

Study of Metabolomic Changes caused by Biotic & Abiotic Stress in Fabaceae

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Abstract

Many biotic and abiotic stresses can be experienced by plants because they are sedentary organisms, which can stunt their growth and result in significant yield losses. For instance, plants are more stressed by the combination of drought and root-infecting pathogens than by either stress alone. While much is known about the modifications to metabolism, chemical technology, and body structure that occur in Fabaceae plants when they are young, little is known about how plants react to multiple stresses when subjected to single stresses. This is crucial for developing genetic propagation strategies that obtain a high and consistent yield within the subject while retaining equilibrium with plant defence reaction mechanisms. More research is needed to fully comprehend how legume plants identify and react to combinations of stress signals that occur simultaneously or sequentially for launching a range of adaptive responses.

Key Terms

Biotic stress, Abiotic stress, Drought, Plant Growth promoting bacteria, grain legumes, signalling.

Introduction

The Leguminosae or Fabaceae plant family includes legumes, which are plant fruits, and the plant is known as a bean or pea plant. The Leguminosae family comprises 19,400 species grouped into approximately 730 clusters, making it the third-largest family of plants that bloom in the world. The main feature that distinguishes members of this family is their fruit, referred to as legumes. This family includes species ranging in size from dwarf herbs found in arctic and alpine vegetation to enormous trees found in tropical forests. Leguminosae is divided into three subfamilies: Mimosoidae, Caesalpinioideae, and Papilionoidea. The Fabaceae family of legumes is used by people all over the world due to their high protein, vitamin, and mineral content, which adds texture to food. Because of their nutritional profile, regular consumption can aid in the reduction of micronutrient deficiencies in individuals residing in developing nations. Because of their ability to adjust atmospheric nitrogen (N), legumes have a promising future in conservative agriculture. This is accomplished by Rhizobium bacteria found in root nodules. Bacteria and legumes have developed symbiotic relationships, allowing them to fix free nitrogen for plants in exchange for legumes providing fixed carbon produced by photosynthesis. Legumes' preference for semi-aerated to aerated habitat is related to a nitrogen-demanding metabolism. This is thought to be an adaptation for unpredictable habitats.

In the roughly 3.7 billion acres of global arable land, different abiotic and biotic stressors always restrict crop productivity. This is an issue that is far from resolved and will only get

worse by limiting plant growth and productivity. Drought-related lower yield problems are severe; large-scale desalinization is not yet practical; and irrigation will not be a long-term viable solution as water becomes scarcer. In many cropping regions, low and high temperatures, acidic soils, and soils high in metal ions all lower productivity. The capacity of plants to detect a variety of environmental factors and initiate signalling pathways that trigger specific reactions is vital. Research on plant-abiotic interactions is still very interesting because it can help us understand plant biology on a fundamental level and facilitate efforts to develop better crop plants.

There may be a variety of ways to solve these issues, but in order to lessen their effects and boost agricultural yields, we must gain a deeper grasp of the physiology and genetics of plant stress tolerance. To maximize yields, it is imperative to breed for tolerance, if not resistance, to biotic and abiotic stress. Growing crop yields is a top priority in developing nations because population growth there is the highest and there is a corresponding increase in demand for food. Furthermore, lower latitudes, which are mainly inhabited by developing nations, will be severely impacted by the effects of climate change.

Study objectives

- To comprehend the difficulties that plants encounter in surviving in their natural habitat.
- To assess the limiting factors through in-depth physiology research on plants.
- Developing new, cutting-edge methods to boost plant productivity in light of changing global conditions and population growth.

Stress: Abiotic and Biotic

According to [1], biotic and abiotic stresses cause distinct and overlapping resistance responses that are shared by many plant species' signalling pathways and genes. As stated by [2], Abiotic stress tolerance is typically regulated **by** polygenic inheritance and may be impacted by several interconnected mechanisms. Plant-pathogen interactions that are compatible or incompatible frequently have quantitative aspects as well. According to recent research, plants may be able to withstand both biotic and abiotic stresses at the same time. However, in order to completely comprehend this ability, it is not possible to simply extrapolate the findings of studies where individual stresses are applied separately.

ABIOTIC STRESS

The vast array of responses that plants have to their environment is controlled by complex signalling and regulatory networks. The levels of molecules, metabolism, cells, physiology, and morphology are all affected by these reactions. One of the most prevalent ways in which plants respond to stress, particularly abiotic stress, is through phenotypic plasticity. This phenomenon arises from an intricate system of endogenous signal transmission between the aerial portion (stem) and the roots. Plant growth and productivity are restricted by the availability of nutrients and water, by conditions that cause a water deficit (such as salinity, temperature, and insolation), and by environmental contaminants. Osmotic stress can arise directly from drought, salinity, and low temperature-induced dehydration; it can also arise indirectly from freezing and hypoxia, which affect water uptake and loss.

Plants must be able to detect stress in order to respond to it. This necessitates both the ability to sense the stress or stimulus that starts the signalling pathway and builds the response, as well as the ability for individual cells to transmit information throughout the entire plant. The last step entails incorporating modifications in cellular gene expression into the plant's overall reaction, which could impact the plant's capacity for growth, development, and even reproduction [3].

Saline Stress

It was found that plants more vulnerable to saline stress showed less proline accumulation, whereas plants with lower tolerance to NaCl showed higher proline accumulation. This is a typical outcome of these kinds of investigations. Plants use osmotic mechanisms to store metabolites like proline, soluble sugars, and specific ions and to help them maintain their water content. This allows plants to withstand salinity stress. Proline therefore functions as a protective molecule when exposed to salt stress.

An additional factor under investigation is the morphological impact caused by salt stress. In this instance, the research using *Glycine max* resulted in a height reduction of up to 76%. Comparable outcomes were seen with *C. siliqua*, where it was noted that the plant's root system and stem had shrunk by 8 and 4 cm, respectively[4]. Cells under salt stress can experience ionic toxicity as well as osmotic stress.

Water Stress

It is discovered that there is a 57, 39, and 42% decrease in grain, pod, and seed yield for *V. unguiculata*, respectively, when comparing studies of water stress caused by drought[5]. Conversely, a decrease in dry weight has been noted in *E. velutina* seeds that have been exposed to varying osmotic potentials, primarily in the stem as opposed to the roots. *A. hypogaea* was the subject of a similar study, in which it was discovered that the species' drought-tolerant variety experienced a nearly 50% drop in dry weight.

The primary indicator of drought is hyperosmotic stress, also known as osmotic stress, because hypoosmotic conditions typically do not pose a serious threat to plant cells. Complex secondary effects of salt stress and drought include metabolic dysfunction, oxidative stress, and damage to cellular constituents like proteins, lipids in membranes, and nucleic acids. Certain cellular reactions originate from primary stress signals, whereas secondary signals are the main cause of other cellular reactions [6].

Thermal Stress

During seed germination, a significant impact of heat stress was observed. When *E. velutina* seeds were subjected to thermal stress, and germination was seen across a broad temperature range. This meant that 5, 40, and 45 °C were the temperatures at which no germination occurred, suggesting that 25 to 30 °C is the ideal range for germination[7].

Metal Stress

Even though some metals are essential to how plants grow and evolve, excessive concentrations of a particular metal can be hazardous and hinder the growth of the plant. In precise terms, cadmium (Cd) hinders plant growth by changing the minerals in the soil, stopping vegetation from absorbing vital nutrients for healthy development. Additionally,

immoderate Cd in the soil depletes the microbial network, further impeding plant growth. [8]. However, the toxicity of the metal Cicer arietinum affected the species and led to a reduction in research done to find tolerance to Cd stress and resulted in a 10% decrease in the germination of seeds.

Table 1.Examination on abiotic stress in Fabaceae plants

Plant Name	Type of Stress Induced	Type of Study	Parameter Studied
<i>Arachis hypogaea</i>	Water Stress	Invitro Seed Germination [9]	Changes in the MDA, H2O2, and proline content, as well as in the enzymatic activity of CAT, POX, GR, APX, and CAT.
<i>Vigna unguiculata</i>	Water stress	Water supply is a limiting factor in a field study[5]	APX, CAT activity. Proline, chlorophyll, and carotenoids quantification.
<i>Erythrina velutina</i>	Salt, hydric and thermic stress	Research on in vitro germination of seeds [7]	Morphological parameters as % of seed germination.
<i>Ceratonia siliqua L</i>	Salt stress	Field investigation of plant growth at varying NaCl concentrations [4]	Chlorophyll, proline, and sugar content
<i>Vicia faba</i>	Salt stress	Analyzing and contrasting how different NaCl concentrations affect the development of plant species varieties [10]	Comparison and analysis of proline, oxidative enzymes, total sugars, total free amino acids, mineral concentration, and seed production
<i>Glycine max</i>	Salt stress	Field investigation of plant growth at varying NaCl concentrations [11][12]&[13]	Biochemical and morphological characteristics like growth, dry weight, ion concentration, proline accumulation, and diamine oxidase

<i>Lotus corniculatus</i>	Salt stress	NaCl concentrations in hydroponic culture [11][12] & [3]	Na ⁺ and Cl ⁻ ions, soluble sugars, proline, and glycine betaine were all analyzed for content.
<i>Cicer arietinum</i>	Toxic heavy metal (Cd) stress	field research conducted during the plant's various reproductive stages [14]	field research conducted during the plant's various reproductive stages [14]
<i>Phaseolus vulgaris</i>	Toxic heavy metal cadmium (Cd)-related stress	Research on seedlings and in vitro germinated seeds [15]	Growth of seedlings, percentage germination, and index of tolerance and phytotoxicity.
<i>Lens culinaris</i>	Stress brought on by Cadmium (Cd), a hazardous heavy metal	Research on seedlings and in vitro germinated seeds [15]	Growth of seedlings, percentage germination, and index of tolerance and phytotoxicity.

BIOTIC STRESS

Certain pathogens target a greater number of stressed plants by exploiting their weakened basal defenses, further damaging the plants; other pathogens need persistently humid conditions to develop and multiply; and plants that are stressed by drought appear to be more resilient. Evidence of a known agronomic interaction between Fusarium wilt and drought exists; dry weather and particularly severe drought favor the disease's progression. Therefore, depending on how much a pathogen interacts physiologically with its plant host, the impact of climate change on the relationship between plants and pathogens may vary [16].

Because they obtain their nutrients from living cells, pathogens that are biotrophic or hemi biotrophic, for example, engage in prolonged physiological interactions with their hosts. As a result, elements that influence plant growth, like a lack of water, may also have an impact on how host tissues colonize.

As was previously mentioned, climate change is already having an effect on the "disease triangle," which describes the relationship among hosts, pathogens, and surroundings. On the other hand, it is predicted that crop quality and productivity will suffer due to increased experience with a combination of abiotic and biotic stresses. To boost crop yield, extensive research is required to comprehend the mechanisms that underlie plant reactions to successive or simultaneous exposure to various stresses, both biotic and abiotic.

Responses of Plant Protection to Abiotic and Biotic Stresses

When a pathogen attacks a plant, it releases a variety of metabolic changes in response, such as proteins involved in pathogenesis, glutathione peroxidase and ascorbate (which scavenge H₂O₂), enzymes, phenols, phytoalexins, xyloglucans, and substances that mimic lignin. These metabolic changes impact morpho-physiological traits, which have been shown to be markedly altered in the context of combined stress. According to [17], these traits include root morphology, stomatal movement, leaf water potential, cell wall reinforcement, cell membrane stability, and plant growth. [18] state that in reaction to infection and injury, the phenylpropanoid pathway is essential for the synthesis of lignin, flavonoids, and phytoalexins. For instance, it has been suggested that genes associated with *A. thaliana*'s secondary cell wall influence how the plant reacts to a combined wilt and drought infection, but not when a combined foliar pathogen and drought infection occurs.

Plant hormone signalling

Salicylic and jasmonic acids (SA and JA, respectively), ethylene signalling, and ABA are the ways in which plants react to both biotic and abiotic stresses. According to reports, *Arabidopsis*' resistance to this fungus is mediated by ERF1. It was also observed that this fungus has the capacity to monopolize the plant JA pathway, exacerbating the illness's symptoms as well as eventually causing the plant to die. Defense and stress-responsive gene expression are modulated in response to combined stresses by a complex balance between the antagonistic interactions of ABA, a major regulator of the drought stress response, and the JA-ethylene signalling pathways.[19] states that when there are mixed strains, the initial signalling things work non-specifically over JA as well as ABA. However, the stress signal's modulation, crosstalk, and the events that follow downstream depends on the confluence of pressures that the plant experiences.

Genes that protect proteins and cellular components under abiotic stress, such as RNA chaperones, LEA proteins, and dehydrins, have been identified to alleviate the antagonistic relationship with the signalling of biotic stress. A more effective way to handle biotic and abiotic interactions is to combine methods to identify genes involved in multiple resistances and multiple sources of stress resistance.

Because auxin affects every facet of a plant's development and growth, it is commonly referred to as a "master hormone." The main way that this phytohormone influences target genes' transcriptional control is via transcription factors known as ARFs. Such transcription factors have been identified as biotic and abiotic stress responses' auxin-acting mediators. But because auxin homeostasis interacts with the ABA and SA signalling pathways, it's also critical for stress adaptation. For example, auxin has a negative effect on defence reactions mediated by SA in pathogen-infected *Arabidopsis*.

In addition to phytohormone balance, additional interrelated signalling pathways, such as those that produce ROS and sense Ca²⁺, the synthesis of kinase cascade activation, and secondary metabolites, are also important for maintaining the balance between defence and development under biotic and abiotic stress conditions. For example, RBoh polypeptides produce reactive oxygen species (ROS) that trigger stomatal closure and hypersensitive cell death brought on by ABA following pathogen elicitor recognition [1]. Furthermore, genes such as kinases and transcription factors that are involved in the crosstalk between signalling

cascades are indirectly regulated by ROS and Ca²⁺ responding to the interaction between abiotic and biotic stress. More specifically, it is well known that the plant responds to biotic and abiotic stresses by means of JA, ET, or SA signalling, which is mediated by WRKY transcription factors. For example, during seed germination, overexpression of AtWRKY30 in *A. thaliana* increased abiotic stress tolerance. ROS-induced oxidative stress and infection assault are the causes of AtWRKY30.

Despite the significance of transcriptional regulation for stress adaptations, microRNAs (miRNAs) mediate post-transcriptional regulation that may be necessary in order to synchronise environmental and developmental reactions [20]. [21] describe miRNAs as small, naturally occurring non-coding RNAs with a nucleotide count of roughly 21–22. By cleaving or suppressing the translation of their mRNA targets, they act as negative regulators of gene expression. One novel way to modulate differential gene expression in plants is to use miRNA control to alter the abundance of mRNA transcripts. As a result, miRNAs are emerging as the next generation of targets for genetic engineering meant to improve the agronomic characteristics of crops.

Literature Review

1. According to studies of [22], [23], plants need an adaptable and energy-efficient system to help them adapt to a particular stress or mixture of stresses at the lowest possible cost. Due to the priming effect, a first stress that comes before another stress may either persist or make the plants more vulnerable to the second stress.

2. [24] suggested Abiotic stresses, like drought or nutrient deprivation, are known to weaken plant defenses and increase vulnerability to necrotic pathogens, which can include facultative pathogens which are otherwise weakly virulent. But it appears that the same abiotic stress minimizes plants' vulnerability to biotrophic pathogens.

3. [25] investigated how down-regulating heat shock transcription factors could reduce the efficiency of a plant's response to heat stress as combined with a viral infection..

4. [26]; [27] studied different genetic loci that may mediate allowance for individual abiotic stresses as well as joined biotic and abiotic stresses, according to research on genome-wide associations using *Arabidopsis thaliana* as a model plant.

5. [28]; [29]; [30]; [31] Research indicates that in order to sustain growth and reproduction under various stressors, contradictory stress reactions are ranked or in balance within the plant's body in a spatially/ temporally specific manner.

Prospects for the Future of Integrated Resistance Breeding with Abiotic and Biotic Stress in Legume

A variety of legumes resistant to multiple stresses would be available for the development of sustainable agriculture by decreasing the need for pesticides and increasing legume production in difficult environments.

Based on existing data and projections about the effects of climate change, plants are expected to be more susceptible to biotic and/or abiotic stress and to experience interactions between stresses more frequently. To sustain high yield potential in this stressed environment, biotic and abiotic stress resistance should be the primary factors driving legume breeding. To

satisfy consumer preferences in a variety of markets, breeding efforts must be synchronized with the need to maintain particular market-class attributes and quality traits.

Site-specific considerations such as soil fertility, temperature, and availability of water are used to determine objectives related to resistance to biotic and abiotic stress. However, some restrictions are becoming more widespread in all regions that grow legumes. A few instances are the diseases that cause wilt and root rot, which are widespread problems exacerbated by the rising frequency of water scarcity. Moreover, biological control has gained more attention lately and may be a helpful addition to integrated resistance breeding and plant defense. Biological control uses antagonistic bacterial and fungal agents to counter pathogens. Moreover, thiophanate-methyl seed coating plus soil treatment with *Trichoderma* spp. reduced the incidence of *F. solani* and *F. oxysporum* in common beans. Researchers discovered a positive correlation between the enhanced capacity of bean plants' peroxidase, polyphenoloxidase, and chitinase enzymes to resist soilborne pathogen infection and the biocontrol activation of *Trichoderma* isolates.

Furthermore, applying growth-promoting rhizobacteria to plants may boost crop yield and fortify the plants' resistance to abiotic stresses. It is commonly known that, in response to certain drought-resistant, rhizosphere-competent bacteria, they enhance plant health and stimulate growth in response to abiotic stressors. For instance, in drought-stressed common beans, rhizobium was able to boost plant growth, nutrient content, and yield [32]. On the other hand, *Pseudomonas putida* was shown to reduce the effects of drought stress and support chickpea recovery by up-regulating several stress-responsive genes and increasing osmolytes and ROS production [33].

However, it is imperative to ensure that the diversity of landrace legumes is collected and conserved in ex situ gene banks, especially with the increasing use of uniform modern cultivars that reduce crop genetic diversity. The same warnings are applicable to native populations of wild relatives.

Research suggestions for future investigation

- Since the issue is quite urgent, governments should devise creative solutions utilizing omics applications to identify the stress marker genes. This is in light of climate change.
- Stress-resistant breeds that have been identified should be developed in accordance with the world's expanding population.
- Crop varieties are rendered ready to withstand stress by early detection of natural disasters.

Summary

Breeding for stress resistance is a challenging task. Each combination of pathogen and host should be treated separately in cases of abiotic stress, as many specific relationships might be required for the phenotypic reaction, although some interactions may be universally applicable. In combined stress environments, multi-trait screening of these genetic resources is necessary to identify advantageous alleles in important genes because, in non-stressful conditions, genotype-by-environment interactions suggestive of adaptive plasticity cannot be evaluated.

The ability to successfully develop legume varieties resistant to biotic and abiotic stresses is contingent upon both the inheritance of resistance and the accessibility of high-quality points of resistance. Based on the current natural variation, association mapping studies can be used to identify and locate the genes governing these traits. These findings can then be verified through functional analysis with data from contrasting accessions' transcriptome, proteome, and metabolomics. These may be genes, such as disease R-genes and, additionally, genes for induced abiotic stress resistance, that contribute to the physical barriers that prevent pathogen penetration. It seems that resilience to abiotic conditions like drought is genetically simpler, given that resistance to pathogens is often attributed to a single major gene.

REFERENCES

1. Fujita M, Fujita Y, Noutoshi Y, Takahashi F, Narusaka Y, Yamaguchi-Shinozaki K, Shinozaki K (2006) Crosstalk between abiotic and biotic stress responses: a current view from the points of convergence in the stress signalling networks. *Curr Opin Plant Biol* 9:436–442. <https://doi.org/10.1016/j.pbi.2006.05.014>
2. Pathania A, Sharma SK, Sharma PN (2014) Common bean. In: Singh M, Bisht I, Dutta M (eds) Broadening the genetic base of grain legumes. Springer, New Delhi
3. Ascencio, J. (2005). Efecto del estrés abiótico sobre la fisiología de malezas y cultivos. *Anales de Botánica Agrícola*, (12), 41-47
4. El Kakhahi, R., Mouhajir, A., Bachir, S., Lemrhari, A., Rachid, Z., Chitt, M., & Errakhi, R. (2015). Morphological and Physiological Analysis of Salinity Stress Response of Carob (*Ceratonia siliqua* L.) in Morocco. *Science international*, 3(3), 73–81.
5. Cardona, C., & Jarma-orozco, A. (2014). Respuestas fisiológicas y bioquímicas del fríjol caupí (*Vigna unguiculata* L. Walp.) bajo déficit hídrico. *Revista Colombiana de Ciencias*, 8(2), 250-261.
6. Zhu J. K. (2016). Abiotic Stress Signalling and Responses in Plants. *Cell*, 167(2), 313-324. <https://doi.org/10.1016/j.cell.2016.08.029>.
7. Sena, E. M. N. D. (2017). Vulnerabilidade de acessos de sementes de *Erythrina velutina* Willd. (Fabaceae) a estresses abióticos. Dissertação (Mestrado Acadêmico em Recursos Genéticos Vegetais) - Universidade Estadual de Feira de Santana, Feira de Santana.
8. Wang, C., Zhang, S. H., Wang, P. F., Qian, J., Hou, J., Zhang, W. J., Lu, J. (2009). Excess Zn Alters the Nutrient Uptake and Induces the Antioxidative Responses in Submerged Plant *Hydrilla verticillata* (L.f Royle). *Chemosphere* 76 (7), 938-945.
9. Akçay, U., Akca, O., Kavas, M., Yıldız Özer, L., Yilmaz, C., Oktem, H., & Yücel, M. (2010). Drought-induced oxidative damage and antioxidant responses in peanut (*Arachis hypogaea* L.) seedlings. *Plant Growth Regulation*, (61), 21–28. <https://doi.org/10.1007/s10725-010-9445-1>.
10. Abdelhamid, M., Sadak, M., Schmildhalte, El-Saad, M. (2013). Interactive effects of salinity stress and nicotinamide on physiological and biochemical parameters of faba bean plant. *Acta Biológica Colombiana*, (18), 499-509.

11. Amirjani, M. (2010). Effect of Salinity Stress on Growth, Mineral Composition, Proline Content, Antioxidant Enzymes of Soybean. *American Journal of Plant Physiology*, (6), 350-360. <https://dx.doi.org/10.3923/ajpp.2010.350.360>
- 12&13. Azarafshan, M., & Abbaspour, N. (2014). Growth and physiological parameters under salinity stress in *Lotus corniculatus*. *Iranian Journal of Plant Physiology*, 4(2), 991-997.
14. Baweja, P., Kumar, D., Maheshwari, V., Singla, M., Ritu, Parul., Akshita. (2020). Effect of Cadmium stress on Growth and Development of *Cicer arietinum* (Fabaceae). *Society for Environment and Development* (India), (15), 49-59.
15. Añazco, K. V. R. (2019). Efecto del cadmio sobre la germinación y crecimiento de *Lens culinaris* Medik. (Lenteja), *Oryza sativa* (Arroz) y *Phaseolus vulgaris* L. (Frejol) (Tesis de Licenciatura, Universidad de Guayaquil, Colombia).
16. Eastburn DM, McElrone AJ, Bilgin DD (2011) Influence of atmospheric and climatic change on plant–pathogen interactions. *Plant Pathol* 60:54–69. <https://doi.org/10.1111/j.1365-3059.2010.02402.x>.
17. Irulappan V, Senthil-Kumar M (2018) Morpho-physiological traits and molecular intricacies associated with tolerance to combined drought and pathogen stress in plants. In: Gosal SS, Wani SH (eds) *Biotechnologies of crop improvement, vol 3. Genomic Approaches*. Springer International Publishing, Cham, pp 59–74.
18. Fraire-Velázquez SI, Rodríguez-Guerra RI, Sánchez-Calderón L (2011) Abiotic and biotic stress response crosstalk in plants. In: Shanker A, Venkateswarlu B (eds) *Abiotic stress response in plants—physiological, biochemical and genetic perspectives*. Intech Open. <https://doi.org/10.5772/23217>
19. Ramegowda V, Senthil-Kumar M (2015) The interactive effects of simultaneous biotic and abiotic stresses on plants: mechanistic understanding from drought and pathogen combination. *J Plant Physiol* 176:47–54. <https://doi.org/10.1016/j.jplph.2014.11.008>
20. Shriram V, Kumar V, Devarumath RM, Khare TS, Wani SH (2016) MicroRNAs as potential targets for abiotic stress tolerance in plants. *Front Plant Sci* 7:817. <https://doi.org/10.3389/fpls.2016.00817>
21. Jones-Rhoades MW, Bartel DP, Bartel B (2006) MicroRNAs and their regulatory roles in plants. *Annual Rev Plant Biol* 57:1, 19–53. <https://doi.org/10.1146/annurev.arplant.57.032905.105218>
22. Pandey P, Irulappan V, Bagavathiannan MV, Senthil-Kumar M (2017) Impact of combined abiotic and biotic stresses on plant growth and avenues for crop improvement by exploiting physiomorphological traits. *Front Plant Sci* 8:537. <https://doi.org/10.3389/fpls.2017.00537>
23. Mauch-Mani B, Baccelli I, Luna E, Flors V (2017) Defense priming: an adaptive part of induced resistance. *Annu Rev Plant Biol* 68:485–512. <https://doi.org/10.1146/annurev-arplant-042916-041132>

24. Saijo Y, Loo EPI (2019) Plant immunity in signal integration between biotic and abiotic stress responses. *New Phytol.* <https://doi.org/10.1111/nph.15989>
25. Anfoka G, Moshe A, Fridman L, Amrani L, Rotem O, Kolot M, Zeidan M, Czosnek H, Gorovits R (2016) Tomato yellow leaf curl virus infection mitigates the heat stress response of plants grown at high temperatures. *Sci Rep.* 6:19715.
26. Thoen MPM, Davila Olivas NH, Kloth KJ, Coolen S, Huang P-P, Aarts MGM, Bac-Molenaar JA, Bakker J, Bouwmeester HJ, Broekgaarden C, Bucher J, Busscher-Lange J, Cheng X, Fradin EF, Jongsma MA, Julkowska MM, Keurentjes JJB, Ligterink W, Pieterse CMJ, Ruyter-Spira C, Smant G, Testerink C, Usadel B, van Loon JJA, van Pelt JA, van Schaik CC, van Wees SCM, Visser RGF, Voorrips R, Vosman B, Vreugdenhil D, Warmerdam S, Wiegiers GL, van Heerwaarden J, Kruijer W, van Eeuwijk FA, Dicke M (2017) Genetic architecture of plant stress resistance: multi-trait genome-wide association mapping. *New Phytol* 213:1346–1362. <https://doi.org/10.1111/nph.14220>
27. Davila Olivas NH, Kruijer W, Gort G, Wijnen CL, van Loon JJA, Dicke M (2017) Genome-wide association analysis reveals distinct genetic architectures for single and combined stress responses in *Arabidopsis thaliana*. *New Phytol* 213:838–851. <https://doi.org/10.1111/nph.14165>
28. Smakowska E, Kong J, Busch W, Belkhadir Y (2016) Organ-specific regulation of growth-defense tradeoffs by plants. *Curr Opin Plant Biol* 29:129–137. <https://doi.org/10.1016/j.pbi.2015.12.005>
29. Karasov TL, Chae E, Herman JJ, Bergelson J (2017) Mechanisms to mitigate the trade-off between growth and defense. *Plant Cell* 29:666–680. <https://doi.org/10.1105/tpc.16.00931>
30. Betsuyaku S, Katou S, Takebayashi Y, Sakakibara H, Nomura N, Fukuda H (2017) Salicylic acid and jasmonic acid pathways are activated in spatially different domains around the infection site during effector-triggered immunity in *Arabidopsis thaliana*. *Plant Cell Physiol* 59:8–16. <https://doi.org/10.1093/pcp/pcx181>
31. Berens ML, Wolinska KW, Spaepen S, Ziegler J, Nobori T, Nair A, Krüler V, Winkelmüller TM, Wang Y, Mine A, Becker D, Garrido-Oter R, Schulze-Lefert P, Tsuda K (2019) Balancing trade-offs between biotic and abiotic stress responses through leaf age-dependent variation in stress hormone cross-talk. *Proc Natl Acad Sci* 116:2364–2373. <https://doi.org/10.1073/pnas.1817233116>
32. Yanni Y, Zidan M, Dazzo F, Rizk R, Mehesen A et al. (2016) Enhanced symbiotic performance and productivity of drought stressed common bean after inoculation with tolerant native rhizobia in extensive fields. *Agric, Ecosyst Environ* 232:119–128. <https://doi.org/10.1016/j.agee.2016.07.006>
33. Tiwari S, Lata C, Chauhan PS, Nautiyal CS (2016) *Pseudomonas putida* attunes morphophysiological, biochemical and molecular responses in *Cicer arietinum* L. during drought stress and recovery. *Plant Physiol Biochem* 99:108–117. <https://doi.org/10.1016/j.plaphy.2015.11.001>