Journal of Cereal Research

Volume 15 (2): 170-176

Homepage: http://epubs.icar.org.in/ejournal/index.php/JWR

Review Article

Role of Cytokinins and Gibberellins in Crops response to Heat and Drought stress

Anukriti Srivastava and Girish Chandra Pandey

Dept. of Bioscience & Biotechnology, Banasthali Vidyapith, Banasthali, Rajasthan

Article history:
Received: 03 Mar., 2023
Revised: 31 Jul., 2023
Accepted: 18 Aug., 2023

Citation:

Srivastava A and GC Pandey. 2023. Role of Cytokinins and Gibberellins in Crops response to Heat and Drought stress. *Journal of Cereal Research* ***15 (2):*** *170-176. http://doi.org/10.25174/2582-2675/2023/136065*

****Corresponding author:***
E-mail: girishchandrapandey@banasthali.in

Abstract

Drought and Heat work together as a coupled form of stresses from abiotic components that decline crop production and create global food insecurity under changing climatic regime. Plants have evolved dynamic morphological, anatomical and syntheticresponses thatenable them to resist heat and drought stress. Even minor heat and drought stress can have a detrimental impact on crop productivity. Currently, the rise in the temperature and drought has been proven by research to affect agricultural yields by as much as 40%. Abiotic stresses cause plants to activate a genetic programme that favours survival through the development of robust adaptation mechanisms. Cytokinins and Gibberellins are plant hormones that control a variety of biological processes, including growth and development. Cytokinins and gibberellins have been discovered for their key function in plant responses to heat stress. Under heat stress, leaf cooling is performed by increased transpiration. Cytokinins play a vital part in this reaction by promoting stomatal opening, which aids in transpiration.There are various proteins that response to heat for example- sHSPs and GLY-rich proteins,are activated by cytokinins under thermal stress. The use of cytokinins enhances thermo-tolerance by lowering the rates of abortion in flowers. The hindrance of heat stress is induced in seed germination and its growth is alleviated by exogenous application of gibberellins. Accordingto a recent study, cytokinins have apart in osmotic stress adaptations with increased plant growth and production, while gibberellin plays a key function as growth hormone and confers heat and drought stress tolerance in crops. The external application and propagation of diverseplant hormones at optimal can help to reduce thermal stress and protect agriculture in adversechange in climate. Because the development of stress tolerance necessitates the activation of hormone-responsive genes in a specific tissue, and hence targeted modification of the plant hormone pool has a better efficacy for modulating plant responses to heat stress.

Phytohormones play a crucial role in imparting heat and drought resistance, establishing a part for a hormone in preserving crop production from heat and drought stress may playimportant role in breeding programs as well as field application of phytohormones.

Keywords: Cytokinins, Gibberellins, Crops, Heat and Drought stress

1. Introduction

According to a recent UN estimate, the world's inhabitation is predicted to grow by 2 billion people over in the next 30 years, from 7.7 billion now to 9.7 billion in 2050(World population prospects 2019). Climate sensitivity of global crop production can face an enormous threat to global food production and food security, particularly if precipitation and adverse temperature regimes, as well as an improve in the number of extreme events such as, droughts, heat waves, storms and floods would occur (Rosenzweig *et al.,* 2001). Agriculturalsector faces a colossal environmental pressure across the world. Elicit from certain figures the environmental factors specifically water scarcity and raise in temperature are responsible for the declination of crops.

Global climate change will increase global average temperature by 2 to 4°C, according to an IPCC report (IPCC Inter-governmental Panel on Climate Change 2007:Impacts, adaptation and vulnerability) Due to elevated anthropogenic activities, the alteration in weather will again elevate and willclearlyhave an effect on the agriculture region as that is frequently being greater vulnerable to weather changes (Abbas, 2013).

In the cell cycle,cytokinins associated Gibberellins are vital sorts of phytohormones that have been discovered for a crucial role and have an effect on the expansion and development of plants. A growing body of evidence suggests that cytokinins can exacerbate the damage to plants caused by a variety of abiotic stress (Mi *et al.,* 2017; Keshishian *et al.,* 2018; Prerostova *et al.,* 2018).

By encouraging osmotic adjustment and inhibiting cell division and proliferation, endosperm growth, photosynthetic reserve, and apical shoot meristem development, cytokinins (CKs) support water deficiency conditions (Kumar *et al.,* 2021).The key positive and negative signalling components were discovered as a result of molecular genetic studies of cytokinin (CK) detection and signalling.CK binds to His-kinase receptors causing them to auto- phosphorylation. Over the last 20 years, substantial research has been conducted on the role of CK in plant response to environmental stresses such as drought.Arabidopsis plants with mutations in the central CK biosynthesis gene, isopentenyl transferase (IPT), exhibit better survival rate in case of water stress. Likewise, mutations in CK signaling components – His- kinase receptors, His phosphotransferase proteins and Type B RR – exhibit increased tolerance to drought.

On the other hand, in some cases, GA signallingis also associatedwith stress tolerance. The relationship between GA status and drought tolerance was investigated by comparing mutant lines of *Arabidopsis thaliana* with varied degrees of GA shortage or over-accumulation. The functional mechanisms of cytokinins and gibberellins, as well as their importance in heat and drought resistance in plants, are discussed in this article.

2. Mechanical response of Cytokinin to Stresses

Heat Stress

The main plant hormone that regulates several growth and development aspects is cytokinin.The involvement of cytokinin in many developmental processes has been carefullycharacterised, as is widely known but its effect on stress tolerance in plants remaininconsistent. This might be because of the complicated relationship between cytokinin and str ess signalling specifically the response to abiotic stress tolerance(Zwack and Rashotte, 2015). Cytokinins and GA are antagonistic in several developmental stages.Despite the fact thatmost research clearly implies AG-regulatory cytokinin activity, evidence for cytokinin AG-regulatory action cannot be overlooked. Cytokinins suppress GA-dependent hypocotylextension and serration in tomatoes (Fleishon *et al.,* 2011).

Cooling leaf is crucial for plants to minimize heat injuries by performing photosynthesis. The amplification of transpiration level under the heat stresscan cool down the leaves. In this intervention,by promoting evaporation, cytokinins haveacrucial role infuelling upthe opening of pores.Cytokinins can induce a variety of heating reactive proteins, including small heat shock proteins (sHSPs) and heat stress proteins.

The overexpression of the cytokinin biosynthetic gene (IPT) increases the endogenous cytokinin level that enhances the tolerance of the heat stress in the grasses (Xing *et al.,* 2009).

Heat stress has the greatest negative impacts during reproductive stage, particularly during the anthesis period, as previously noted (Pandey *et al.,* 2019). The flower will abort if the plant is stressed during anthesis, resulting in a considerable yield loss.

For example, revelation of the primary flower of the edible fruit *Passiflora* (granadilla) to high surrounding temperatures induces termination of the whole flower (Sobol *et al.,* 2014). Twophytohormones such as GA and cytokinins play distinct parts in this disease.Treatment with GA 3 induced termination of flowers, but treatment of cytokinins improved heat tolerance by lowering the rate of abortions in flowers.Furthermore, heat-tolerant edible fruit genotypes have been demonstrated to have large quantities of cytokinin in their leaves.

Transgenic plants with low cytokinin content were vulnerable to heat stress in *Arabidopsis,*whereas transgenic plants with high cytokinin content displayed improved thermal resistance tolerance during flowering.The important fact is, heat resistant edible fruit genotypes havebeen shown to contain high levels of cytokinin in their leaves.Furthermore, the introductionof exogenous cytokinins in wild-type Arabidopsis plants has shown that cytokinins have adefence function against high air temperature during flower formation.In order to improve heat tolerance, cytokinin may lower endogenous GA levels otherwise; it will only alter the GA signalling pathway's downstream branches, with no effect on active GA levels (Fleishon *et al.,* 2011; Sobol *et al.,* 2014). Despite this, the defensive impact of cytokinin is rather inconsistent when contrasted to its role in other conditions such as drought. *Arabidopsis* contains low cytokinin mutants that are more resistant to water stress, implying that low cytokinin levels can boost ABA susceptibility, hence improving drought tolerance in plants (Nishiyama *et al.,* 2011).

Studies have disclosed that the quickreceiving of thermal stimuli and its followingsignal transduction are important for the rapid enabling of plant defences. These processes, however, are mediated by a complicated signalling network in which phytohormones play a key role. For example, heat stress fuel up the HSF current, with HSFA2 serving as the primary regulator of HSR (Liu and Charng, 2013). The various genes expression in HSP synthesis and other molecular processes are rapidly regulated by HSF activation. There are many genes involved in HSP production act as molecular chaperones, inhibiting protein break-down (Mittler *et al.,* 2012).In the case of Arabidopsis, thermal stress has a significant impact on the plant's biological response, whether it is applied to the entire plant or to certain parts such as shoots and roots (Dobra *et al.,* 2015). Endogenous phytohormones such as cytokinin are thought to have a role in these reactions. When the stressed organelle was exposed to thermal stress, the transcription levels of the HSFA2 and thermal stress related protein 32kD(HSA32) genes were quickly induced.

On the other hand, at least 2 h after non-stressed organs are exposed to heat, the concentrations of ABA and active cytokinin are gradually reduced, while leaves release more active cytokinin,moreover, heat stress inflicted on a neighbourhood of the plant prompts the expression of components of the cytokinin signaling pathways. Therefore, these changes are related to the stimulation of transpiration.Plants also react to heat stress by increasing cytokinin level that are active and up-regulating genes that are required in photosynthesis andglycolysis until the strain becomes severe (Dobra *et al.,* 2015).

Drought stress

Drought may have a number of negativeimpacts on plant physiological activitiessuch as reduced photosynthesis, decreased crop production, hastened senescence and others (Liu *et al.,* 2012; Zheng *et al.,* 2017; Chen *et al.,* 2010).

The prospect of enhancing drought tolerance in plants by modulating cytokinin levels is directly proportional to the length of the stress, soil water potential, and pace of transpiration (Veselov *et al.,* 2017). The up-regulationas well as down regulation of endogenous cytokinin in response to drought has improved the drought tolerance (Zhang *et al.,* 2018; Werner *et al.,* 2010).The research stated that in the period of drought stress, the build-up of endogenous cytokinin is decreased (Calvo-Polanco *et al.,* 2019)and this limitation can improve the drought tolerance through various anatomical reactions such as closing of stomata (Naidoo *et al.,* 2018)early leaf maturation, and leaf excision (Rivero *et al.,* 2009 ; Xu *et al.,* 2016; Shen *et al.,* 2014). Since cytokinin is an adverse modulator of root growth in plants and bifurcation of branchesby boosting the break-down of cytokinin in the root, it can generate plant with a larger root system, promote the basis to shoot ratio, and show persistent drought tolerance (Pospisilova *et al.,* 2016; Ramireddy *et al.,* 2018).

Over-expression of CKX helps in down-regulation of cytokinin (Werner *et al.,* 2010)due to this, plant growth tends to slower in rate and drought tolerance of *Arabidopsis*

(Werner *et al.,* 2010; Nishiyama *et al.,* 2011), chickpea (Khandal *et al.,* 2020), tobacco (Mackova *et al.,* 2013) and barley (Pospisilova *et al.,* 2016; Ramireddy *et al.,* 2018) and content of protective compounds such proline and betaine are increased .Several mutant genotypes (ipt 1,3, 5 and 7) in *Arabidopsis* also display a reduced endogenous cytokinin content and increased drought tolerance (Nishiyama *et al.,* 2011).

3. Mechanical Response of Gibberellins to Stress

Heat Stress

Gibberellins (GAs) are a category of natural diterpenoids that has been discovered for its importance in seed germination and its growth, blooming induction, and fruit formation in plants. (Sun and Gubler, 2004).The degradation of DELLA protein induces the GA-mediated growth promotion. As stated before, GA is also required in retaliation of plants to thermal stress. Heat exposure for 3 hours at 50°C has a significant effect on *Arabidopsis* seed germination and growth. Exogenous treatment of GA 3 (50 µM) inhibits heat stress induced suppression of seed germination and its growth (Alonso-Ramirez *et al.,* 2009).

GA inhibits seed germination and seedling development in heat-stressed seedlings through changing SA production and signalling. GA 3 - or the over-expression of GASA-mediated Fs causes enhanced heat tolerance and SA accumulation in Arabidopsis under heat stress.

The fact is properly devised that quick lengthening of the stem is a flexible retaliation of plants to high surrounding climate. Repressed GA production in *Arabidopsis* deals with hypocotyl elongation influenced by high temperatures, demonstrating that quick GA amendment is crucial for hypocotyl elongation driven by high temperatures in addition to auxin. The BR pathway is also required at a later stage of growth. Furthermore, the PIF4 action at post-translational levels under high temperature is promoted by GA pathway (Stavang *et al.,* 2009).

The blooming season is important for structuring the life cycle of plants as well as for speciesinvolved in pollination. In higher plants, hot temperatures speed up the flowering transition, while this acceleration in flowering depends on the flowering plant .PIF4 activates FT under heat, facilitating transition in flowers. The breakdown of DELLA protein, which causes PIF4 activity, is energised by phytohormonal AG whereas PIF4 can turn on FT via a plausible process in which GA levels influence blooming (Kumar *et al.,* 2012).

Drought Stress

In plants, symptoms of GA deficiency and drought stress can appear phenotypically similar. During prolonged drought, the height in plants reduced including flowering and reduction in gibberellins content produces dwarfed plants with reduced plants organ including fruit set (Olimpieri *et al.,* 2011; Vettakkorumakankav *et al.,* 1999).

The dry weight of the plants could be decreased by 30% in some cultivars of Barley due to drought stress andthe cells tend to expand and developed slowly (Vettakkorumakankav *et al.,* 1999). Gibberellins can induce elongation and development in stem to offset the drought symptoms to an extent but application of gibberellins does not remedy the negative effects of long term drought.This clearly shows that the down-regulation in the expression of genes involvedin gibberellins biosynthesis and there is reduced production of GA 20-oxidase enzymes (Zeevaart *et al.,* 1993).The results suggest that during drought stress, there is down regulation of gibberellin biosynthesis by plants in order to prevent aggressive growth.

As water availability decreases due to the drought stress, gibberellins can be reduced and that leads to decline in stem elongation (Liu and Charng, 2013). Reduction of GA production is advantageous for plantings because dwarfed plants can easily tolerate and survive in stressed conditionsand dwarfism in plants is reported as more suitable for environments where drought and heat stress occur more frequently (Vettakkorumakankav *et al.,*1999). Also, compact size plants can be denser and have better efficiency of resources during drought stress.

4. Hormone responsive protein mediated stress responses

Phytohormonesandsome proteinsplayanefficient role, as these can be used for communication in plant stress hormone. The domain containing proteins C1-(cysteine rich protein family) aresaid to play a rolein plant hormone-mediated stress responses (Bhaskar *et al.,* 2015).

The C1-clan protein family is involved in hormone-mediated stress repair, according to a study published in the several journals. There are 72 other kinds of proteins in *Arabidopsis* that included all three distinct signature domains.

Conclusion and future prospects

As a result of global change in climatic conditions the crop yields are expected to be adversely effected by heat and drought conditions in coming days. Therefore, to understand the mechanical functions required in plant resistance to drought and heat stress is significant. The development of new varieties with improved heat tolerance will cut down negative effects of heat stress. Modification of plant hormones via breeding or exogenous treatment of various plant hormones at an appropriate dose may aid in the management of heat and drought stress and hence assisting crop production in the climatic changes. It is important to understand that genes which are hormone responsive are activated in a certain tissue is important for inducing the stress tolerance and that's why plant hormones are exposed to alteration toimprove their efficacy in controlling plant response to heat and drought stress.

Compliance with ethical standards.

There is no violation of ethics by any means.

Conflict of Interest

No.

Author Contributions

Anukriti Srivastava wrote the manuscript and Girish Chandra Pandey critically reviewed it.

References

1. Abbas F. 2013. Analysis of a historical (1981-2010) temperature record of the Punjab province of Pakistan. *Earth Interactions* **17**: 1-23.
2. Alonso-Ramirez A, D Rodriguez, D Reyes, JA Jimenez, G Nicolas, M Lopez-Climent, A Gomez-Cadenas, C Nicolas. 2009. Evidence for a role of gibberellins in salicylic acid- modulated early plant responses to abiotic stress in *Arabidopsis* seeds. *Plant Physiology* **150(3)**: 1335–44.
3. Bhaskar RV, B Mohanty, V Verma, E Wijaya, PP Kumar. 2015. A hormone-responsive c1-domain-containing protein At5g17960 mediates stress response in *Arabidopsis thaliana*. PLOS ONE **10(1)**: e0115418.
4. Chen L, F Ren, H Zhong, W Jiang, X Li. 2010. Identification and expression analysis of genes in response to high-salinity and drought stresses in *Brassica napus. Acta Biochimica et Biophysica Sinica* **42:** 154–164.
5. Calvo-Polanco M, E Armada, AM Zamarreno, JM Garciamina, R Aroca, 2019. Local root ABA/ cytokininstatus and aquaporins regulate poplar responses to mild drought stress independently of the ectomycorrhizal fungus *Laccaria bicolor. Journal of Experimental Botany* **70**: 6437–6446.
6. Dobra J, M Cerny, H Storchova, P Dobrev, J Skalak, PL Jedelsky, H Luksanova, A Gaudinova, B Pesek, J Malbeck, T Vanek, B Brzobohaty, R Vankova. 2015. The impact of heat stress targeting on the hormonal and transcriptomic response in *Arabidopsis. Plant science an international journal of experimental plant biology* **231**: 52–61.
7. Fleishon S, E Shani, N Ori, D Weiss, 2011.Negative reciprocal interactions between gibberellin and cytokinin in tomato. *New Phytologist* **190(3)**: 609–17.
8. IPCC Intergovernmental Panel on Climate Change. Climate change 2007:Impacts, adaptation and vulnerability.In: *Perry* ML, OF Canziani, PJ van der Linden, CE Hanson, editors.2007.Contribution of Working Group IIto Fourth Assessment Report of theInter- governmental Panel on Climate Change. Cambridge: *Cambridge University* Press, p. 1000.
9. Keshishian EA, HT Hallmark, T Ramaraj, L Plackova, A Sundararajan, FD Schilkey, O Novak, AM Rashotte, 2018.Salt and oxidative stresses uniquely regulate tomato cytokinin levels and transcriptomic response. *Plant Direct* **2(7)**: e00071.
10. Khandal H, SK Gupta, V Dwivedi, D Mandal, NK Sharma, NK Vishwakarma, L Pal, M Choudhary, A Francis, P Malakar. 2020. Root-specific expression of chickpea cytokinin oxidase/dehydrogenase 6 leads to enhanced root growth, drought tolerance and yield without compromising nodulation. *Plant Biotechnology Journal* **18(11)**: 2225-2240.
11. Kumar SV, D Lucyshyn, KE Jaeger, E Alos, E Alvey, NP Harberd, PA Wigge. 2012. Transcription factor PIF4 controls thethermo-sensory activation of flowering. *Nature* **484(7393)**: 242–5.

12. Kumar S, S Mahapatra, S Chakraborty, S Mukharjee. 2021. Effect of abiotic stresses and mitigation strategy associated with their tolerance in wheat. *Journal of Cereal Research* **13**(**1**): 16-37.

13. Liu J, F Zhang, J Zhou, F Chen, B Wang, X Xie. 2012. Phytochrome B control of totalleaf area and stomatal density affects drought tolerance in rice. *Plant Molecular Biology* **78**(**3**): 289-300.

14. Liu HC, YY Charng. 2013. Common and distinct functions of *Arabidopsis* class A1 and A2 heat shock factors in diverse abiotic stress responses and development. *Plant Physiology* **163**(**1**): 276– 90.

15. Lubovska Z, J Dobra, H Storchova,N Wilhelmova, R Vankova. 2014. Cytokininoxidase/dehydrogenase overexpression modifies antioxidant defense against heat, drought and their combination in *Nicotianatabacum* plants. *Journal of Plant Physiology* **171**(**17**): 1625-33.

16. Mackova H, M Hronkova,J Dobra,V Tureckova, O Novak, Z Lubovska, V Motyka, D Haisel, T Hajek, IT Prasil. 2013. Enhanced drought and heat stress tolerance of tobacco plants with ectopically enhanced cytokinin oxidase/dehydrogenase gene expression. *Journal of Experimental Botany* **64**(**10**): 2805-15.

17. Mittler R, A Finka,P Goloubinoff. 2012. How do plants feel the heat? *Trends Biochemical Sciences* **37**(**3**): 118–25.

18. Mi X, X Wang,H Wu,L Gan, J Ding,Y Li. 2017. Characterization and expression analysis of cytokinin biosynthesis genes in *Fragaria vesca. Plant Growth Regulation* **82**: 139–149.

19. Naidoo G, KK Naidoo. 2018. Drought stress effects on gas exchange and water relations of the invasive weed *Chromolaena odorata. Flora* **248**: 1–9.

20. Nishiyama R, Y Watanabe, Y Fujita, DT Le, M Kojima, T Werner, R Vankova, K Yamaguchi-Shinozaki, K Shinozaki, T Kakimoto. 2011. Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. *Plant Cell* **23**: 2169–2183.

21. Olimpieri I, R Caccia, ME Picarella, A Pucci, E Santangelo, GP Soressi, A Mazzucato. 2011. Constitutive co-suppression of the GA 20-oxidase1 gene in tomato leads to severe defects in vegetative and reproductive development. *Plant Science* **180**: 496–503.

22. Pandey GC, G Mehta, P Sharma, V Sharma. 2019. Terminalheat tolerance in wheat: An overview. *Journal of Cereal Research* **11**(**1**): 1–16.

23. Pospisilova H, E Jiskrova, P Vojta, K Mrizova, F Kokas, MM Cudejkova, V Bergougnoux, O Plihal, J Klimesova, O Novak. 2018. Transgenic barley over-expressing a cytokinin dehydrogenase gene shows greater tolerance to drought stress. *New Biotechnology* **33**: 692–705.

24. Prerostova S, PI Dobrev, A Gaudinova, V Knirsch, N Korber, R Pieruschka, F Fiorani, B Brzobohatý, M Cerný, L Spichal, 2018. Cytokinins: Their Impact on molecular and growthresponses to drought stress and recovery in *Arabidopsis. Frontiers of Plant Science* **9**: 655.

25. Ramireddy E, SA Hosseini, K Eggert, S Gillandt, H Gnad, NV Wiren, T Schmulling. 2018. Root engineering in Barley: Increasing cytokinin degradation produces a larger root system, mineral enrichment in the shoot and improved drought tolerance. *Plant Physiology* **177**: 1078–1095.

26. Rivero RM, V Shulaev, E Blumwald, 2009. Cytokinin-dependent photorespiration and the protection of photosynthesis during water deficit. *Plant Physiology* **150**: 1530–1540.

27. Rivero RM, J Gimeno, A Van Deynze, H Walia, E Blumwald. 2010. Enhanced cytokinin synthesis in tobacco plants expressing PSARK::IPT prevents the degradation of photosynthetic protein complexes during drought. *Plant and Cell Physiology* **51**: 1929–1941.

28. Rosenzweig C, A Iglesius, XB Yang, PR Epstein, E Chivian. 2001.Climate change andextreme weather events-Implications for food production, plant diseases, and pests. *Global change & Human Health* **2**: 90-104.

29. Sobol S, N Chayut, N Nave, D Kafle, M Hegele, R Kaminetsky, JN Wunsche, A Samach. 2014.

Genetic variation in yield under hot ambient temperatures spotlights a role for cytokinin in protection of developing floral primordia. *Plant, Cell and Environment* **37(3)**: 643–57.

30. Shen X, Z Wang, X Song, J Xu, C Jiang, Y Zhao, C Ma, H Zhang. 2014. Transcriptomic profiling revealed an important role of cell wall re-modeling and ethylene signalling pathway during salt acclimation in *Arabidopsis. Plant Molecular Biology* **86**: 303-317.

31. Sun T-p, F Gubler. 2004. Molecular mechanism of gibberellin signaling in plants. *Annual Review of Plant Biology* **55**: 197–223.

32. Stavang JA, J Gallego-Bartolomé, MD Gómez, S Yoshida, T Asami, JE Olsen, JL García-Martínez, D Alabadí, MA Blázquez. 2009. Hormonal regulation of temperature- induced growth in *Arabidopsis. Plant Journal* **60(4)**: 589–601.

33. Veselov DS, GR Kudoyarova, NV Kudryakova, VV Kusnetsov. 2017. Role of cytokinins in stress resistance of plants. *Russian Journal of Plant Physiology* **64**: 15–27.

34. Vettakkorumakankav N, D Falk, P Saxena, RA Fischer. 1999. A crucial role for gibberellins in stress protection of plants. *Plant and Cell Physiology* **40**: 542-548.

35. Werner T, E Nehnevajova, I Kollmer, O Novak, M Strnad, U Kramer, T Schmulling. 2010. Root-specific reduction of cytokinin causes enhanced root growth, drought tolerance, and leaf mineral enrichment in *Arabidopsis* and Tobacco. *Plant Cell* **22**: 3905–3920.

36. Xing J, Y Xu, J Tian, T Gianfagna, B Huang. 2009. Suppression of shade-or heat- induced leaf senescence in creeping bent grass through transformation with the *ipt* gene for cytokinin synthesis. *Journal of American Society for Horticulture Science* **134(6)**: 602–9.

37. Xu Y, R Liu, N Sui, W Shi, L Wang, C Tian, J Song, 2016. Changes in endogenous hormones and seed-coat phenolics during seed storage of two *Suaeda salsa* populations. *Australian Journal of Botany* **64**: 325–332.

38. Zeevaart JA, DA Gage, M Talon. 1993. Gibberellin A1 is required for stem elongation in spinach. *Proceedings of the National Academy of Sciences of the United States of America* **90**: 7401-7405.

39. Zhang W, J Wang, L Xu, A Wang, L Huang, H Du, L Qiu, R Oelmuller. 2018. Drought stress responses in maize are diminished by *Piriformospora indica. Plant Signaling Behavior* **13**: e1414121.

40. Zheng Y, C Liao, S Zhao, C Wang, Y Guo. 2017. The glycosyl transferase QUA1 regulates chloroplast-associated calcium signaling during salt and drought stress in Arabidopsis. *Plant and Cell Physiology* **58**: 329–341.

41. Zwack PJ, AM Rashotte. 2015. Interactions between cytokinin signalling and abiotic stress responses. *Journal of Experimental Botany* **6(16)**: 4863–71.