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Plants Signaling Pathways against Biotic and Abiotic Stresses in Challenging Environment

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Sessile plants confront the fluctuating harsh environmental conditions and react to alterations in biotic and abiotic components of environments by symbiotic association between plant and biosphere. The origins of stresses are the vicinal environment, which is composed of biotic and abiotic agents. A wide range of molecular mechanisms are opted by the plants for their self-defense. The plant faces harsh conditions due to its molecular battery. Signaling molecules engineer the plants to tolerate the stresses. Transposable elements become active due to living and nonliving agents. Physical and chemical agents cause induction in mutation. These changes are the first driving step in the evolution of plants. During evolution, environmental changes force the plants to adapt or succumb to stress. The plants respond to the ecological conditions by modulating the gene programmer.

Keywords: Signaling pathways, Crosstalk, Defense, Challenges, UPS, Evolution.

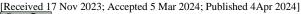
INTRODUCTION

Natural and anthropogenic factors are the main events to cope with the biotic and abiotic challenges (Minakshi et al., 2011). Natural disasters, including extreme rainfall events, floods, cold waves, heat waves, and cyclones, are severe threats to economic losses. The alterations in climate patterns can influence the spread of pathogens and it can also affect the plant's response to biotic stresses (Nicol, 2011; Russell et al., 2004). The enhancement in pathogen infestation is a major constraint in crop production (Minakshi et al., 2011). The effects of stress may vary depending on time, nature severity. and prevailing environmental conditions (Gupta et al., 2016; Sharma and Dubey, 2005). Stress factors hijack the plant system in a combination or interactive way (Niinemets. 2010). In interactive mode, the initial stress factor alters the plant behavior for the attack of another stress (Mittler, 2002). The damages caused by stress are more severe when more than one-factor attacks synergism. Plants respond to the environment in specific and non-specific ways (Newton et al., 2011). There are many common threats and damages in signaling pathways of specific and general responses to stresses (Miller et al., 2010). The plant faces a wide array of biotic and abiotic challenges, e.g., insects, herbivores, fungal, bacterial, and viral attacks by specific, general, or overlapping defense mechanisms. Biotic agents interfere with the plantwater relationship to increase the pathogenesis. Plants their remodel anatomy, morphology, physiologies, biomolecules and gene expressions due to environmental stress conditions (Wang et al., 2001; Shao et al., 2009). Biotic stresses also stimulate the plant protoplast, chloroplast and peroxisomes to raise the reactive oxygen species (ROS) level (Bolwell, 1999). The changes in ubiquitous/proteome (UPS) help the plant to survive under harsh biotic and abiotic conditions, e.g., Arabidopsis, cereals and French beans. Both factors impose severe pressure on our global agents. The central theme behind this title is to find the targets of crop plants and how they tolerate environmental stress.

Ways of defense mechanism: Avirulence factor (Avr) and plant defense protein (R-resistance) become susceptible if they lack cognate R gene in response to particular Avr. The plant produces SAR (Systematic Acquired Resistance) when a pathogen attack (Durrant and Dong, 2004). Plants fend off future attacks from fungi and bacteria when customized by colonizing non-pathogenic bacteria (Durrant and Dong, 2004). There are the following types of defense mechanisms:

- 1. Basal Defense: In this, the plant recognizes and responds to a wide range of non-host pathogens by PAMPs (pathogen-associated molecular Patterns).
- 2. Gene-for-Gene

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3. R-mediated Resistance

types of defense mechanism biochemical defense mechanism: Biotic and abiotic agents are coordinated via cross-talk and signaling pathways (Fig.1). The critical components of this cross-talk are transcription factor. HSF (Heat shock factor), ROS, and mitogen-activated protein kinase (MAPK) to minimize the damages by conserving valuable resources (Nicky and Peter, 2012; Rizhsky et al., 2004). When the NADPH level falls, the uptake of oxygen in plants (Bolwell, 1996). (Diphenyleneiodonium Chloride) is the inhibitor of NADPHoxidase, which facilitates the alleviation of the effects of ROS (Bolwell et al., 1998). ROS are produced in response to both biotic and abiotic stresses (Anjum et al., 2011). The crop plants either mutated transgenically (transcription factor-TF) or conventional breeding (Maize) and embryogenesis abundant (EA) in potatoes, bananas, and rice are the best defenders against stresses (Newton et al., 2011; Anderson et al., 2004).

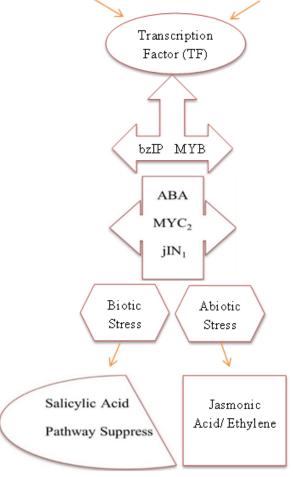


Figure 1. Combine TF and Phytohormones to deal with biotic and abiotic stresses.

Phytohormonal/Regulator Roles in Defense Mechanism:

Endogenous phytohormones are LMW molecules that regulate the protective mechanism in plants in a synergistic or antagonistic manner (Figure 2) (Abe et al., 2012). The ABA, Ethylene, Gibberelline and Auxin facilitate the plant in alteration of UPS, transcriptional and post-transcriptional changes in response pathway (Kate and Judy, 2007). The ABA produced in response to biotic and abiotic factors strongly interacts with the ET in an intricate defense mechanism (Jonathan et al., 2004). ABA causes drought stress. It is exaggerated by climatic, edaphic and agronomic factors. The unavailability of water induces the change in stomatal aperture due to ion transport, growth, vield, membrane integrity, pigment content, osmotic adjustment water relations, photosynthetic activity and reduction in turgor pressure (Figure 3) (Roelfsema, 2004; Praba et al., 2009). It weakened germination and poor stand establishment (Harris et al., 2002). The plants become more susceptible to disease pathogens when drought occurs in Sorghum, Beans and Date palms (Suleman et al., 2001). Drought and heat stress cause the opening of chromatin conformation). Jasmonic acid and ethylene act synergistically and antagonistically during the biotic stresses. The ethylene is produced primarily in biotic and abiotic stresses (Van et al., 2015). UPS programs are important against pathogens and favor the plant defense systems because several pathogens hijack the UPS components (Zheng et al., 2006). This component plays an essential role in many plant processes (Imaizumi et al., 2005; Van et al., 2015). It helps in identification by different bioinformatics tools (Moon et al., 2004).

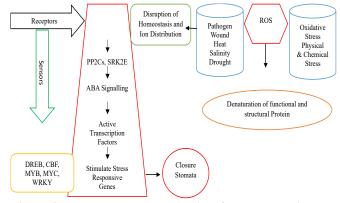


Figure 2. Drought, Heat and ABA defense mechanism

Bioagents Role in plant protection against stress:

Microorganisms are the primary strategy to cope with abiotic and biotic stresses. They play a crucial role in plant growth promotion, nutrient management and disease control by colonizing the rhizosphere/endo-rhizosphere of plants (Saxena et al., 2005). PGPR including Rhizobium, Bradyrhizobium, Azotobacter, Azospirillum, Pseudomonas



and Bacillus, Pantoea, Paenibacillus, Burkholderia, Achromobacter, Microbacterium, Methylobacterium, variovorax, Enterobacter Upadhyay et al., (2009) have been reviewed recently to tolerate abiotic stresses.

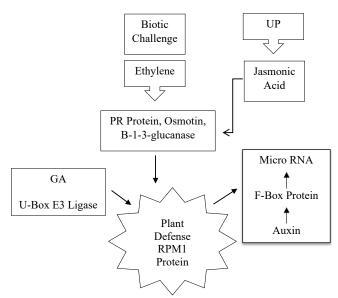


Figure 3. Crosstalk between UPS and Hormones to activate the Plant Defense System.

The viral infection protects the plants from drought in tobacco, beet, and rice. Drought, heat and salinity cause severe threats to 50% of arable land. Rhizobacterial-treated plants resist the attack of drought and bacteria (Timmusk and Wagner, 1999). Nematode ameliorates drought stress (Smith et al., 2007). Different types of signaling have been discussed in the latest supporting literature to confront the environmental challenges (Table 1 and Figure 4). Stresstargeted or exposed areas of the plants are dwelling sites of rhizobacteria (Lifshitz et al., 1986).

- Thermomicrophiles and halomicrophiles can optimize metabolic activities (enzymatic activities, membrane stability) (Madigen, 1999).
- 2. Cytoplasmic osmolarity is modulated by the rhizobacteria for the production of osmoprotectants (Blanco, 1994).
- 3. Oligosaccharides of these bio-agents sustain the turgor pressure (Sandhya *et al.*, 2009a, b).
- 4. Exopolysaccharides can hold water holding and nutrients cementing.
- 5. Keeps the *Pseudomonas* hydric stress (Roberson and Firestone, 1992).
- Pseudomonas aeruginosa strain AMK-P6 formulate the chaperons (heat shock (HSPs/thermoprotective proteins) and few bacteria (Serratia marscescens strain SRM and Pantoea dispersa) release cryoprotective protein (cold shock proteins-CSP) (Koda et al., 2001; Castiglioni et al.,

- 2008), which prevent the denaturation of proteins and proteases during extreme temperature (Ali *et al.*, 2009).
- Root length and number of tips increased by indole acetic acid, gibberellins and some PGPR in drought stress (Egamberdieva and Kucharova, 2009), Paenibacillus polymyxa in Azospirillum thaliana (Timmusk and Wagner, 1999) and A. brasilense Sp245 in Triticum aestivum.
- 8. Salinity tolerance in tomato, pepper, canola, bean and lettuce by the cooperation of PGPB (Barassi *et al.*, 2006).
- 9. Production of trehalose metabolism in rhizobia enhances the abiotic stress signaling pathway of leguminous plants (Suarez *et al.*, 2008).
- Plant physiology and the expression of plant genes become improved by arbuscular mycorrhizal (AM) during water deficiency and drought stress (Ruiz-Lozano and Azcon, 2000).
- 11. Drought and heat stress in alpine and arid grassland habitats increase by the endophytic symbionts of dark septate fungi (DSF) (Porras-Alfaro *et al.*, 2008).
- 12. Brassinosteroids cause pleiotropic effects on plant development (Bishop, 2002).

Plant Modifications to Confront the Varietal Stresses:

- Stomata open in heat stress and closed in cold and water stress (Beattie, 2011). The closed stomata also prevent microbial invasion (Melotto *et al.*, 2006) by induction of ABA (Rizhsky *et al.*, 2004).
- 2. Callose deposition starts on the cell wall during fungal attack.
- 3. Transcription factors and effectors proteins (Dubos *et al.*, 2010) increased to overcome the damages caused by heat, salt and heavy metals (Miller *et al.*, 2010).
- 4. Production of proline to tolerate heat, salt and osmotic stress. Proline and soluble sugar levels elevate during cold stress (Gilmour *et al.*, 2000).
- 5. Production of secondary metabolites (Osmoprotectants, antioxidants, anthocyanin) to mound the array of stresses (Atkinson *et al.*, 2011).
- 6. Antioxidants scavenge ROS.
- 7. Regulation of phytohormonal signal to overcome or interaction (Asselbergs *et al.*, 2007).
- 8. The plant attracts AMF by secreting strigolactones in its microenvironment, which produces antioxidants (Catalase, superoxide dismutase, Ascorbate peroxidase, glutathione reductase, carotenoids, alpha-tocopherol, proline oxidase, r-glutanyl kinase) osmolytes (Jitender, 2011).
- 9. Genetical changes help in stress tolerance among crop plants (Swindell, 2006).
- 10. Heat Shock protein (HSP)-a chaperon, protects the plants from oxidative stress (Rizhsky *et al.*, 2004).
- 11. Anti-stress plants produce small non-coding RNA to overcome cold stress (Sunkar *et al.*, 2007).



Table 1. Different types of mechanism signaling to ameliorate the stresses via bioagents.

Bio-Agent	Crop	Targeted Stress	Mechanism	References
Bacillus subtilis	A. thaliana	Drought	Proline accumulation	Chen et al., (2007)
Rhizobium and Pseudomonas	Zea mays	salinity	Proline accumulation	Bano and Fatima, (2009)
Rhizobium tropici, P. polymyxa	Phaseolus vulgaris L.	Drought	Overexpressing trehalose-6-phosphate synthase gene	Figueiredo <i>et al.</i> , (2008)
Pseudomonas chlororaphis	Arabidopsis thaliana	Drought	Volatile metabolite, 2R, 3R-butanediol, salicylic acid (SA), ethylene and jasmonic acid-signalling pathways	Cho et al., (2008)
Burkholderia phytofirmans PsJN	Grapevine tissue	Cold/ chilling stress	Epiphytic and endophytic colonization of grapevine tissue and organs	Compant et al., (2005)
Glomus versiforme	Citrus	Drought	Osmotic adjustment of the plant under drought stress through enhanced levels of non-structural carbohydrates, K, Ca and Mg.	Wu and Xia, (2006)
Glomus intraradices and Glomus sp. strain	Lavender	Water Deficiency	Overproduction of glutathione and ascorbate	<u>Marulanda <i>et al.</i>,</u> (2007)
Gigaspora margarita .	Sorghum	Drought on salt Stressed Soil (Dual)	Promoted stomatal conductance	Minakshi <i>et al.</i> , (2011)
Glomus spp.	Maize/ mung bean/ clover	Salt Stress	proline accumulation	Ben Khaled <i>et al.</i> , (2003)
Glomus intraradices	Pterocarpus officinalis	Flood Stress	Limited the overproduction of acetaldehyde (causing agent of flood injury)	Fougnies et al., (2007)
AM fungi and Bradyrhizobium	Casuarina equisetifolia	Flood	Development of adv. roots, aerenchyma and hypertrophied lenticels	Rutto et al., (2002)
Pseudomonas putida, Enterobacter cloacae, P. putida	Tomato	Flood	Synthesis of ACC-deaminase	Grichko and Glick (2001)
PGPR	Chickpea	Metal toxicity	Sequestration of metal ions	Gupta et al., (2004)
Scytonema	Rice	Coastal Salinity	Gibberellic acid and extracellular products	Rodriguez et al., (2006)
Piriformaspora indica (DSF)	Arabidopsis thaliana, P. indica	Diverse Set of Stress	upregulation of the message levels for phospholipase Ddelta, calcineurin B-like proteins (CBL 1) and histone acetyltransferase (HAT)	Sheramati et al., (2008)
Paraphaeosphaeria quadriseptata	Arabidopsis thaliana	Heat Stress	induction of HSP101 and HSP70	McLellan <i>et al.</i> , (2007)
Endophytic fungi Cuvularia spp.	Dichanthelium lanuginosum	Heat Stress	Curvularia thermotolerance virus (CatahTV).	Redman et al., (2002)

- 12. SiRNA regulates both bio and abiotic stresses (Ruiz, 2009).
- 13. NT26 keeps away pathogens during the cold period of the year (Zhang *et al.*, 2009).
- 14. Transgenes are successful candidates in plants during tolerance (Wei *et al.*, 2011).
- 15. SnRK1 is an array sensor that maintains photosynthesis and yields plants (Bartels and Sunkar, 2005).
- 16. Hydrated amorphous silica in the epidermis of various tissues facilitates the plant to tolerate biotic and abiotic stress (Jian, 2004).
- 17. Production of stress protein and compatible solutes (Bohnert and Shen, 2000), HSP, late embryogenesis abundant (LEA) protein (Mathur *et al.*, 2008), and osmoprotectants.

- 18. Three types of compatible solutes improved stress tolerance.
- 19. For nutrient balance, plants uptake proton as a coupling ion in an ion transport system (Lorenzo *et al.*, 2004).
- 20. The chemical composition of lignin is changed during the stress.
- 21. Jasmonate is a defense during the reproductive stages of plants to promote resistance against insects and pathogens (Creelman and Johne, 1995).
- 22. Fungal chitin and bacterial flagellin show callose deposition and oxidative burst (Flexas *et al.*, 2004) through pathogenesis in many plants (Kim *et al.*, 2006).
- **23.** Plants produce specific proteins in hypersensitive response (HR) to encounter pathogenicity.



24. Heavy metals, nitric acid and Ca signaling play a vital role in plant immunity response.

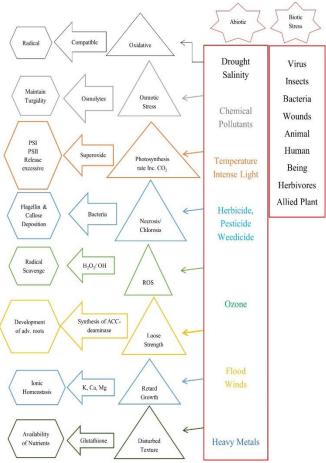


Figure 4. Biotic and abiotic stresses and prevention action

Conclusion and Future Perspectives: Experimental conditions to check the tolerance in plants must be homogenous to natural conditions. It is possible to induce a broad spectrum of changes in crop plants. A significant body of research suggests that there is still a need to determine the mastermind that can play the cross-talk between abiotic and biotic stress. Taking the available current leads, future research is still needed in this area, particularly on field evaluation and application of potential organisms.

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REFERENCES

Abe H, Y. Tomitaka, T. Shimoda, S. Seo, T. Sakurai, S. Kugimiya, S. Tsuda and M. Kobayashi 2012. Antagonistic plant defense system regulated by phytohormones assists interactions among vector insect, thrips and a tospovirus. Plant and Cell Physiology 53:204-12. doi: 10.1093/pcp/pcr173

Ali, S.Z., V. Sandhya, M. Grover, N. Kishore, L.V. Rao and B. Venkateswarlu. 2009. Pseudomonas sp. strain AKM-P6 enhances tolerance of sorghum seedlings to elevated temperatures. Biology and Fertility of Soils 46:45-55. https://doi:10.1007/s00374-009-0404-9

Anderson, J.P., E. Badruzsaufari, P.M. Schenk, J.M. Manners, O.J. Desmond, C. Ehlert, D.J. Maclean, P.R. Ebert and K. Kazan. 2004. Antagonistic interaction between abscisic acid and jasmonate-ethylene signaling pathways modulates defense gene expression and disease resistance in Arabidopsis. Plant Cell 16:3460-3479. https://doi.org/10.1105/tpc.104.025833

Anjum, S.A., X. Xie, L.C. Wang, M.F. Saleem, C. Man and W. Lei. 2011. Morphological, physiological and biochemical responses of plants to drought stress. Morphological, physiological and biochemical responses of plants to drought stress. African Journal of Agricultural Research 6:2026-2032. http://dx.doi.org/10.5897/AJAR10.027

Asselbergs, F.W., S.M. Williams, P.R. Hebert, C.S. Coffey, H.L. Hillege, G. Navis, D.E. Vaughan, W.H. Van Gilst and J.H. Moore. 2007. Epistatic effects of polymorphisms in genes from the renin-angiotensin, bradykinin, and fibrinolytic systems on plasma t-PA and PAI-1 levels. Genomics 89:362-369. https://doi.org/10.1016%2Fj.ygeno.2006.11.004

Atkinson, N.J., T.P. Dew, C. Orfila and P.E. Urwin. 2011. Influence of combined biotic and abiotic stress on nutritional quality parameters in tomato (*Solanum lycopersicum*). Journal of Agricultural and Food



- Chemistry 59:9673-9682. https://doi.org/10.1021/jf202081t
- Bano, A. and M. Fatima. 2009. Salt tolerance in Zea mays (L). following inoculation with Rhizobium and Pseudomonas. Biology and Fertility of Soils 45:405-413. http://dx.doi.org/10.1007/s00374-008-0344-9
- Barassi, C.A., G. Ayrault, C.M. Creus, , R.J. Sueldo and M.T. Sobrero. 2006. Seed inoculation with Azospirillum mitigates NaCl effects on lettuce. Scientia Horticulturae 109:8-14. https://doi.org/10.1016/j.scienta.2006.02.025
- Bartels, D. and R. Sunkar. 2005. Drought and salt tolerance in plants. Critical reviews in plant sciences 24:23-58. https://doi.org/10.1080/07352680590910410
- Beattie, G.A. 2011. Water relations in the interaction of foliar bacterial pathogens with plants. Annual of Review of Phytopathology 49:533-555. https://doi.org/10.1146/annurev-phyto-073009-114436
- Ben Khaled, L., A.M. Gomez, E.M. Ourraqi and A. Oihabi. 2003. Physiological and biochemical responses to salt stress of mycorrhized and/or nodulated clover seedlings (Trifolium alexandrinum L.). Agronomie 23:571-580. (Google Scholar)
- Bishop, G.J. 2007. Refining the plant steroid hormone biosynthesis pathway. Trends in Plant Science 12:377-380. https://doi.org/10.1016/j.tplants.2007.07.001
- Blanco, B.T. 1994. Osmoadaptation in rhizobia: ectoineinduced salt tolerance. Journal of Bacteriology 176:5210-5217. https://doi.org/10.1128%2Fjb.176.17.5210-5217.1994
- Bohnert, H.J, and B. Shen. 2009. Transformation and compatible solutes. Scientia Horticulturae 78:237-260. https://doi.org/10.1016/S0304-4238(98)00195-2
- Bolwell, G. P., D.R. Davies, C. Gerrish, C.K. Auh and T.M. Murphy. 1998. Comparative biochemistry of the oxidative burst produced by rose and French bean cells reveals two distinct mechanisms. Plant Physiology 116:1379-1385. https://doi.org/10.1104/pp.116.4.1379
- Bolwell, G.P. 1996. The origin of the oxidative burst in plants. Biochemical Society Transactions 24:438-442. https://doi.org/10.1042/bst0240438
- Bolwell, G.P. 1999. Role of active oxygen species and NO in plant defense responses. Current Opinion in Plant Biology 2:287-294. https://doi.org/10.1016/s1369-5266(99)80051-x
- Castiglioni, P., D. Warner, R. J. Benson, D. C. Anstrom, J. Harrison, M. Stoecker, M. Abad, G. Kumar, S. Salvador, R. D'Ordine, S. Navarro, S, Back, M. Fernandes, J. Targolli, S. Dasgupta, C. Bonin, M.H. Luethy and J.E. Heard. 2008. Bacterial RNA chaprones confer abiotis stress tolerance to plants and improved grain yield in maize under water-limited conditions. Plant Physiology 147:446-455. https://doi.org/10.1104/pp.108.118828
- Chen, M., H. Wei, J, Cao, L. Liu, Y. Wang and C. Zheng. 2007. Expression of Bacillus subtilis proAB genes and

- reduction of feedback inhibition of proline synthesis increases proline production and confers osmotolerance in transgenic Arabdopsis. Journal of Biochemistry and Molecular Biology 40:396-403.
- https://doi.org/10.5483/bmbrep.2007.40.3.396
- Cho, SM., B.R. Kang, S.H. Han, A.J. Anderson, J.Y. Park, Y.H. Lee, B.H. Cho, K.Y. Yang, C.M. Ryu and Y.C. Kim. 2008. 2R, 3r-butanediol, a bacterial volatile produced by Pseudomonas chlororaphis O6, is invoplved in induction of systemic tolerance to drought in Arabdopsis thaliana. Molecular Plant-Microbe Interactions 21:1067–1075. https://doi.org/10.1094/mpmi-21-8-1067
- Compant, S., B. Reiter, A. Sessitsch, J. Nowak, C. Clement and E. Ait Bakra. 2005. Endophytic coloniozation of Vitis vinifera L. by plant growth promoting bacterium Burkholderia sp. strain PsJN. Applied and Environmental Microbiology 71:1685-1693. https://doi.org/10.1128/aem.71.4.1685-1693.2005
- Creelman, R.A., and M. Johne. 1995. Jasmonic acid distribution and action in plants: Regulation during development and response to biotic and abiotic stress. Proceedings of the National Academy of Sciences of the United States of America 92:4114-4119. https://doi.org/10.1073%2Fpnas.92.10.4114
- Dubos, C., R, Stracke, E. Grotewold, B. Weisshaar, C. Martin and L. Lepiniec. 2010. MYB transcription factors in Arabidopsis. Trends in Plant Science 15:573-81. https://doi.org/10.1016/j.tplants.2010.06.005.
- Durrant, W.E., and X. Dong. 2004. Systemic acquired resistance. Annual Review of Phytopathology 42:185-209.
 - https://doi.org/10.1146/annurev.phyto.42.040803.14042
- Egamberdieva, D., and Z. Kucharova. 2009. Selection for root colonizing bacteria stimulating wheat growth in saline soils. Biology and Fertility of Soil 45:563-571 https://doi.org/10.1007/s00374-009-0366-y
- Figueiredo, M.V.B., H.A. Burity, C.R. Martinez and C.P. Chanway. 2008. Alleviation of drought stress in common bean (Phaseolus vulgaris L.) by co-inoculation with Paenibacillus polymyxa and Rhizobium tropici. Applied Soil Ecology 40:182-188. http://dx.doi.org/10.1016/j.apsoil.2008.04.005
- Flexas, J., J. Bota, F. Loreto, G. Cornic and T.D. Sharkey. 2004. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. Plant Biology 6:1-11. http://dx.doi.org/10.1055/s-2004-820867
- Fougnies, L., S. Renciot, F. Muller, C. Plenchette, Y. Prin,
 S.M. de Faria, J.M. Bouvet, S. Sylla, B. Dreyfus and
 A.M. Ba. 2007 Arbuscular mycorrhizal colonization and
 nodulation improve tolerance in Pterocarpus officinalis



- Jacq. seedlings. Mycorrhiza 17:159-166. https://doi.org/10.1007/s00572-006-0085-2
- Gilmour, S.J., M.S. Audrey, P.S. Maite, D.E. John and F.T. Michael. 2000. Overexpression of the Arabidopsis *CBF3* Transcriptional Activator Mimics Multiple Biochemical Changes Associated with Cold Acclimation. Plant Physiology 124:1854-1865. https://doi.org/10.1104/pp.124.4.1854
- Grichko, V.P., and B.R. Glick. 2001. Amelioration of flooding stress by ACC deaminase containing plant growth promoting bacteria. Canadian Journal of Microbiology 47:77-80. http://dx.doi.org/10.1016/S0981-9428(00)01212-2
- Gupta, A., S.K. Dixit and M. Senthil-Kumar. 2016. Drought stress predominantly endures *Arabidopsis thaliana* to *Pseudomonas syringae* infection. *Frontiers in Plant Science* 7:808. https://doi.org/10.3389/fpls.2016.00808
- Gupta, D.K., U.N. Rai, S. Sinha, R.D. Tripathi, B.D. Nautiyal, P. Rai and M. Inouhe. 2004. Role of Rhizobium (CA-1) inoculation in increasing growth and metal accumulation in Cicer arietinum L. growing under fly-ash stress condition. Bulletin of Environmental Contamination and Toxicology 73:424-431. https://doi.org/10.1007/s00128-004-0446-5
- Harris, D., R.S. Tripathi and A. Joshi. 2002. On-farm seed priming to improve crop establishment and yield in dry direct-seeded rice, in: Pandey S., Mortimer M., Wade L., Tuong T.P., Lopes K., Hardy B. (Eds.), Direct seeding: Research Strategies and Opportunities, International Research Institute, Manila, Philippines, pp. 231-240. Google Scholar
- Imaizumi, T., T.F. Schultz, F.G. Harmon, L.A. Ho and S.A. Kay. 2005. FKF1 F-box protein mediates cyclic degradation of a repressor of CONSTANS in Arabidopsis. Science 309:293-7. https://doi.org/10.1126/science.1110586
- Jian, F.M. 2004. Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. Soil Science and Plant Nutrition 50:11-18.
- http://dx.doi.org/10.1080/00380768.2004.10408447 Jitender, G. 2011. Glycinebetaine and abiotic stress
- tolerance in plants. Plant Signaling & Behavior 6:1746-1751. https://doi.org/10.4161%2Fpsb.6.11.17801
- Jonathan, P.A., B. Ellet, M.S. Peer, M.M. John, J.D. Olivia, E. Christina, J.M. Donald, R.E. Paul and K. Kemal. 2004. Antagonistic Interaction between Abscisic Acid and Jasmonate-Ethylene Signaling Pathways Modulates Defense Gene Expression and Disease Resistance in Arabidopsis. Plant Cell 16:3460-3479. https://doi.org/10.1105/tpc.104.025833
- Kate, D., and C. Judy. 2007. Ubiquitin, Hormones and Biotic Stress in Plants, Annals of Botany 99:787-822. https://doi.org/10.1093/aob/mcl255

- Kim, Y.J., D.G. Kim, S.H. Lee and I. Lee. 2006. Wound-induced expression of the ferulate 5-946 hydroxylase gene in Camptotheca acuminata. Biochimica et Biophysica Acta, 947:182-190. https://doi.org/10.1016/j.bbagen.2005.08.015
- Koda, N.A., K. Yamade, H. Kawahara and H. Obata. 2001. A novel cryoprotective protein (CRP) with high activity from the icenucleating bacterium, Pantoea agglomerans IFO12686. Bioscience, Biotechnology, and Biochemistry 65:888–894. https://doi.org/10.1271/bbb.65.888
- Lifshitz, R., J.W. Kloepper, F.M. Scher, E.M. Tipping and M. Laliberte. 1986. Nitrogen-fixing pseudomonads isolated from roots of plants grown in the Canadian high arctic. Applied and Environmental Microbiology 51:251–255. https://doi.org/10.1128/aem.51.2.251-255.1986
- Lorenzo, O., J.M. Chico, J.J. Sanchez-Serrano and R. Solano. 2004. JASMONATE-INSENSITIVE1 encodes a MYC transcription factor essential to discriminate between different jasmonate regulated defense responses in Arabidopsis. Plant Cell 16:1938-1950. https://doi.org/10.1105/tpc.022319
- Madigen, O. 1999 Thermophilic and halophilic extremophiles. Current Opinion in Microbiology 2:265–269. https://doi.org/10.1016/s1369-5274(99)80046-0
- Marulanda, A., R. Porcel, J.M. Barea and R. Azcon. 2007. Drought tolerance and antioxidant activities in lavender plants colonized by native drought tolerant or drought sensitive Glomus species. Microbial Ecology 54:543–552. https://doi.org/10.1007/s00248-007-9237-y
- Mathur, P.B., V. Vadez and K.S. Kiran. 2008. Transgenic approaches for abiotic stress tolerance in plants: retrospect and prospects. *Plant Cell Reports* 27:411–424. https://doi.org/10.1007/s00299-007-0474-9
- McLellan, C.A., T.J. Turbyville, K. Wijeratne, Kerschen A., Vierling E., Queitsch C., Whiteshell L. and Gunatilaka A. A. L. 2007 A rhizosphere fungus enhances Arabidopsis thermotolerance through production of an HSP90 inhibitor. Plant Physiology 145:174-182. https://doi.org/10.1104/pp.107.101808
- Melotto, M., W. Underwood, J. KoczanJ., Nomura K. and He SY. 2006. Plant stomata function in innate immunity against bacterial invasion. Plant Cell 126:969-80. https://doi.org/10.1016/j.cell.2006.06.054
- Miller, G., N. Suzuki S. Ciftci-Yilmazand R. Mittler. 2010. Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell Environment 33:453-67. https://doi.org/10.1111/j.1365-3040.2009.02041.x
- Minakshi, G., Z. Sk, V. Ali, A.R. Sandhya and B. Venkateswarlu. 2011. Role of microorganisms in adaptation of agriculture crops to abiotic stresses. World Journal of Microbiology and Biotechnology 27:1231-1240. https://doi.org/10.1007/s11274-010-0572-7



- Mittler, R. 2002. Oxidative stress, antioxidants and stress tolerance. Trends in Plant Science 7:405-410. https://doi.org/10.1016/s1360-1385(02)02312-9
- Moon, J., G. Parry and M. Estelle. 2004. The ubiquitin-proteasome pathway and plant development. Plant Cell 16:3181-95. https://doi.org/10.1105%2Ftpc.104.161220
- Newton, A.C., S.N. Johnson and P.J. Gregory. 2011. Implications of climate change for diseases, crop yields and food security. Euphytica 179:3-18. http://dx.doi.org/10.1007/s10681-011-0359-4
- Nicky, J.A. and E.U. Peter. 2012. The interaction of plant biotic and abiotic stresses: from genes to the field. *Journal of Experimental Botany* 63:3523-3543. https://doi.org/10.1093/jxb/ers100
- Nicol, J.m., s. j. turner, d.l. coyne, l. nijs, s. hockland and z.t. maafi. 2011. Current nematode threats to world agriculture. In: Jones J, Gheysen G, Fenoll C, eds. *Genomics and molecular genetics of plant–nematode interactions*. Amsterdam, the Netherlands: Springer 21-43. http://dx.doi.org/10.1007/978-94-007-0434-3_2
- Niinemets, U. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. Forest Ecology and Management 260:1623-1639.
 - http://dx.doi.org/10.1016/j.foreco.2010.07.054
- Porras-Alfaro, A., J. Herrera, R.L. Sinsabaugh, K.J. Odenbach, T. Lowrey and D.O. Natvig. 2008. Novel root fungal consortium associated with a dominant desert grass. Applied and Environmental Microbiology 74:2805–2813. https://doi.org/10.1128%2FAEM.02769-07
- Praba, M. L., J.E. Cairns, R.C. Babu and H.R. Lafitte. 2009. Identification of physiological traits underlying cultivar differences in drought tolerance in rice and wheat. Journal of Agronomy and Crop Science 195:30-46. http://dx.doi.org/10.1111/j.1439-037X.2008.00341.x
- Redman, R.S., S. Freeman, D.R. Clifton, J. Morrel, G. Brown and R.J. Rodriguez. 1999. Biochemical analysis of plant protection afforded by a nonpathogenic endophytic mutant of Colletotrichum magna. Plant Physiology 119:795-804. https://doi.org/10.1104/pp.119.2.795
- Rizhsky, L., Liang H. J., Shuman J., Shulaev V., Davletova S. and Mittler R. 2004. When defense pathways collide. The response of Arabidopsis to a combination of drought and heat stress. Plant Physiology 134:1683-1696. https://doi.org/10.1104/pp.103.033431
- Roberson, E., and M. Firestone. 1992. Relationship between desiccation and exopolysaccharide production in soil Pseudomonas sp. Applied and Environmental Microbiology 58:1284-1291. https://doi.org/10.1128/aem.58.4.1284-1291.1992

- Rodriguez, A. A., Stella A. M., Storni M. M., Zulpa G. and Zaccaro M. C. 2006. Effect of cyanobacterial extracellular products and gibberellic acid on salinity tolerance in Oryza sativa L. Saline System 2:1-4. https://doi.org/10.1186%2F1746-1448-2-7
- Roelfsema, M.R., V. Levchenko and R. Hedrich. 2004. ABA depolarizes the guard cells in intact plants, through a transient activation of R- and S-type anion channels. Plant Journal 37:578-588.
 - https://doi.org/10.1111/j.1365-313x.2003.01985.x
- Ruiz, V. F., Olivier V. 2009. Roles of Plant Small RNAs in Biotic Stress Responses. Annual Review of Plant Biology, 60:485-510.
 - https://doi.org/10.1146/annurev.arplant.043008.092111
- Ruiz-Lozano, J.M. and R. Azcon. 2000. Symbiotic efficiency and infectivity of an autochthonous arbuscular mycorrhizal Glomus sp. from saline soils and Glomus deserticola under salinity. Mycorrhiza 10:137-143. http://dx.doi.org/10.1007/s005720000075
- Russell, J., R. Rodriguez, J. Redman and M. Henson. 2004. The role of fungal symbiosis in the adaptation of plants to high stress environments. Mitigation and Adaptation Strategies for Global Change 9:261-272. http://dx.doi.org/10.1023/B:MITI.0000029922.31110.97
- Rutto, K. L., Mizutani F. and Kadoya K. 2002 Effect of root-zone flooding on mycorrhizal and non-mycorrhizal peach (Prunus persica Batsch) seedlings. Scientia Horticulturae 94:285-295.
- http://dx.doi.org/10.1016/S0304-4238(02)00008-0
 Sandhya, V., S.Z. Ali, M. Grover, G. Reddy and B.
- Venkateswarlu. 2009. Alleviation of drought stress effects in sunflower seedlings by exopolysaccharides producing Pseudomonas putida strain P45. Biology and Fertility of Soils 46:17-26.
 - http://dx.doi.org/10.1007/s00374-009-0401-z
- Sandhya, V., S.Z. Ali, M. Grover, N. Kishore and B. Venkateswarlu. 2009. Pseudomonas sp. strain P45 protects sunflowers seedlings from drought stress through improved soil structure. Journal of Oilseeds Research 26:600-601. http://dx.doi.org/10.1007/s00374-009-0401-z
- Saxena, A.K., S.R. Lata and A.K. Pandey. 2005. Culturing of plant growth promoting rhizobacteria. In: Gopi KP, Varma A (eds) Basic research applications of mycorrhizae. I K International Pvt Ltd, New Delhi, pp 453-474. Google Scholar
- Shao, H.B., L.Y. Chu, C.A. Jaleel, P. Manivannan, R. Panneerselvam and M.A. Shao. 2009. Understanding water deficit stress-induced changes in the basic metabolism of higher plants-biotechnologically and sustainably improving agriculture and the ecoenvironment in arid regions of the globe. Critical Reviews in Biotechnology 29:131-151. https://doi.org/10.1080/07388550902869792



- Sharma, P. and R.S. Dubey. 2005. Drought induces oxidative stress and enhances the activities of antioxidant enzyme in growing rice seedling. Plant Growth Regulation 46:209-221. http://dx.doi.org/10.1007/s10725-005-0002-2
- Sheramati, I., S. Tripathi, A. Varma and R. Oelmuller. 2008. The rotcolonizing endophyte Piriformaspora indica confers drought tolerance in Arabidopsis by stimulating the expression of drought stress-related genes in leaves. Molecular Plant-Microbe Interactions 21:799-807. https://doi.org/10.1094/mpmi-21-6-0799
- Smith, A.H., W.M. Gill, E.A. Pinkard and C.L. Mohammed. 2007. Anatomical and histochemical defence responses induced in juvenile leaves of Eucalyptus globulus and Eucalyptus nitens by Mycosphaerella infection. Forest Pathology 37:361-373. http://dx.doi.org/10.1071/AP06070
- Suarez, R., A. Wong, M. Ramirez, A. Barraza, C. OrozcoMdel, M,A, Cevallos, M. Lara, G. Hernandez and G. Iturriaga. 2008. Improvement of drought tolerance and grain yield in common bean by overexpressing trehalose-6-phosphate synthase in rhizobia. Molecular Plant-Microbe Interactions 21:958– 966. https://doi.org/10.1094/mpmi-21-7-0958
- Suleman, P., A. Al-Musallam and C.A. Menezes. 2001. The effect of solute potential and water stress on black scorch caused by Chalara paradoxa and Chalara radicicola on date palms. Plant disease 85:80-83. https://doi.org/10.1094/PDIS.2001.85.1.80
- Sunkar, R., C. Viswanathan, Z. Jianhua and Z. Jian-Kang. 2007. Small RNAs as big players in plant abiotic stress responses and nutrient deprivation. Annual review 12:301-309.
 - https://doi.org/10.1016/j.tplants.2007.05.001
- Swindell, W.R. 2006. The Association Among Gene Expression Responses to Nine Abiotic Stress Treatments in *Arabidopsis thaliana*. Genetics 174:1811-1824; https://doi.org/10.1534/genetics.106.061374
- Timmusk, S. and E.G.H. Wagner. 1999. The plant growth-promoting rhizobacterium Paenibacillus polymyxa

- induces changes in Arabidopsis thalianan gene expression: a possible connection between biotic and abiotic stress responses. Molecular Plant-Microbe Interactions 12:951-959. https://doi.org/10.1094/mpmi.1999.12.11.951
- Upadhyay, S. K., D. P. Singh and R. Saikia. 2009. Genetic diversity of plant growth promoting rhizobacteria from rhizospheric soil of wheat under saline conditions. Current Microbiology 59:489-496. https://doi.org/10.1007/s00284-009-9464-1
- Van de P.B., D. Smet and S, D. Van Der. 2015. Ethylene and hormonal crosstalk in vegetative growth and development. Plant Physiology 169:61-72. https://doi.org/10.1104/pp.15.00724
- Wang, Z.Y., H. Seto, S. Fujioka, S. Yoshida and J. Chory. 2001. BRI1 is a critical component of a plasma membrane receptor for plant steroids. Nature 410:380-383. https://doi.org/10.1038/35066597
- Wei, Q., Y. Guo, H. Cao and B. Kuai. 2011. Cloning and characterization of an *AtNHX2*-like Na⁺/H⁺ antiporter gene from *Ammopiptanthus mongolicus* (Leguminosae) and its ectopic expression enhanced drought and salt tolerance in *Arabidopsis thaliana*. Plant Cell Tissue Organ Culture 105:309-316. https://doi.org/10.1007/s11240-010-9869-3
- Wu, Q.S., and R.X. Xia. 2006. Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well-watered and water stress conditions. Journal of plant physiology:163:417-425. https://doi.org/10.1016/j.jplph.2005.04.024
- Zhang, J., X. Yunyuan, H. Qing and C. Kang. 2009. Deep sequencing of *Brachypodium* small RNAs at the global genome level identifies microRNAs involved in cold stress response. *BMC Genomics* 10:449. https://doi.org/10.1186/1471-2164-10-449
- Zheng, Z., S.A. Qamar, Z. Chen and T. Mengiste. 2006. Arabidopsis WRKY33 transcription factor is required for resistance to necrotrophic fungal pathogens. The Plant Journal 48:592-605.
 - https://doi.org/10.1111/j.1365-313X.2006.02901.x

