumber calcium dependent protein kinase gene *CsCDPK5* is a waterlogging stress response gene and has the highest expression in the hypocotyl of cucumber, so it may be involved in the formation of adventitious roots in the hypocotyl of cucumber (Xu et al., 2016), and more than 27 000 transcripts were detected in the hypocotyl of cucumber, 1 494 and 1 766 genes of 'Zaoer-N' and 'Pepino' were differentially expressed 2 d after waterlogging (Xu et al., 2017b). Comparative analysis showed that genes related to carbohydrate mobilization, nitrate assimilation, hormone production and signal pathway, transcription factors and cell division may be involved in the formation of adventitious root primordia under waterlogging stress. After that, *QTLARN6.1*, the major gene of waterlogging tolerance, was found by the Bulk Segregant Analysis of the whole genome sequencing. This gene can promote the formation of 'Zaoer-N' adventitious roots and improve the waterlogging tolerance of plants (Xu et al., 2018).

2 Effects of Waterlogging on Respiration of Cucurbit Crops

After *Cucurbi* crops were flooded, the kurtosis in mitochondria disappeared, the contents gradually decreased, the activity of respiratory related enzymes decreased, the production of ATP decreased, the citric acid cycle (TCA)

was inhibited, and the aerobic respiration was weakened. After waterlogging stress, the activities of aerobic respiration related enzymes malate dehydrogenase (MDH) and succinate dehydrogenase (SDH) of muskmelon decreased, and the decrease range of sensitive muskmelon ‘Shijimi’ was larger than that of waterlogging tolerant muskmelon ‘Cuixi’ (Zhang et al., 2019). After waterlogging, the expression of genes involved in the citric acid cycle in cucumber roots, such as genes encoding pyruvate dehydrogenase, citrate hydrolase, isocitrate dehydrogenase, succinyl CoA ligase, succinate dehydrogenase and malate dehydrogenase decreased. After 8 hours’ waterlogging treatment, the gene expression of succinyl CoA ligase decreased by 66.1% (Qi et al., 2012).

Under anoxic conditions, the structure of proteins will change, some special proteins will be synthesized into anaerobic peptides (ANPs), and the respiratory pathway will be transformed from TCA to anaerobic fermentation. Although anaerobic respiration can be used as a temporary remedy for plants to maintain cell activity, long-term anaerobic respiration can not meet the needs of plants for energy and intermediate metabolites. At the same time, it will accumulate a large amount of ethanol and acetaldehyde, which will be toxic to plants. After 48 hours’ waterlogging of cucumber, the activities of alcohol dehydrogenase (ADH), pyruvate decarboxylase (PDC) and lactate dehydrogenase (LDH) were up-regulated, and the concentrations of ethanol, acetaldehyde and lactate increased. After the waterlogging stress was relieved, the content gradually decreased (Xu et al., 2014). In addition, relevant studies have found that the expression of genes involved in pentose phosphate and glyoxylate pathways first increased and then decreased after 8 hours’ waterlogging (Qi et al., 2012).

3 Effects of Waterlogging on Photosynthesis of *Cucurbit* Crops

After waterlogging stress, photosynthesis of *Cucurbit* crops decreased, and both stomatal and non-stomatal limitations played a role. In the early stage of waterlogging of cucumber (2 d), the stomata of leaves contracted or partially closed, the diffusion and exchange of O₂ and CO₂ were blocked, the intercellular CO₂ concentration and transpiration rate decreased, which showed stomatal limitation; After long-term waterlogging stress (10 d), the photosynthetic rate continued to decrease, the stomatal conductance recovered, the intercellular CO₂ concentration increased, and there was no significant difference in transpiration rate from the control group, which showed non-stomatal limitation (Barikman et al., 2019).

With the extension of waterlogging stress time, the activity of proteins related to photosynthesis in *Cucurbit* crops decreased, the synthesis of photosynthetic pigments was blocked (Zhu, 2014), the transportation of photosynthetic products slowed down, the formation of new leaves was inhibited, the abscission rate of old leaves accelerated, and the total leaf area of plants decreased (Kato-noguchi and Morokuma, 2007); At the same time, transpiration weakened, relative water content decreased, and leaves wilted in varying degrees (Lin et al., 2014). The activity of ribulose-1,5-bisphosphate carboxylase (Rubisco) was higher than that before treatment after 1 day’s waterlogging, but due to the decrease of CO₂ solubility in leaf cells, Rubisco’s affinity for CO₂ decreased and its activity decreased to a lower level (Liao and Lin, 1994). The contents of chlorophyll a, chlorophyll b, carotenoid and total chlorophyll of cucumber decreased after waterlogging (Barikman et al., 2019). In addition, the death of plants after waterlogging stress is directly related to the sharp decline of chlorophyll content. The stronger the chlorophyll preservation ability of plants, the less damage to physiological functions (Qi et al., 2011). At the same time, the expression of genes encoding photosystem II subunit S (*CU10576*), photosystem I psaG/psaK (*Contig885*) and ferredoxin (*CU9779*) are significantly down-regulated (Figure 1) (Qi et al., 2012).

4 Active Oxygen Metabolism

4.1 Production of reactive oxygen species

Under normal conditions, the production and clearance of reactive oxygen species (ROS) are in equilibrium. ROS mainly include O₂⁻, H₂O₂, OH⁻ (Asada, 1999; Dat et al., 2000) and NO (Lamattina et al, 2000). Under waterlogging stress, the root, stem and other root organs are subjected to hypoxia stress, the biochemical environment in the plant is changed, the aerobic respiration is inhibited, the electron transfer chain is blocked, and the excess electron reduces O₂, resulting in excessive O₂⁻, resulting in damage such as lipid membrane oxidation, hindered photopigment synthesis, DNA strand breakage and protein denaturation, affecting the normal growth of

the plant, and even causing plant death in severe cases. One of the main sources of ROS in plants is the reaction mediated by NAPDH oxidase, which converts O_2 to $O_2^{\cdot-}$ and produces H_2O_2 . Respiratory burst oxidase gene (*RBOH*) plays an important role in ROS mediated signal transduction, such as defense response, programmed cell death and plant development (Torres et al., 2002; Takeda et al., 2008). *RBOH* gene was significantly up-regulated in cucumber during waterlogging treatment (Qi et al., 2012).

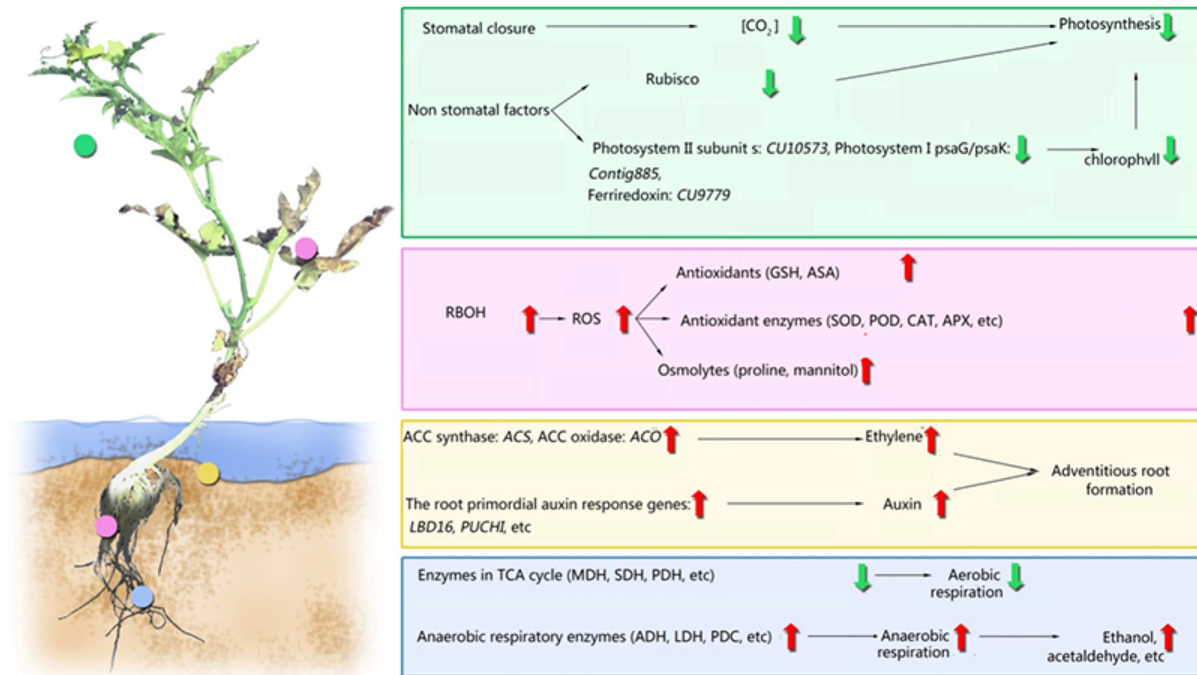


Figure 1 Physiological response of *Cucurbit* crops to waterlogging stress

Note: the green box: photosynthesis; the red box: reactive oxygen species metabolism; the yellow box: adventitious root formation; the blue box: respiration

4.2 Active oxygen removal

4.2.1 Antioxidant enzymes

After plants are stressed, endogenous enzyme systems play a role in scavenging reactive oxygen species, mainly including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), peroxidase (POD), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR) and so on (Blokhina et al., 2003). At the beginning of waterlogging, the SOD activity of watermelon leaves decreased, the content of ROS increased, and the activities of SOD and POD increased; With the deepening of waterlogging stress, the content of ROS further increased, malondialdehyde accumulated, the activity of protective enzyme decreased, and plasma membrane was damaged (Liu et al., 2016). After waterlogging stress, the expression of *APX* was up-regulated, the enzyme activity was increased, and the scavenging capacity of reactive oxygen species was enhanced (Chih et al., 2014). Similar results were found in the study on white gourd (Lin et al., 2013).

4.2.2 Antioxidants

Antioxidants are an important part of the active oxygen scavenging system, mainly including ascorbic acid (ASA), glutathione (GSH), α -tocopherol et al. (Apel and Hirt, 2004). Ascorbic acid and glutathione play an important role in ROS clearance. They can not only directly remove ROS, but also participate in ROS clearance as substrates of enzymes; At the same time, it can also participate in the regeneration of antioxidants, such as ASA acting as reducing agents in the regeneration cycle of α -tocopherol and zeaxanthin. Relevant studies have found when the roots of non-heading Chinese cabbage seedlings were under short-term waterlogging stress, the contents of ASA and GSH were significantly higher than those in the control group (Guo et al., 2015).

4.2.3 Osmolytes

Osmolytes in plants mainly include inorganic ions and organic solutes, such as polyols and nitrogen-containing compounds. A large number of studies have shown that osmoregulation substances have a certain impact on the scavenging of reactive oxygen species. For example, proline and mannitol can scavenge ROS (Liang et al., 2018; Geng et al., 2011), and Ca^{2+} can improve the activity of antioxidant enzymes (Shen et al., 1997). After being flooded, the content of free proline in cucumber increased significantly. After 10 days' treatment, the content of free proline increased by 58.9%, indicating that under the short-term waterlogging environment, the free proline in the plant accumulated rapidly to remove hydroxyl radical, reduce cell osmotic potential and alleviate the damage of waterlogging to the plant (Barikman et al., 2019).

5 Identification Index of Waterlogging Tolerance of *Cucurbit* crops

At present, there is no unified standard for the identification of waterlogging tolerance of *Cucurbit* crops. Various morphological, physiological and biochemical indexes of flooded crops are used as the standard for the identification of waterlogging tolerance, including single index identification and compound multiple index analysis and identification. Chen (2009) found that there was a significant positive correlation between mortality and chlorophyll loss rate, with a correlation coefficient of 0.4051, and chlorophyll loss rate was taken as an index of waterlogging tolerance, the waterlogging tolerance of 40 cucumber germplasm resources was comprehensively evaluated. Due to the low correlation of single index, researchers tend to use multi factor membership function to identify the waterlogging tolerance of *Cucurbit* crops. Qi et al. (2011) comprehensively evaluated the waterlogging tolerance of 40 cucumber germplasm resources of 6 ecological types based on the average membership function values of 5 indexes, that is, plant mortality, chlorophyll loss rate, SOD growth rate, POD loss rate and CAT growth rate.

6 Genetic Breeding Study on Waterlogging Tolerance of *Cucurbit* Crops

6.1 Conventional breeding

Cultivating new varieties is the most direct and effective method to improve the waterlogging tolerance of *Cucurbit* Crops. Martin et al. (2008) studied the genetic law of waterlogging tolerance in early growth stage of cucumber through two cucumber parents 'pw00832' (waterlogging tolerance) and 'pw0801' (sensitive), and conducted a one-week waterlogging test on plants of P₁, P₂, F₁, F₂, B₁ and B₂ generations. Super parental segregation was observed in most waterlogging tolerance traits of F₂ generation, and the estimated values of tolerance score and narrow heritability of adventitious root formation were high. The backcross of F₁ parents showed good gene fusion, indicating that selecting super parent population in this hybrid combination can breed varieties with high tolerance.

6.2 Molecular marker assisted breeding

Marker assisted selection (MAS) can be used as a useful additional tool in plant breeding to optimize selection efficiency (Dwivedi et al., 2007). Song et al. (2013) hybridized waterlogging tolerant gourd 'JZS' with sensitive gourd 'T2002' to obtain F₂ population. Using bulked segregant analysis (BSA), combined with random amplified polymorphic DNA marker (RAPD) and simple sequence repeat marker (SSR), a molecular marker related to gourd waterlogging tolerance (S87/88) was screened. Xu (2017) constructed a genetic linkage map consisting of 149 simple sequence repeat markers spanning 550.8 cM and divided it into 7 linkage groups. Three QTLs related to waterlogging tolerance (*ARN3.1*, *ARN5.1*, *ARN6.1*) distributed on chromosomes 3, 5 and 6 were identified by complex interval mapping method. Among them, the main effect QTL (*ARN6.1*) was located between *SSR12898* and *SSR04751*. By using 5 single nucleotide polymorphism (SNP) markers, *ARN6.1* was reduced to 0.79 Mb and marked by *SSR12898* and *SNP25558853*.

6.3 Genetic engineering of waterlogging tolerant *Cucurbit* crops

Some waterlogging tolerant genes were introduced into plants through genetic transformation to obtain waterlogging tolerant materials. Xia (2015) found that after waterlogging treatment, the relative expression of *CmHSP83* gene in waterlogging tolerant muskmelon 'M19' was significantly higher than that in sensitive

muskmelon ‘M63’, so it was speculated that this gene may be related to waterlogging tolerance of muskmelon; Through bioinformatics analysis of *CmHSP83* gene, it was found that the gene had high homology and conservation with *HSP90* family genes of different species, belonging to *HSP90* family; *CmHSP83* was introduced into ‘M63’ by agrobacterium mediated method to obtain waterlogging tolerant transgenic plants. Xu et al. (2018) transferred the waterlogging tolerance related gene *ARN6.1* into wild cucumber Pepino’ to obtain transgenic plants. It was found that under waterlogging conditions, the number of adventitious roots of the transgenic cucumber was significantly increased compared with the wild cucumber.

7 Progress

In recent years, China’s weather and climate situation is complex, with frequent rainstorms, high overlap and strong extremes, which has seriously affected the growth, yield and quality of *Cucurbit* crops and caused a certain degree of economic losses. However, at present, researchers mostly reduce the damage caused by waterlogging stress from the aspect of cultivation management, and there is less research on the waterlogging tolerance of *Cucurbit* crops. Therefore, it is an urgent problem to determine the waterlogging tolerance phenotype of *Cucurbit* crops and breed waterlogging tolerant *Cucurbit* varieties. Future research should combine plant physiology, molecular biology and genetics, comprehensively analyze the waterlogging tolerance mechanism of *Cucurbit* crops, determine the rapid identification method of waterlogging tolerance, screen waterlogging tolerance related genes through whole gene association analysis, and obtain varieties with strong waterlogging tolerance based on gene editing, hybridization and other technologies, so as to provide theoretical basis and technical support for the sustainable production of *Cucurbit* crops.

Authors’ Contributions

ZJW was the executor of this study and completed the first draft of the manuscript; HY was the designer and person in charge of the project, guiding the writing and revision of the manuscript. Both of the authors read and approved the final manuscript.

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References

- Ahsan N., Lee D.G., Lee S.H., Kang K.Y., Bahk J.D., Choi M.S., Lee I.J. Renaut J., and Lee B.H., 2007, A comparative proteomic analysis of tomato leaves in response to waterlogging stress, *PlantPhysiol.*, 131(4): 555-570
<https://doi.org/10.1111/j.1399-3054.2007.00980.x>
PMid:18251847
- Apel K., and Hirt H., 2004, Reactive oxygen species: metabolism oxidative stress and signal transduction, *Annual Review of Plant Biology*, 55: 373-399
<https://doi.org/10.1146/annurev.arplant.55.031903.141701>
PMid:15377225
- Asada K., 1999, The water-water cycle in chloroplasts: scavenging of active oxygens and dissipation of excess photons, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 50: 601-639
<https://doi.org/10.1146/annurev.arplant.50.1.601>
PMid:15012221
- Barikman T.C., Simpson C.R., and Sams C.E., 2019, Waterlogging causes early modification in the physiological performance, carotenoids, chlorophylls, proline, and soluble sugars of cucumber plants, *Plants*, 8(160): 1-15
<https://doi.org/10.3390/plants8060160>
PMid:31181725 PMCID:PMC6630288
- Blokhina O., Virolainen E., and Fagersterstedt K.V., 2003, Antioxidants, oxidative damage and oxygen deprivation stress: a review, *Annals of Botany*, 91(2): 179-194
<https://doi.org/10.1093/aob/mcf118>
PMid:12509339 PMCID:PMC4244988
- Chen R.F., 2009, The Waterlogging tolerance evaluation and preliminary QTL mapping of traits associated with waterlogging tolerance of cucumber, Thesis for M.S., Yangzhou University, Supervisor: Chen X.H., pp.21-28
- Chih M.C., Kuo W.S., and Lin K.H., 2014, Cloning and gene expression analysis of sponge gourd sscorbate peroxidase gene and winter squash superoxide dismutase gene under respective flooding and chilling stresses, *Horticulture, Environment, and Biotechnology*, 55(2): 129-137
<https://doi.org/10.1007/s13580-014-0116-4>

- Dat J., Vandennebee S., Vranová E., Montagu M.V., Inzé D., and Breusegem F.V., 2000, Dual action of the active oxygen species during plant stress responses, *Cell. Mol. Life Sci.*, 57(5): 129-137
<https://doi.org/10.1007/s13580-014-0116-4>
- Dawood T., Yang X.P., Visser J.W.E., Beek T.A.H.T., Kensch P.R., Cristescu S.M., Lee S., Floková K., Nguyen D., Mariani C., and Rieu I., 2016, A co-opted hormonal cascade activates dormant adventitious root primordia upon flooding in *Solanum dulcamara*, *Plant Physiol.*, 170(4): 2351-2364
<https://doi.org/10.1104/pp.15.00773>
PMid:26850278 PMCid:PMC4825138
- Dwivedi S.L., Crouch J.H., Mackill D.J., Xu Y.B., Blair M.W., Ragot M., Upadhyaya H.D., and Ortiz R., 2007, The molecularization of public sector crop breeding: progress, problems and prospects, *Advances in Agronomy*, 95(7): 163-318
[https://doi.org/10.1016/S0065-2113\(07\)95003-8](https://doi.org/10.1016/S0065-2113(07)95003-8)
- Er B.B., Wu F.F., Xie L.L., Dai X.Z., and Zhou H.X., 2018, Differences in morphological structure and physiological response of wax gourd seedlings under waterlogging stress (*Journal of Southern Agriculture*), 49(12): 2419-2424
- Fang B.S., 2015, Identification of waterlogging tolerance and its mechanism of different watermelon varieties, Thesis for M.S., Zhejiang University, Supervisor: Zhang M.F., pp.15-48
- Geng H., Wang S.L., Guo L., and Han X.D., 2011, Effect of mannitol on wheat germination and seedling growth under seawater stress, *Jiyinzuxue yu Yingyong Shengwuxue (Genomics and Applied Biology)*, 30(2):218-223
- Guo X.X., Li X.F., Zhu H.F., Zhu Y.Y., and Liu J.P., 2015, Effects of waterlogging stress on ascorbate-glutathione cycle in *Brassica campestris* ssp. chinensis, *Zhiwu Shengli Xuebao (Plant Physiology Journal)*, 51(12):2181-2187
- He C.J., Morgan P.W., and Drew M.C., 1996, Transduction of an ethylene signal is required for cell death and lysis in the root cortex of maize during aerenchyma formation induced by hypoxia, *Plant Physiol.*, 112(2): 463-472
<https://doi.org/10.1104/pp.112.2.463>
PMid:12226403 PMCid:PMC157969
- Kato-Noguchi H., and Morokuma M., 2007, Ethanolic fermentation and anoxia tolerance in four rice cultivars, *Journal of Plant Physiology*, 164(2): 168-173
<https://doi.org/10.1016/j.jplph.2005.09.017>
PMid:16483690
- Lamattina L., García-Mata C., Graziano M., and Pagnussat G., 2003, Nitric oxide: the versatility of an extensive signal molecule, *Annual Review of Plant Biology*, 54(1): 168-173
<https://doi.org/10.1016/j.jplph.2005.09.017>
PMid:16483690
- Li S.Y., 2011, The cause types of flood disaster in China and the counter measures for flood control and disaster reduction, *Zhongguo Xinjishu Xinchangping (China New Technologies and Products)*, (1): 253-254
- Liang L.N., Liu X., Tang X., Wen Y.K., Si H.J., and Zhang N., 2018, Effect of drought stress on physiological and biochemical indexes of potato leaves, *Jiyinzuxue yu Yingyong Shengwuxue (Genomics and Applied Biology)*, 37(3): 1343-1348
- Liao C.T., and Lin C.H., 1994, Effect of flooding stress on photosynthetic activities of momordica charantia, *Plant Physiology and Biochemistry*, 32(4): 479-485
- Lin K.H., Kuo W.S., Chiang S.M., Hsiung T.C., Chiang M.C., and Lo H.F., 2013, Study of sponge gourd ascorbate peroxidase and winter squash superoxide dismutase under respective flooding and chilling stresses, *Scientia Horticulture*, 162(8): 333-340
<https://doi.org/10.1016/j.scienta.2013.08.016>
- Lin Y., Zhang W., Qi F., Cui W.T., Xie Y.J., and Shen W.B., 2014, Hydrogen-rich water regulates cucumber adventitious root development in a heme oxygenase-1/carbon monoxide-dependent manner, *Plant Physiology*, 171(2): 1-8
<https://doi.org/10.1016/j.jplph.2013.08.009>
PMid:24331413
- Liu N.J., and Ding Y., 2007, Analysis of natural disasters in the first three quarters of 2017, *Zhongguo Jianzai (Disaster Analysis)*, (21): 58-61
- Liu W.G., Yan Z.H., Wang C., and Zhang H.M., 2016, Response of antioxidant defense system in watermelon seedling subjected to waterlogged stress, *Guoshu Xuebao (Journal of Fruit Science)*, 23(6): 860-864
- Martin A.Y., Chen X.H., Liang G.H., Gu M.H., and Xu C.W., 2008, Inheritance of waterlogging tolerance in cucumber, *Euphytica*, 162(1): 1-8
<https://doi.org/10.1016/j.jplph.2013.08.009>
PMid:24331413
- Mergenmann H., and Sauter M., 2000, Ethylene induces epidermal cell death at the site of adventitious root emergence in rice, *Plant Physiol.*, 124(2): 609-614
<https://doi.org/10.1104/pp.124.2.609>
PMid:11027711 PMCid:PMC59167
- Qi X.H., Chen R.F., and Xu Q., 2011, Preliminary analysis of cucumber submergence tolerance at seedling stage, *Zhongguo Shucai (China Vegetables)*, 31(4): 23-28
- Qi X.X., Xu X.W., Lin X.J., Zhang W.J., and Chen X.H., 2012, Identification of differentially expressed genes in cucumber (*Cucumis sativus* L.) root under waterlogging stress by digital gene expression profile, *Genomics*, 99(3): 609-614
<https://doi.org/10.1104/pp.124.2.609>
PMid:11027711 PMCid:PMC59167

- Setter T.L., Waters I., Sharma S.K., Singh K.N., Kulshreshtha N., Yaduvanshi N.P.S., Ram P., Singh B.N., Rane J., McDonald G., Khabaz-Saberi H., Biddulph T.B., Wilson R., Barclay I., McLean R., and Cakir M., 2009, Review of wheat improvement for waterlogging tolerance in Australia and India: the importance of anaerobiosis and element toxicities associated with different soils, *Annals of Botany*, 103(2): 609-614
<https://doi.org/10.1104/pp.124.2.609>
PMid:11027711 PMCID:PMC59167
- Shen B., Jensen R.G., and Bohnert H.J., 1997, Mannitol protects against oxidation by hydroxyl radicals, *Plant Physiology*, 115(2): 527-532
<https://doi.org/10.1104/pp.115.2.527>
PMid:12223821 PMCID:PMC158511
- Song H., Zhang X.Q., Gao X., and Wang M.H., 2013, Inheritance of waterlogging tolerance and molecular marker linked to related root trait in bottle gourd, *Huabei Nongxuebao (Acta Agriculture Boreali-sinica)*, 28(4): 65-68
- Takeda S., Gapper C., and Kaya H., 2008, Local positive feedback regulation determines cell shape in root hair cells, *Science*, 319(5867): 1241-1244
<https://doi.org/10.1126/science.1152505>
PMid:18309082
- Torres M.A., Dangl J.L., and Jones J.D.G., 2002, Arabidopsis gp91^{phox} homologues *AtrbohD* and *AtrbohF* are required for accumulation of reactive oxygen intermediates in the plant defense response, *Proc. Natl. Acad. Sci. USA*, 99(1): 1241-1244
<https://doi.org/10.1126/science.1152505>
PMid:18309082
- Xia X.X., 2015, Cloning of the melon' *CmHSP83* gene and genetic transformation, Thesis for M.S., Huazhong Agriculture University, Supervisor: Wang L.P., pp.12-62
- Xu X.W., Chen M.Y., Ji J., Xu Q., Qi X.H., and Chen X.H., 2017a, Comparative RNA-seq based transcriptome profiling of waterlogging response in cucumber hypocotyls reveals novel insights into the de novo adventitious root primordia initiation, *BMC Plant Biology*, 17(1): 129
<https://doi.org/10.1186/s12870-017-1081-8>
PMid:28747176 PMCID:PMC5530484
- Xu X.W., Ji J., Lu L., Qi X.H. and Chen X.H., 2016, Cloning and expression analysis of cucumis sativus calcium-dependent protein kinase 5 gene (*CsCDPK5*) under waterlogging stress, *Yuanyi Xuebao (Acta Horticulturae Sinica)*, 43(4): 704-714
- Xu X.W., Ji J., Xu Q., and Chen X.H., 2017b, Inheritance and quantitative trait loci mapping of adventitious root numbers in cucumber seedlings under waterlogging conditions, *Molecular Genetics and Genomics*, 292(2): 353-364
<https://doi.org/10.1007/s00438-016-1280-2>
PMid:27988808
- Xu X.W., Ji J., Xu Q., Qi X.H., Weng Y.Q., and Chen X.H., 2018, The major-effect quantitative trait locus CsARN6.1 encodes an AAA ATPase domain-containing protein that is associated with waterlogging stress tolerance by promoting adventitious root formation, *The Plant Journal*, 93(5): 917-930
<https://doi.org/10.1111/tpj.13819>
PMid:29315927
- Xu X.W., Wang H.H., Qi X.H., Xu Q., and Chen X.H., 2014, Waterlogging-induced increase in fermentation and related gene expression in the root of cucumber, *Scientia Horticulturae*, 179(10): 917-930
<https://doi.org/10.1111/tpj.13819>
PMid:29315927
- Zhang X.C., Shabala S., Koutoulis A., Shabala L., Johnson P., Hayes D., Nichols D.S., and Zhou M.X., 2015, Waterlogging tolerance in barley is associated with faster aerenchyma formation in adventitious roots, *Plant and Soil*, 394(1-2): 355-72
<https://doi.org/10.1007/s11104-015-2536-z>
- Zhang Y.P., Diao Q.N., Zhang W.X., Tian S.B., Xu S., and Fan H.W., 2019, Effects of flooding and stress relief on physiological metabolism of muskmelon seedlings, *Zhongguo Shucai (China Vegetables)*, 39(11): 41-48
- Zhu J., 2014, Effects of waterlogging stress on the growth of loofah seedlings, *Hubei Nongye Kexue (Hubei Agricultural Sciences)*, 53(9): 2067-2069