Check for updates

Received: 11 February 2024 | Revised: 7 April 2024 | Accepted: 10 April 2024

DOI: 10.1111/ppl.14307

REVIEW

Physiologia Plantarum

Harnessing Phytohormones: Advancing Plant Growth and Defence Strategies for Sustainable Agriculture

Jamin Ali[1] | Mohammad Mukarram[2] | James Ojo[3] | Nancy Dawam[4] | Riyazuddin Riyazuddin[5] | Hamed A. Ghramh[6,7] | Khalid Ali Khan[6,8] | Rizhao Chen[1] | Daniel Kurjak[9,10] | Ahmet Bayram[11]

[1]College of Plant Protection, Jilin Agricultural University, Changchun, PR China

[2]Food and Plant Biology Group, Department of Plant Biology, Universidad de la República, Montevideo, Uruguay

[3]Department of Crop Production, Kwara State University, Malete, Nigeria

[4]Department of Zoology, Faculty of Natural and Applied Sciences, Plateau State University Bokkos, Diram, Nigeria

[5]Instituto de Bioingeniería, Universidad Miguel Hernández, Elche, Spain

[6]Centre of Bee Research and its Products, Research Centre for Advanced Materials Science, King Khalid University, Abha, Saudi Arabia

[7]Biology Department, Faculty of Science, King Khalid University, Abha, Saudi Arabia

[8]Applied College, King Khalid University, Abha, Saudi Arabia

[9]Institute of Forest Ecology, Slovak Academy of Sciences, Zvolen, Slovakia

[10]Faculty of Forestry, Technical University in Zvolen, Zvolen, Slovakia

[11]Plant Protection, Faculty of Agriculture, Technical University in Zvolen, Zvolen, Slovakia

Correspondence
Rizhao Chen,
Email: rizhaochen@jlau.edu.cn

Funding information
Slovak Research and Development Agency, Grant/Award Number: APVV-21-0224; Slovak Grant Agency for Science, Grant/Award Number: VEGA 1/0392/22

Edited by R. Gupta

Abstract

Phytohormones, pivotal regulators of plant growth and development, are increasingly recognized for their multifaceted roles in enhancing crop resilience against environmental stresses. In this review, we provide a comprehensive synthesis of current research on utilizing phytohormones to enhance crop productivity and fortify their defence mechanisms. Initially, we introduce the significance of phytohormones in orchestrating plant growth, followed by their potential utilization in bolstering crop defences against diverse environmental stressors. Our focus then shifts to an in-depth exploration of phytohormones and their pivotal roles in mediating plant defence responses against biotic stressors, particularly insect pests. Furthermore, we highlight the potential impact of phytohormones on agricultural production while underscoring the existing research gaps and limitations hindering their widespread implementation in agricultural practices. Despite the accumulating body of research in this field, the integration of phytohormones into agriculture remains limited. To address this discrepancy, we propose a comprehensive framework for investigating the intricate interplay between phytohormones and sustainable agriculture. This framework advocates for the adoption of novel technologies and methodologies to facilitate the effective deployment of phytohormones in agricultural settings and also emphasizes the need to address existing research limitations through rigorous field studies. By outlining a roadmap for advancing the utilization of phytohormones in agriculture, this review aims to catalyse transformative changes in agricultural practices, fostering sustainability and resilience in agricultural settings.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Authors. *Physiologia Plantarum* published by John Wiley & Sons Ltd on behalf of Scandinavian Plant Physiology Society.

1 | INTRODUCTION

Plants are remarkable organisms that possess an intricate system of chemical signaling to regulate various physiological processes (Tuteja and Sopory, 2008). Among these signaling molecules, phytohormones, also known as plant hormones, stand out as key players. They orchestrate crucial aspects of plant growth, development, and responses to environmental challenges (Weyers and Paterson, 2001). Phytohormones are naturally occurring organic compounds produced in specific plant tissues, where they act as messengers, transmitting information and coordinating responses throughout the entire organism (Koepfli et al., 1938; Fahad et al., 2015).

The discovery of phytohormones dates back to the early 20th century when scientists observed that specific chemicals had profound effects on plant growth and behaviour, even when present in minute concentrations (Koepfli et al., 1938; Torrey, 1985; Pérez and Goossens, 2013). Since then, extensive research has unveiled multiple classes of phytohormones, each with distinct functions and regulatory roles (Letham, 1969; Hirsch et al., 1997; Pérez and Goossens, 2013; Wani et al., 2016). The complex interplay of these phytohormones ensures the harmonious development of plants from germination to reproduction (Fahad et al., 2015; Zhao et al., 2021). Understanding these intricate hormonal networks carries significant implications for agriculture and sustainable food production. Harnessing phytohormones has the potential to improve crop yield, quality, and resilience to environmental challenges (Choudhary et al., 2021; Hirayama and Mochida, 2022).

Similarly, phytohormones play a crucial role in plant defense against both abiotic and biotic stresses (Checker et al., 2018; Ku et al., 2018; Kumari et al., 2023). Previous studies have demonstrated their efficacy in safeguarding plants against biotic stressors, particularly insect herbivores, by modulating insect performance and behavior (War et al., 2012; Divekar et al., 2022). Phytohormone-induced direct defenses in plants involve the production of antifeedant, deterrent, or antibiotic compounds, such as alkaloids, benzoxazinoids, cyanogenic glycosides and glucosinololates, which directly impact insect physiology and behaviour (Loake and Grant, 2007; Fürstenberg-Hägg et al., 2013; Ibrahim et al., 2018). Additionally, phytohormone-induced indirect defenses include the release of volatile compounds from plants, which attract natural enemies of insect pests (Verma et al., 2016; Ali et al., 2023a). Such applications of phytohormones in plant defense highlight their potential for developing sustainable pest management programs in agricultural production (Razo-Belman and Ozuna, 2023).

An accumulating body of research focusing on the effects of phytohormones on plant growth and defence has been conducted globally. However, despite the promising potential of phytohormones as defense elicitors in plant defence mechanisms, agricultural production still struggles to adopt practical solutions (Agudelo-Morales et al., 2021; Hirayama and Mochida, 2022). The reliance on toxic chemical insecticides for pest control persists, highlighting a significant gap between research findings and practical application in the field (Fan et al., 2015). One contributing factor to this gap is the predominant focus of phytohormone research in laboratory settings, with limited dedicated efforts towards field trials and real-world application (Ciura and Kruk, 2018; Ali et al., 2023b). Consequently, there is an urgent need to reassess the current research landscape and redirect efforts towards providing practical solutions and establishing sustainable agricultural approaches (Han and Kahmann, 2019; Wyckhuys et al., 2023). By bridging the gap between laboratory studies and field applications, researchers can facilitate the translation of phytohormone research into actionable strategies for pest management and crop protection, thereby contributing to the advancement of sustainable agriculture practices and global food security.

In this review, we aim to explore the diverse world of phytohormones and illuminate their pivotal roles in plant growth and defence. The first part of this review focuses on the role of phytohormones in enhancing plant growth. Subsequently, we shift our attention to the intricate realm of plant defence strategies, where phytohormones play a central role in coordinating responses to various biotic stressors such as pathogens and herbivores. Moreover, we explore the concept of phytohormonal crosstalk; the integration of these signaling pathways allows plants to allocate resources efficiently and maintain a balance between growth and defence. By delving into the complexities of these hormonal networks, we aim to stimulate further research and innovation in the field of plant science, ultimately contributing to sustainable agricultural practices and global food security. Furthermore, we emphasize the untapped potential of phytohormones as a promising option for pest management. Despite their recognized effectiveness, agricultural practices still lag in implementing phytohormone-based solutions in the field. Consequently, farmers continue to rely heavily on toxic chemical insecticides. We also shed light on the limitations of phytohormone research conducted under real-world field conditions and the failure to translate current findings into actionable strategies for developing sustainable agriculture.

2 | UNDERSTANDING PHYTOHORMONES

Phytohormones, essential chemical messengers in plants, intricately regulate growth, development, and responses to environmental stimuli (Wani et al., 2016; Ku et al., 2018). Operating in complex networks, phytohormones interact synergistically or antagonistically to finely tune plant growth and defense (Pieterse et al., 2009; Checker et al., 2018; Y. Zhang et al., 2022). Classified into several major classes - Auxins, Gibberellins (GAs), Cytokinins (CKs), Abscisic Acid (ABA), and Ethylene (ET) - phytohormones collectively orchestrate adaptive responses and defense against stressors (Nadeem et al., 2016; Mearaji et al., 2021) (Figure 1). While auxin promotes cell division and tissue differentiation, ABA and auxins often exhibit antagonistic effects (Gehring et al., 1990; Asghar et al., 2019). Additionally, salicylic acid (SA) and jasmonic acid (JA) contribute significantly to both plant defense and growth (Ruan et al., 2019; Ding and Ding, 2020). These intricate interactions ensure plants adapt to varying conditions, balancing growth and stress responses (Verma et al., 2016; Zhao et al., 2021).

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

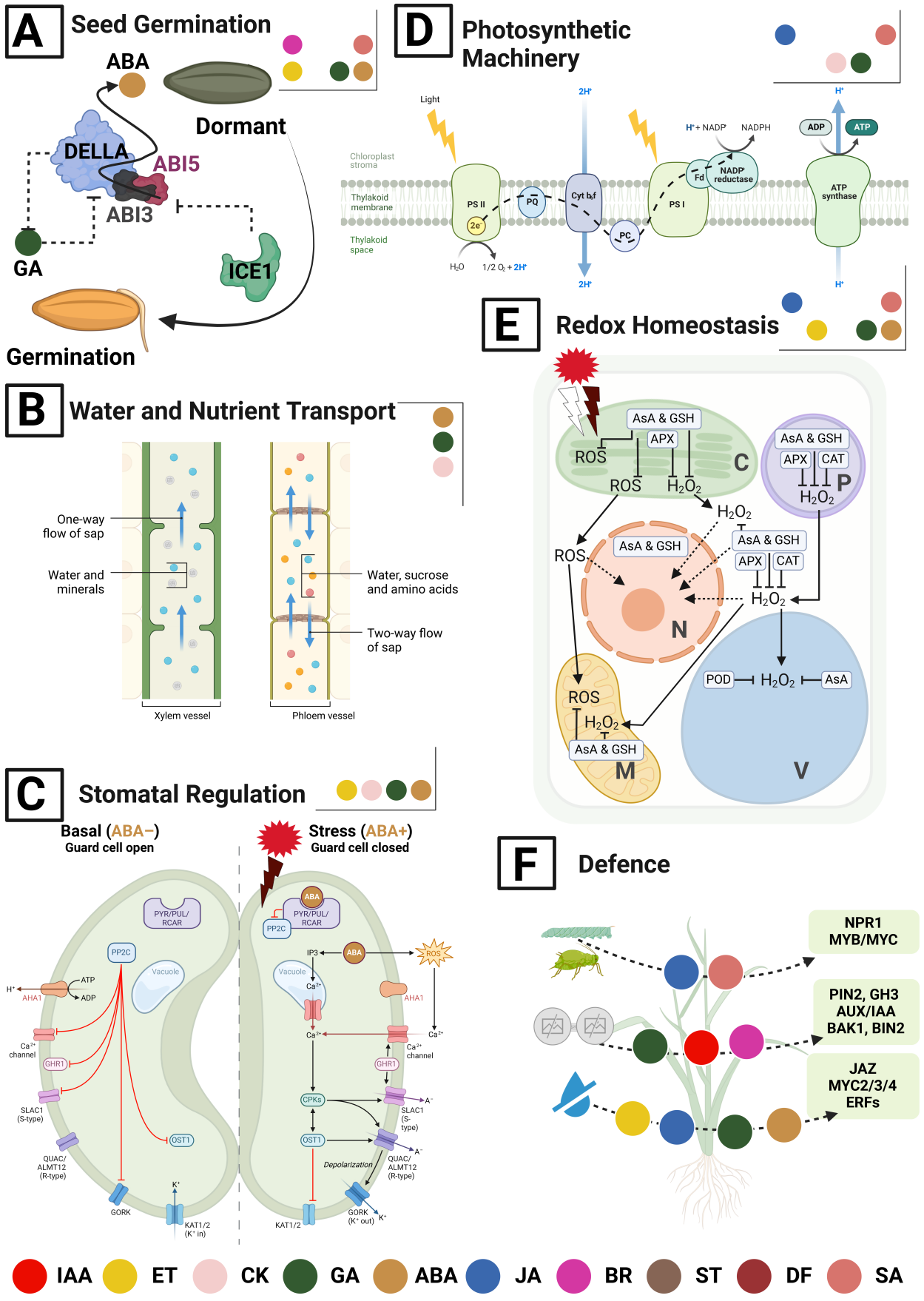


FIGURE 1 Legend on next page.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Phytohormones encompass distinct classes, each crucial for diverse plant processes, with context-dependent functions subject to modulation by hormone concentrations and environmental factors (Erb et al., 2012). These chemical messengers regulate cell division, tissue formation, fruit yield, stem elongation, root development, and stress responses (Yamaguchi and Kamiya, 2000; Tanimoto, 2005; Perrot-Rechenmann, 2010; Finkelstein, 2013). Notably, SA and JA contribute to plant defense while positively impacting growth by influencing chlorophyll fluorescence, photosynthesis-related activities, and promoting the growth of vegetative and reproductive organs (Rivas-San Vicente and Plasencia, 2011; Ghorbel et al., 2021; Sheteiwy et al., 2021). A recent study further supports the positive impact of JA on plant growth (Hewedy et al., 2023). Additional research is needed to unravel the intricate interactions and specific mechanisms by which these phytohormones modulate plant growth and adaptation to environmental challenges.

Phytohormones initiate complex signaling pathways, beginning with hormone perception at the cellular level, binding to specific receptors, and activating downstream responses (Santner and Estelle, 2009; Erb et al., 2012). Binding to distinct receptors, each class of phytohormones activates specific signal transduction pathways involving secondary messengers like calcium ions, cyclic nucleotides, or reactive oxygen species (Demidchik et al., 2017). These pathways lead to the activation of transcription factors, regulating gene expression and influencing various physiological processes such as cell division, elongation, differentiation, and defense responses (Dharmasiri et al., 2013) (Figure 1). Phytohormonal signaling pathways do not operate in isolation; they interact and crosstalk to finely modulate plant responses, allowing the integration of signals from multiple hormones and environmental cues (Santner and Estelle, 2009). The equilibrium between auxin and CK signaling determines growth patterns, and the interplay between salicylic acid and jasmonic acid pathways influences defense responses against pathogens and herbivores (Moubayidin et al., 2009; Schweiger et al., 2014). Transport and distribution of hormones throughout the plant further contribute to the regulation of growth and defense (Anfang and Shani, 2021). In conclusion, phytohormone signaling pathways intricately regulate plant growth and defense, providing valuable insights into plant physiology and adaptive responses.

3 | THE IMPACT OF PHYTOHORMONES ON PLANT GROWTH

Phytohormones collectively coordinate and regulate plant growth and development, facilitating adaptation to dynamic environmental conditions and defence against various stressors (Beveridge et al., 2003; Pozo et al., 2015; Lymperopoulos et al., 2018) (Table 1). For instance, auxin orchestrates precise control over cell division (Perrot-Rechenmann, 2010; Huang et al., 2019) as well as root and shoot formation (Perrot-Rechenmann, 2010; Martínez-de la Cruz et al., 2015), and leaf development (Peer et al., 2011; Zhang et al., 2020). Gibberellic acid (GA) exerts regulatory influence over critical processes such as fruit yield modulation (Sharma and Singh, 2009; Abbas et al., 2020), stem elongation (Yamaguchi and Kamiya, 2000; Sun, 2004), and root development, concurrently acting to alleviate abiotic stresses (Tanimoto, 2005; Rizza et al., 2017). **Cytokinins (CKs)** intricately govern cellular proliferation and differentiation and lateral shoot growth stimulation (Perilli et al., 2010; Skalák et al., 2019). Ethylene (ET) assumes a pivotal role in seed germination, flower development, leaf senescence, inhibiting root growth and orchestrating responses to environmental stressors (Dolan et al., 1994; Achard et al., 2003; Lin et al., 2009; Feng et al., 2015; Iqbal et al., 2017). Abscisic acid (ABA) profoundly influences dormancy, germination dynamics, and the enhancement of stress- responsive pathways (Finkelstein, 2013; Chen et al., 2020; Muhammad Aslam et al., 2022). Strigolactones, as plant-derived signaling compounds, play a pivotal role in orchestrating plant development and fostering symbiotic relationships between plant roots and soil microbes, serving as key components of

FIGURE 1 **The role of phytohormones on morpho-physiological aspects of higher plants under optimal and stressed conditions.** **A.** Ethylene (ET), brassinosteroids (BR), and salicylic acid (SA) influence seed physiology. However, abscisic acid (ABA) and gibberellin (GA), biosynthesis dominates seed physiology. GA and ABA signalling are antagonistic: where ABA promotes dormancy and GA germination. In dormant seeds, DELLA protein inhibits GA signalling and GA inactivates DELLA protein. DELLA, together with ABI3 and ABI5, trigger dormancy-inducing factors and promotes ABA biosynthesis genes while inhibiting GA biosynthesis genes. On the other hand, ICE1 (INDUCER OF CBF EXPRESSION 1) inactivates the binding of DELLA-ABI5 protein. Further, GA induces disassociation of DELLA-ABI5 and promotes germination. For further reading: (Waadt et al., (2022). **B.** Phytohormones influence the ascent of sap. Several studies have reported that cytokinin (CK), gibberellins, and abscisic acid can regulate water and nutrient transport during physiological and stressed environments. **C.** Stomatal regulation is largely controlled by abscisic acid. Nonetheless, ethylene, cytokinins, and gibberellin can interact with guard cell opening and closing under different environmental settings. ABA mediates stomatal regulation through signal transduction system consisting of PYR/PYL/RCAR type ABA receptors, group A 2C-TYPE PROTEIN PHOSPHATASE (PP2C) and SNF-1 (SUCROSE NON-FERMENTING 1) related protein kinase 2 (SnRK2) family of proteins. For further reading: (Mukarram et al., (2021). **D.** Similarly, jasmonates (JA), cytokinins, gibberellins, and salicylic acid interfere with photosystem II (PSII) and electron transport chain (ETC) of photosynthetic machinery. **E.** Jasmonates, ethylene, gibberellin, abscisic acid, and salicylic acid mediate redox homeostasis under stress conditions. These phytohormones are suggested to upregulate antioxidant activities, including superoxide dismutase (SOD), catalase (CAT), ascorbic peroxidase (APX), and peroxidase (POD) activities and glutathione (GSH) and ascorbic acid (AsA) contents in cellular organelles. These enzymatic and non-enzymatic antioxidants scavenge reactive oxygen species (H_2O_2, $^1O_2$, O_2^-, OH^-) suppressing oxidative damage. **F.** Several independent studies have established that auxins (IAA), ethylene, cytokinins, gibberellin, abscisic acid, jasmonates, brassinosteroids, systemin (ST), defensin (DF), and salicylic acid promote optimal growth and defend against several (a) biotic stresses including pest and pathogen attack, herbivory, salinity, drought, trace elements, and UV radiation. Done with Biorender.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Role of Phytohormones on Plant Growth.

Phytohormones	Plant species	Effect	References
Auxin	*Oryza sativa*	Inhibited growth of tiller buds	(Liu et al., 2009)
	Lactuca sativa	Plant development - aid cell elongation, division and differentiation, and enhance signal transduction and flower development	(Wang et al., 2022)
	Triticum aestivum	Enhanced CO_2 assimilation rate and ultimately grain yield	(Iqbal and Ashraf, 2007)
Gibberellins	*L. sativa*	Enhanced biomass accumulation, leaf expansion, stomatal conductance, water use efficiency, and nitrogen use efficiency	(Miceli et al., 2019)
	Pisum sativum	Influenced gas exchange and chlorophyll contents through exogenous mode of application	(Javed et al., 2021)
	Solanum melongena	Enhanced seed germination	(Demir et al., 1994)
	S. lycopersicum	Mitigated drought-induced oxidative damage by maintaining relative water content, balancing the antioxidant mechanism system, and conserving the Chl concentration	(Jayasinghe et al., 2019)
	T. aestivum	Increased relative leaf water content, stomatal density, and Chlorophyl content	(Al Mahmud et al., 2019)
Cytokinins	*Zea mays*	Promoted sprouting of tiller buds	(Wang et al., 2012)
	Arabidopsis thaliana	Increased resistance to disease	(Choi et al., 2010)
	O. sativa	Improved growth and yield	(Zahir et al., 2001)
	Vitis vinifera	Inhibited ABA-induced stomatal closure	(Stoll et al., 2000; Tanaka et al., 2006)
	Epipremnum aureum	Increased net carbon assimilation, net photosynthesis, and dry matter accumulation	(Di Benedetto et al., 2015)
Ethylene	*Pyrus* spp.	Improved the activity of CAT, APX, and SOD and reduced the activity of polyphenol oxidase (PPO) and POX	(Ma et al., 2017)
	Glycine maximum	Mitigated waterlogging stress by promoting the initiation of adventitious roots and by increasing root surface area, expression of glutathione transferases, and relative glutathione activity	(Kim et al., 2018)
	L. sativa	Increased germination at a high temperature	(Nascimento et al., 2004)
	Cajanus cajan	Increased the germination percentage under Cd stress conditions	(Sneideris et al., 2015)
	Sinapis alba, O. sativa	High production of ethylene inhibited root growth	(Konings and Jackson, 1979)
	A. thaliana	Inhibited root growth and regulated root hair formation	(Dolan et al., 1994; Achard et al., 2003; Feng et al., 2015)
	Eruca sativa	Ethylene treatment caused Leaf chlorophyll loss	(Koukounaras et al., 2006; Khan et al., 2017)
	S. tuberosum	Caused severe leaf senescence symptoms, including yellowing, epinasty, and stunted growth	(Özgen et al., 2005; Khan et al., 2017)
	A. thaliana, Zea mays, S. lycopersicum	Provided protection against salinity stress	(Riyazuddin et al., 2020)
Abscisic acid (ABA)	*T. aestivum*	Increased the amount of endogenous ABA in the tiller nodes	(Cai et al., 2013)
	T. aestivum, Sorghum bicolor	Enhanced salinity tolerance and increased growth	(Gurmani et al., 2011)

(Continues)

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 (Continued)

Phytohormones	Plant species	Effect	References
	Hordeum vulgare	Promoted leaves growth by reducing water loss by transpiration under saline conditions using seed priming method	(Fricke et al., 2004)
Brassinosteroids	*Medicago sativa*	Improved seed germination and seedling growth under salinity stress	(Zhang et al., 2007)
	Arachis hypogea	Improved drought tolerance and increase the yield of peanut	(Huang et al., 2020)
Salicylic acid	*G. maximum*	Regulated physiological processes - activate, modulate, and regulate numerous responses during plant exposure to abiotic and biotic stresses	(Senaratna et al., 2000)
	S. lycopersicum, *Vigna* spp.	Enhanced productivity under low-temperature stress	(Khan et al., 2003)
	Zea mays	Enhanced germination and growth parameters of seedlings under salinity stress	(Habibi and Abdoli, 2013)
	Lepidium sativum	Mitigated drought stress and enhance vegetative growth	(Chavoushi et al., 2019)
	Carthamus tinctorius, *T. aestivum*	Increase photosynthetic pigment under Boron toxicity	(El-Shazoly et al., 2019)
Jasmonic acid	*O. sativa*	Increased chlorophyll content and photochemical efficiency	(Sheteiwy et al., 2018)
	Brassica oleracea	Improved the growth of broccoli sprouts under salinity stress	(Hassini et al., 2017)
	S. lycopersicum	Protected tomato seedlings against fusarium wilt	(Król et al., 2015; Galviz-Fajardo et al., 2020)
Defensins	*T. aestivum*	Promoted plant growth and development	(Zélicourt et al., 2007; Graham et al., 2008)
	A. thaliana	Possesses antimicrobial activity against bacteria, fungi, and viruses and even show cytotoxic and insecticidal activities	(Berrocal-Lobo et al., 2002; Hwang et al., 2010; Aboye et al., 2015)
Systemin	*S. lycopersicum*	Translates a locally perceived wounding signal into distal, (damage-associated molecular patterns) DAMP-triggered PTI (pattern triggered immunity) responses	(Ryan and Pearce, 2003)
	S. lycopersicum	Responsible for signalling in wound response and the cooperative regulation of strong systemic response	(Narváez-Vásquez et al., 2007)
	A. thaliana	Suppressed root growth and enlarges meristematic cells by inducing jasmonic acid synthesis in the companion cell-sieve element complex, triggering systemic protease inhibitor induction	(Heldt and Piechulla, 2011; Yamaguchi et al., 2013)
Strigolactones	*A. thaliana*	Regulated shoot architecture	(Wang et al., 2015; Waters et al., 2017)
	O. sativa	Regulated root architecture	(Arite et al., 2012; Waters et al., 2017)
	Striga lutea	Stimulated seed germination	(Huang and Osbourn, 2019; Das, 2024)

root exudates (Xie et al., 2010; Smith, 2014; Al-Babili and Bouwmeester, 2015). In terms of plant growth, strigolactones exhibit multifaceted functions. They contribute to various aspects of plant development, including branching, root architecture, and responses to environmental stimuli (Xie et al., 2010). By modulating the allocation of resources and coordinating physiological processes, strigolactones ensure optimal growth and adaptation to changing environmental conditions. Their role as signaling molecules facilitates crosstalk between different plant organs and enables the fine-tuning of growth patterns in response to internal and external cues (Smith, 2014).

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 Role of Phytohormones in Plant Defense.

Phytohormones	Plant species	Effect	References
Jasmonic acid	*Oryza sativa*	Emitted volatiles attract natural enemies; Mymarid egg parasitoid *Anagrus nilaparvatae*	(Lou et al., 2005)
	Zea mays	Increased foraging behaviour of *Cotesia kariyai* against *Mythmina separata*	(Ozawa et al., 2004)
	Brassica oleracea	Induced volatile emission that attracts natural enemies: *Cotesia glomerata*, *C. rubecula*, and *Diadegma semiclausum* against *P. rapae*	(Bruinsma et al., 2009)
	Arabidopsis thaliana	Increased attraction of parasitoid *C. rubecula* against *P. rapae*	(Van Poecke and Dicke, 2002)
	Phaseolus lunatus	Induced volatiles emission, that attracts predatory mite *Phytoseiulus persimilis* against *Tetranychus urticae*	(Dicke et al., 1999; Heil, 2004)
	Gerbera jamesonii	Induced the production of a complex odour blend that attracts *P. persimilis* against *T. urticae*	(Gols et al., 1999)
	Pinus sylvestris	Induced volatile emission that attracts parasitoid *Chrysonotomyia ruforum* against pine sawfly *Diprion pini*	(Hilker et al., 2002)
	Solanum lycopersicum	Delayed nymphal development in *Bemisia tabaci*	(Zhang et al., 2018)
	Chrysanthemum indicum	Site-dependent plant defence against *Frankliniella occidentalis*	(Chen et al., 2020)
	Cucumis sativus	JA treatments induced an increase in leaf thickness, trichome density, and phenol content against *Liriomyza sativae*	(Doostkam et al., 2023)
Methyl jasmonate	*Ananas comosus*	Reduction in microbial growth, targeting bacteria, yeasts, and molds	(Martínez-Ferrer and Harper, 2005)
	B. oleracea	Induced plant resistance by altering oviposition preference of *Pieris brassicae* and *P. rapae*	(Bruinsma et al., 2007)
	Picea abies	Reduced egg deposition and pupal weight of Spruce bark beetle *Ips typographus*	(Erbilgin et al., 2006)
	P. sylvestris	Enhanced plant defense through increased emission of monoterpene, β-pinene, and limonene, against Sawfly *Neodiprion sertifer* and *D. pini*	(Heijari et al., 2008)
	Triticum aestivum	Reduced densities of pests including aphids, thrips, and stem sawfly; while attracting biological control agents i.e. *Collyria coxator*	(Bayram and Tonğa, 2018a)
	T. aestivum	Increased polyphenol oxidase and proteinase inhibitor in host plant, affecting the preference and probing behavior of the grain aphid *Sitobion avenae*	(Cao et al., 2014)
	Gossypium hirsutum	Reduced the densities of sucking insect pests such as *Thrips tabaci*, *Aphis gossypii*, *Empoasaca decipiens*, while increasing natural enemies including *Coccinella septempunctata*, *Aeolothrips intermedius*, and *Chrysoperla carnea*	(Tonğa et al., 2022)

(Continues)

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 (Continued)

Phytohormones	Plant species	Effect	References
***cis*-Jasmone (CJ)**	*Solanum tubersoum*	Reduced growth of *Macrosiphum euphorbiae* on treated plants	(Sobhy et al., 2017; Sobhy et al., 2020)
	S. lycopersicum	Reduced oviposition of *S. exigua*	(Disi et al., 2017)
	Capsicum annuum	No significant effect on relative mean growth rate of *M. persicae* and *A. solani*	(Dewhirst et al., 2012)
	T. aestivum	Reduced growth rate and settlement of *S. avenae* and *O. melanopus*, while and increasing biological control agents *Collyria coxator*	(Bruce et al., 2003; Delaney et al., 2013; Bayram and Tonğa, 2018b)
	Z. mays	Made the plant less attractive to *Cicadulina storeyi*	(Oluwafemi et al., 2013)
	A. thaliana	Made the plant less attractive to *M. persicae*, while more attractive to *Lipaphis erysimi*	(Bruce et al., 2008)
	B. napus, *B. oleracea*, *B. rapa*	Reduced fecundity, survival, and settlement of *M. persicae*, while attracting parasitoid *Diaeretiella rapae*	(Ali et al., 2021)
	G. hirsutum	Induced direct and indirect plant defense against *Aphis gossypii*, *T. tabaci*, *Empoasca decipiens*	(Hegde et al., 2012; Tonğa et al., 2020)
	Glycine max	Reduced weight of *E. heros* when fed on CJ treated plant	(Vieira et al., 2013)
Salicylic acid	*Nicotiana tabacum*	Induced defense gene expression against *Pseudomonas syringae* pathovar	(Mur et al., 1996)
	C. sativus	Induced plant resistance against *Colletrichum lagenarium*	(Mills et al., 1986)
	S. lycopersicum	Induced defense related-gene expression and activated systemic acquired resistance against *Alternaria solani*	(Spletzer and Enyedi, 1999)
	Cicer arietinum	Induced plant defenses against a variety of biotic stresses including *Helicoverpa armigera* and *Spodoptera litura*	(War et al., 2011)
	Citrus sinensis	Altered the emission of volatile organic compounds, which influenced the behavior of *Diaphorina citri*	(Patt et al., 2018)
Methyl salicylate	*Helianthus annuus*	Induced oxidative defense reactions in roots against biotic stress	(Garrido et al.,2009)
	Vitis vinifera	Attracts biological control agents, such as coccinellids, against powdery mildew	(Gadino et al., 2012)
	G. max	Attracted natural enemies and reduced pest population of *Aphis glycines* Matsumura	(Mallinger et al., 2011)
	B. rapa	Attracted natural enemies of Diamondback moth and lacewing i.e. *Diadegma semiclausum* Hellén, *Anacharis zealandica* Ashmead	(Orre et al., 2010)
Benzothiadiazole	*N. tabacum*	Induced systemic resistance against tobacco mosaic virus, *Cercospora nicotianae*, *Pseudomonas syringae*, *Erwinia carotovora*, *Phytophthora parasitica* and *Peronospora tabacina*	(Bodenheimer and Swirski, 1957; Friedrich et al., 1996)

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 (Continued)

Phytohormones	Plant species	Effect	References
	N. tabacum	Inhibited catalase and ascorbate, scavenging enzymes against microbial pathogens	(Wendehenne et al., 1998)
	T. aestivum	Activateed defense genes and resistance against *Erysiphe graminis*	(Stadnik and Buchenauer, 2000)
Brassinosteroids	*S. tuberosum* and *S. lycopersicum*	Enhanced plant defenses against *Phytophthora infestans* and *Verticillium dahliae*	(Krishna, 2003; Xia et al., 2009; Vardhini et al., 2010)
	N. tabacum and *O. sativa*	Induced resistance against tobacco mosaic virus, and bacterial pathogens *Pseudomonas syringae*, *Oidium* sp. *Maganoprothe grisea*	(Nakashita et al., 2003a)
	C. sativus	Induced stress tolerance by enhancing NADPH oxidase activity and elevated H_2O_2 level in apoplast against cucumber mosaic virus	(Xia et al., 2009)
	O. sativa	Lead activation of defense genes, such as chitinase RCH10 and Phenylalanine ammonia-lyase against *Xanthomonas oryzae* pv. oryzae	(He et al., 2000)
Systemin	*S. tuberosum*	Activated innate immunity and orchestrates defense mechanisms against pests and pathogens	(Ryan, 2000)
	S. lycopersicum	Induced metabolic alterations at the molecular level, primarily linked to increased transcription of pattern-recognition receptors, signaling enzymes, and transcription factors in adjacent plants against *Spodoptera littoralis*	(Coppola et al., 2017)
Defensins	*S. lycopersicum*	Enhanced overexpression of proteins induces resistance against *Botrytis cineria*	(Stotz, et al., 2009; Van der Weerden and Anderson, 2013; Lacerda et al., 2014)
	N. alata	Inhibits the growth of *B. cinerea* and *Fusarium oxysporum*	(Lay et al., 2003; Lay et al., 2003)
	A. thaliana	Possess antimicrobial activity against bacteria, fungi, and viruses, even showing cytotoxic and insecticidal activities	(Berrocal-Lobo et al., 2002; Aboye et al., 2015)
	N. tabacum	Suppresses infection of *Pseudomonas syringae* and the performance of *Manduca sexta*	(Rayapuram and Baldwin, 2008)
	C. annuum	Induces dose-dependent reductions in larval and pupal mass, delayed metamorphosis, and significantly impaired fecundity in *H. armigera*	(Mulla and Tamhane, 2023)
	Pisum sativum	α-Amylase inhibitor-type plant defensins protect plants from biotic stresses including *Callosobruchus chinensis*	(Shade et al., 1994; da Silva et al., 2023)
Ethylene	*A. thaliana*	Enhanced plant resistance against *Gossypium babadense*	(Stotz et al., 2000)
	Zea mays	Inhibition of ethylene synthesis and perception increases susceptibility of plant to *Spodoptera frugiperda*	(Harfouche et al., 2006)

(Continues)

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 (Continued)

Phytohormones	Plant species	Effect	References
	Solanum lycopersicum	Ethylene response factors 15 and 16 in tomato initiate jasmonate biosynthesis, thereby enhancing plant resistance against *H. armigera*	(Hu et al., 2021)
	Vicia faba L.	The combined treatment of jasmonic acid and ethylene induces a resistance effect in plant against *Frankliniella occidentalis*	(Jia et al., 2022)
	A. thaliana	Ethylene's receptor ETR2 controls trichome branching by regulating microtubule assembly, influencing plant defense against insect herbivores	(Plett et al., 2009; Song et al., 2022)
	A. thaliana	Ethylene signaling mutants show increased anthocyanin levels compared to wild-type plants potentially affecting plant defense against insect herbivores	(Meng et al., 2018; Song et al., 2022)
	N. attenuata	A synergistic regulation by both jasmonic acid (JA) and ethylene, enhances resistance against *Spodoptera litura*	(Yang et al., 2023)
Auxin	*C. morifolium* Ramat	Auxin-coated chrysanthemum cuttings in water reduced *F. occidentalis* feeding damage	(Mouden et al., 2020)
	N. attenuata	IAA swiftly triggers specific JA-dependent secondary metabolites in plants attacked by herbivores, enhancing plant defense against *M. sexta*	(Machado et al., 2016)
	O. sativa	2,4-D, an auxin analogue widely used in monocot crops, boosts rice defenses by triggering increased trypsin proteinase inhibitor activity and volatile production (Table 2), leading to enhanced resistance against *Chilo suppressalis*	(Xin et al., 2012)
	A. thaliana	Induces defense by promoting the biosynthesis and signaling of JA in plants against *Pythium irregulare*, *Pseudomonas syringae* and *M. sexta*	(Tiryaki and Staswick, 2002; Nagpal et al., 2005; Grunewald et al., 2009; Erb et al., 2012)
	Medicago sativa	Dicamba, a synthetic analogue of auxin, effectively reduced populations of insect herbivores *Acyrthosiphon pisum* and *Empoasca fabae (Table 2)*	(Egan et al., 2014; Johnson et al., 2023)
Cytokinins (CK)	*Populus trichocarpa* Torr. and Gray x *P. deltoides* Bartr. ex Marsh	CK priming in plants reduces weight gain in *Lymantria dispar* larvae by enhancing the biosynthesis of JA (Table 2) and its fatty acid precursor linolenic acid	(Dervinis et al., 2010)
	N. attenuata	CK-mediated reactions have been documented across different species including the tobacco hornworm *M. sexta* and the green peach aphid *M. persicae*, resulting in deterring insect feeding, delaying larval development, and decreasing weight gain	(Hui et al., 2003; Giron et al., 2013; Akhtar et al., 2020).

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 (Continued)

Phytohormones	Plant species	Effect	References
	N. tabacum	CKs regulate plant resistance by modulating secondary metabolic pathways to produce insecticidal compounds against *M. sexta* and *M. persicae*	(Smigocki, 1995)
	O. sativa	Enhanced defense in rice by activating the JA pathway against *Nilaparvata lugens*	(Zhang et al., 2022)
Abscisic acid (ABA)	*S. lycopersicum*	ABA-deficient plants exhibit decreased resistance against insects, such as *Spodoptera exigua*	(Thaler and Bostock, 2004)
	A. thaliana	ABA (*aba-1-1*) mutant plants display enhanced defense responses against aphid *M. persicae*	(Hillwig et al., 2016)
	A. thaliana	Upon *P. rapae* feeding, ABA activates the MYC-branch and suppresses the ERF-branch of the JA pathway, boosting plant defense against caterpillars	(Vos et al., 2013, 2019)
	Manihot esculenta	An integrative transcriptomic analysis reveals the interplay between abscisic acid and lignin pathways in cassava, inducing defense against *Aleurotrachelus socialis* infestation	(Nye et al., 2023)
	O. sativa	Exogenous ABA suppressed *S. avenae* nymph feeding in rice, likely due to heightened trichome density, upregulated gene expression, and emission of seven pest-resistant compounds.	(Liang et al., 2024)
Strigolactones	*A. thaliana*	Strigolactones appear to have a priming effect on *Arabidopsis thaliana*, initiating salicylic acid-mediated disease resistance against *P. syringae*	(Kusajima et al., 2022)
	N. attenuata	Regulate anthocyanin and induce plant defense against *Trichobaris mucorea*	(Li et al., 2020)
	P. sativum	Pea plants (strigolactones mutants) exhibited a significant increase in fecundity of aphid *Acyrthosiphon pisum*	(Swiegers et al., 2020, 2022)
	S. lycopersicum	Strigolactone-deficient tomato plants exhibit reduced resistance to *B. cinerea* due to decreased levels of defense-related hormones JA and SA	(Torres-Vera et al., 2014)
	O. sativa	Enhances rice defense against *Pyricularia oryzae* by inducing the accumulation of jasmonate, sugar, and flavonoid phytoalexins	(Lahari et al., 2024)
	S. lycopersicum	Regulate defense against soil-borne pathogens like root-knot nematodes *Meloidogyne incognita*	(Xu et al., 2019)

Salicylic acid (SA) and jasmonic acid (JA), widely acknowledged for their remarkable contributions to plant defence, are of significant importance in enhancing plant growth (Ruan et al., 2019; Ding and Ding, 2020; Ali et al., 2021; Ali et al., 2023a). These phytohormones intricately regulate a spectrum of physiological and biochemical processes that positively impact growth (Rivas-San Vicente and Plasencia, 2011). Notably, they modulate chlorophyll fluorescence and seed germination dynamics (Sheteiwy et al., 2021), augment

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

activities related to photosynthesis (Rivas-San Vicente and Plasencia, 2011; Nazim et al., 2021) and stimulate the growth in both vegetative and reproductive plant organs (Ghorbel et al., 2021). Recent investigations by Hewedy et al. (2023) further substantiate the affirmative influence of JA on plant growth. Further research is needed to explore the intricate interactions and specific mechanisms by which these phytohormones modulate plant growth and adaptation to environmental challenges.

Brassinosteroids, a crucial plant hormone, play diverse roles in regulating plant growth and development across various species. Brassinosteroids both enhance seed germination and seedling growth in *Medicago sativa*, particularly under salinity stress conditions (Zhang et al., 2007). Similarly, in *Arachis hypogaea*, brassinosteroids contribute to improved drought tolerance and increased peanut yield (Huang et al., 2020). Defensins, another essential hormone, exhibit significant effects on plant growth and defense mechanisms. In *Triticum aestivum*, defensins promote overall plant growth and development (Zélicourt et al., 2007; Graham et al., 2008). Meanwhile, in *A. thaliana*, defensins demonstrate antimicrobial activity against various pathogens and also possess cytotoxic and insecticidal properties (Berrocal-Lobo et al., 2002; Hwang et al., 2010; Aboye et al., 2015). Systemin, on the other hand, serves as a key signaling molecule in wound responses. In *Solanum lycopersicum*, it translates locally perceived wounding signals into distal damage-associated molecular pattern (DAMP)-triggered pattern-triggered immunity (PTI) responses (Ryan and Pearce, 2003). Furthermore, in *A. thaliana*, systemin suppresses root growth and induces jasmonic acid synthesis, leading to systemic protease inhibitor induction (Heldt and Piechulla, 2011; Yamaguchi et al., 2013). Overall, these hormones intricately regulate various aspects of plant growth, highlighting their importance in plant physiology.

4 | PHYTOHORMONES AND PLANT DEFENCE

In the ongoing battle against plant pathogens and environmental stressors, phytohormones play a crucial role in coordinating plant defense (War et al., 2012; Zhao et al., 2021; Vaishnav and Chowdhury, 2023). Understanding this has led to sustainable strategies for crop protection and resilience (Chen and Pang, 2023), as modern agriculture leverages phytohormones to enhance immunity, reduce pesticide use, and promote sustainable crop management.

Jasmonic acid (JA) and its derivatives, collectively known as jasmonates, are vital plant hormones that strengthen plant resistance against herbivores (Howe and Jander, 2008) (Table 2). This includes compounds such as methyl jasmonate (MeJA), *cis*-Jasmone (CJ), and prohydrojasmon (PDJ), proven to induce defense responses against insect attacks (Birkett et al., 2000; Thaler et al., 2001; Uefune et al.,2014). Jasmonates activate defense-related genes and secondary metabolites, enhancing plant defense (Vijayan et al., 1998; Wasternack, 2014). They also modulate volatile emissions, attracting natural enemies and stimulate extrafloral nectar production, reinforcing the "*attract and reward strategy*" (Rodriguez-Saona et al., 2001; Rodriguez-Saona et al., 2012). The application of jasmonic acid and its derivatives holds promise for enhancing plant defences and sustainable pest management in agriculture (Ali et al., 2021; Ali et al., 2023b) (Table 2). Efficacy depends on factors like timing, cultivars, and dosage (Thaler et al., 2002; Doostkam et al., 2023). Plants treated with jasmonic acid (JA) emit volatile blends, mimicking the scent of herbivore-damaged plants, which attracts natural enemies and contributes to improved pest management (Ament et al., 2004; Bruinsma et al., 2009). These compounds induce direct and indirect plant defenses when applied to both roots and shoots (Li et al., 2013; Pierre et al., 2013). Moreover, jasmonate treatment enhances extrafloral nectar production, supporting natural enemies' nutrition and fitness (Gols et al., 2003; Bruinsma et al., 2008) (Table 2).

In particular, methyl jasmonate (MeJA), a crucial component in plant defense against herbivores, is a naturally occurring volatile compound that coordinates stress and herbivore response (Seo et al., 2001; Wasternack, 2007). Synthesized from jasmonic acid (JA), MeJA is pivotal in the plant's defense signaling network (Jiang and Yan, 2018). MeJA activates defense enzymes (SOD, PAL, PPO) and induces protease inhibitors, disrupting herbivore feeding (Lomate and Hivrale, 2012). It also prompts the production of chemical deterrents like flavonoids and glucosinolates (Belhadj et al., 2006; Bi et al., 2007). MeJA directly impacts herbivore performance, affecting reproduction, survival, and feeding (Erbilgin et al., 2006; Bayram and Tonğa, 2018a; Tonğa et al., 2022). Indirectly, MeJA increases volatile emissions, attracting natural enemies for enhanced pest control (Rodriguez-Saona et al., 2001; Martin et al., 2003; Bayram and Tonğa, 2018a; Tonğa et al., 2022). Applied exogenously, MeJA holds promise for pest management and sustainable agriculture, providing a tool to enhance plant resistance and promote eco-friendly pest control (Bayram and Tonğa, 2018b; Wei et al., 2021; Tonğa et al., 2022).

cis-Jasmone (CJ) is a naturally occurring stress signal primarily induced by herbivory or external stimuli (Koch et al., 1997; Tanaka et al., 2009). It activates unique genes distinct from the MeJA-induced signalling pathway (Matthes et al., 2010), and induces plant defence against pests, both through direct and indirect mechanisms (Blassioli Moraes et al., 2008; Bruce et al., 2008; Ali et al., 2021). CJ treatment alters plant volatile emissions, making them less appealing to herbivores while attracting natural enemies, thus reducing herbivore performance and population density (Bruce et al., 2003; Pickett et al., 2007; Bruce et al., 2008; Dewhirst et al., 2012; Bayram and Tonğa., 2018b; Tonğa et al., 2020; Ali et al., 2021). Moreover, CJ enhances tritrophic interactions by attracting natural enemies and primes plants for the increased production of defensive volatile organic compounds, such as (E)-2-hexenal, 6-methyl-5-hepten-2-one (MHO), (Z)-3-hexenyl acetate, myrcene, (E)-ocimene, (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT), methyl salicylate (MeSA), caryophyllene, (E)-β-farnesene, and (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) (Hegde et al., 2012; Sobhy et al., 2017; Bayram and Tonğa, 2018b; Tonğa et al., 2020; Ali et al., 2021). The exogenous application of CJ demonstrates its potential for pest control management and sustainable agriculture, making it a valuable tool in enhancing plant defences against herbivores (Ali, 2023; Ali et al., 2021; Sobhy et al., 2022).

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Salicylic acid (SA), a key phytohormone, plays a central role in a plant's immune system, acting as a defense mechanism against biotrophic pathogens (Raskin, 1992; Ding and Ding, 2020). Synthesized through the phenylpropanoid pathway, SA rapidly increases in response to pathogen invasion, activating defense-related genes and metabolic pathways to protect the plant (Hayat et al., 2007; Tripathi et al., 2019; Mohamed et al., 2020). Derivatives like methyl salicylate contribute by synthesizing defensive compounds and activating relevant genes (Park et al., 2007). SA is crucial in establishing systemic acquired resistance (SAR), providing long-lasting immunity against various pathogens (Malamy et al., 1990; Gaffney et al., 1993). Upon pathogen recognition, local SA levels increase, triggering systemic signaling and activating pathogenesis-related (PR) genes, fortifying the plant's immune system (Wang et al., 2012; Zhu et al., 2014; Ding et al., 2022). SA-mediated defense is effective against biotrophic pathogens (An and Mou, 2011) and extends to mitigating abiotic stresses, including drought, heat, and heavy metal toxicity (Khan et al., 2015; Shokat et al., 2021b). SA signaling interacts with ABA and ET pathways, fine-tuning the plant's response to diverse stressors (Yang et al., 2015; Nguyen et al., 2016). These attributes make SA and its derivatives valuable for pest control and sustainable agriculture. SA derivatives, including methyl salicylate (MeSA) and acetyl salicylic acid (aspirin), bolster plant defense responses. MeSA, released by plants during pathogen attacks, acts as a mobile signal, inducing defense in neighboring plants and attracting beneficial insects for natural pest control (Park et al., 2007; Ali et al., 2023) (Table 2). Aspirin, a derivative of SA, enhances plant defense mechanisms and increases resistance to various pathogens (White, 1979; Senaratna et al., 2000) (Table 2).

Brassinosteroids (BRs), a class of steroid hormones (Table 2), play a crucial role in regulating diverse physiological processes in plants, encompassing growth, development, reproduction, and stress responses (Krishna, 2003; Hayat et al., 2019; Nolan et al., 2020). Particularly, BRs enhance plant defenses against both abiotic and biotic stress (Krishna, 2003; Vardhini et al., 2010). In the context of biotic stress, BRs orchestrate plant defense mechanisms against pests and pathogens, contributing to PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI) responses (Zipfel, 2009; Naveed et al., 2020). BRs promote PTI by enhancing reactive oxygen species (ROS) accumulation, callose deposition, and the expression of defense-related genes (Xia et al., 2009; Lu et al., 2020; Benitez-Alfonso and Caño-Delgado, 2023). Furthermore, BRs enhance ETI responses by amplifying recognition and signaling cascades initiated by specific plant resistance (R) proteins, leading to hypersensitive response (HR) and systemic acquired resistance (SAR) (He et al., 2000; Grant and Lamb, 2006; Yu et al., 2018). The interplay between BRs and other phytohormones, such as SA and JA, adds complexity to plant immune responses, fine-tuning the balance between SA and JA-dependent defense strategies (Divi et al., 2010; Yang et al., 2019). As key regulators in the intricate network of plant immune responses, BRs offer promising opportunities for developing eco-friendly and targeted strategies to safeguard crops, enhance resistance, and ensure agricultural sustainability against evolving pests and pathogens (Krishna, 2003; Manghwar et al., 2022).

Systemin and defensins are other important key players that play a vital role in activating innate immunity in plants and orchestrating defence mechanisms against herbivores and microbial invaders, respectively (Stotz et al., 2009; Choi and Klessig, 2016). Systemin, a small peptide, and defensins, antimicrobial peptides, trigger a cascade of events that lead to the synthesis of JA and the activation of defence-related genes, providing rapid and targeted protection against pests and pathogens (Ryan, 2000; Choi and Klessig, 2016). The structural diversity of defensins allows them to combat a wide range of pathogens, and their crosstalk with other defence pathways fine-tunes the plant's response to specific threats (Odintsova et al., 2019). Understanding the molecular mechanisms of systemin and defensins opens avenues for sustainable pest and pathogen management in agriculture, including the development of biopesticides and elicitor-based strategies (Anderson et al., 2016; Vincent et al., 2020; Leannec-Rialland et al., 2022). Harnessing these natural defence inducers offers promising eco-friendly and targeted solutions to ensure crop health, resistance, and global food production sustainability amidst changing environmental challenges.

Ethylene, a vital plant hormone, plays a pivotal role in orchestrating defense mechanisms against insect herbivores. Upon herbivory by insects from various feeding guilds, plants release ethylene as a response (Von Dahl and Baldwin, 2007; Ali et al., 2024). This hormone stands out as a key regulator in inducing protective responses upon insect feeding, altering defense mechanisms against herbivores (Guo and Ecker, 2004). For instance, in lima beans exposed to *Tetranychus urticae*, ethylene induction serves as a defensive measure against the herbivore, accompanied by the expression of defense-related genes (Arimura et al., 2000; Kahl et al., 2000). Ethylene's role extends to maize, where it forms part of the signal transduction pathway leading to defense against insect herbivory (Harfouche et al., 2006). Ethylene induces the emission of specific volatile organic compounds, the accumulation of phenolic compounds, and proteinase inhibitor activity, thereby bolstering plant defenses (Von Dahl and Baldwin, 2007). Furthermore, it enhances jasmonic acid accumulation and regulates the expression of defense-related genes, including chitinase, β-1,3 glucanase, and pathogenesis-related genes (Guo and Ecker, 2004; Harfouche et al., 2006). Ethylene's interaction with JA, SA, and ABA contributes to plant defense against various biotic stresses (Adie et al., 2007). Moreover, ethylene modulates defense pathways by activating specific defenses, priming distant plant parts, and regulating volatile signals for attracting carnivorous enemies or warning neighboring plants (Broekgaarden et al., 2015). In maize, ethylene regulates the expression of defensive genes such as maize insect resistance1 (*mir1*) in defense against insect herbivores (Louis et al., 2015). Recent studies also highlight ethylene's role in anthocyanin accumulation, trichome development, and defenses against insects in *Arabidopsis thaliana*, as well as triggering jasmonate biosynthesis in response to infestation in tomato (Tian et al., 2014; Hu et al., 2021; Song et al., 2022). Overall, ethylene emerges as a central player in plant

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

defense, inducing multifaceted responses to combat insect herbivores and enhance plant resilience (Table 2).

Abscisic acid (ABA) (CK priming in plants 2) serves as a pivotal regulator in plant defense mechanisms, extending beyond its traditional functions in seed germination and abiotic stress responses (Anderson et al., 2004) (Table 2). Contrasting effects of ABA levels on plant susceptibility to herbivory have been observed: while ABA-deficient plants exhibit decreased resistance against insects like *Spodoptera exigua*, they display enhanced defense responses against pests such as *Myzus persicae* (Thaler and Bostock, 2004; Hillwig et al., 2016). Under biotic stress conditions, ABA plays a dual role by antagonizing jasmonic acid (JA)-ethylene signaling while also inducing JA responses through MYC2 transcription factors, thereby influencing defense pathways (Dinh et al., 2013). ABA primes JA-regulated defense responses upon secondary herbivore attack, enhancing plant resistance against insects like *Pieris rapae* (Vos et al., 2013, 2019). However, recent findings suggest that insects exploit ABA to manipulate nutrient allocation mechanisms or suppress host-plant defenses (Seng et al., 2023). Mutants impaired in ABA synthesis, such as *aba2-1*, exhibit increased weight gain of herbivorous larvae like *Spodoptera littoralis* and altered feeding behaviour, highlighting the crucial role of ABA in regulating plant-insect interactions (Thaler and Bostock, 2004; Christmann et al., 2006). Additionally, the downregulation of ABA-regulated genes in *aba2-1* mutants affects the development and mortality of insect herbivores, further underscoring ABA's significance in plant defense (D'Ovidio et al., 2004; Liu et al., 2005; Bodenhausen and Reymond, 2007). Overall, these findings emphasize the multifaceted role of ABA in orchestrating plant defense strategies against herbivorous insects.

Auxin, along with other phytohormones like ABA and ethylene (Table 2), not only regulate plant growth but also play crucial roles in plant defense mechanisms. ABA initiates defense pathways early, while ethylene's multifaceted role includes both promoting wound-response gene expression and inhibiting nicotine production. Conversely, auxin acts as a negative regulator of wound responses. Moreover, indole-3-acetic acid (IAA), a type of auxin, enhances plant responses to herbivore attacks by influencing other hormonal pathways and defense mechanisms (Erb et al., 2012). IAA not only enhances JA signaling but also specifically regulates a plant's defensive network, aiding in precise responses to various attackers (Machado et al., 2016). Additionally, auxins like indole-3-butyric acid (IBA) provide protection against pests such as thrips and leaf miners in chrysanthemum plants, showcasing an unconventional role beyond root promotion (Mouden et al., 2020). Auxin is pivotal in plant mechanical defense, promoting lignin formation and reinforcing cell walls to resist herbivores and pathogens (Huang et al., 2013). In response to herbivory, auxin levels rise, inducing the production of anthocyanin, a chemical repellent (Machado et al., 2016). Furthermore, auxin indirectly contributes to plant defense by stimulating ethylene production, which is crucial in defense responses (Perez-Alonso and Pollmann, 2018). Auxin also facilitates plant defense by interacting with microbial biocontrol agents. Microbial agents produce auxins like IAA, influencing plant physiology and triggering defense responses such as enhanced root growth and basal defense against pathogens. For instance, *Pseudomonas fluorescens* enhances auxin production in barley tissues during its interaction with the Fusarium head blight (FHB) fungus, enhancing disease resistance (Mainali and Nyaupane, 2023). This multifaceted role of auxin underscores its significance in plant defense strategies.

Cytokinins (CKs) (Table 2) play a crucial role in regulating plant defense responses against insect herbivores and pathogens. Studies have shown that CKs are involved in the biosynthesis of JA, which is a key signaling molecule in plant defense mechanisms (Hare et al.,1997; Cortleven et al., 2019). Additionally, CKs induce the expression of wound-induced genes and directly affect the performance of insect herbivores. For example, CK-mediated responses have been observed in various species, such as the tobacco hornworm *Manduca sexta*, the gipsy moth *Lymantria dispar*, and the green peach aphid *M. persicae*, leading to the deterrence of insect feeding, delayed larval development, and reduced weight gain (Hui et al., 2003; Dervinis et al., 2010; Akhtar et al., 2020). Furthermore, CKs serve as crucial regulators of insect resistance in plants by influencing secondary metabolic pathways that produce compounds with insecticidal properties (Smigocki, 1995). This priming effect of CKs enhances plant defense against herbivory by reducing weight gain in insect larvae and altering the expression of defense-related genes (Dervinis et al., 2010). Elevated levels of CKs are often detected following insect or pathogen infestations, indicating their pivotal role in orchestrating plant metabolism associated with induced defense mechanisms (Giron et al., 2013). Moreover, CKs mediate long-distance systemic processes in response to herbivory, suggesting their integral involvement in wounding and herbivore-associated molecular pattern (HAMP)-triggered responses across plant species (Schäfer et al., 2015). In conclusion, CKs significantly influence plant defense against insect herbivores by altering plant nutrient allocation and impacting plant quality for biotic invaders. Additionally, they can be utilized by biotic invaders to disrupt plant defense mechanisms and exploit plant resources for their own benefit (Giron et al., 2013). Recent studies, such as the one conducted by Zhang et al. (2022), have further highlighted the role of CKs in conferring resistance against insect pests, such as the brown planthopper, by elevating the JA pathway in rice. These findings underscore the importance of CKs in plant defense and their potential applications in pest management strategies.

Strigolactones emerge as crucial players in bolstering plant defense against biotic stresses (Al-Babili and Bouwmeester, 2015; Francis et al., 2024). Research indicates that strigolactones actively participate in plant defense responses by modulating systemic acquired resistance through SA-mediated signaling pathways (Kusajima et al., 2022). Deficiencies in strigolactone signaling compromise the plant's ability to mount effective defense responses, leading to increased susceptibility to pathogens and herbivores (Torres-Vera et al., 2014; Nasir et al., 2019; Kusajima et al., 2022). Furthermore, strigolactones play a critical role in enhancing plant resistance against specific pests and pathogens. For instance, strigolactone deficiency in tomato plants results in decreased levels of defense-related hormones such as JA, SA, and ABA, along with diminished expression of jasmonate-dependent genes involved in resistance against pathogens like *Botrytis cinerea* (Torres-Vera et al., 2014). Additionally, studies have demonstrated that strigolactone deficiency

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

induces the accumulation of phytoalexins, sugars, and flavonoids, thereby enhancing rice defense mechanisms against the blast fungus *Pyricularia oryzae* (Lahari et al., 2024). This multifaceted role of strigolactones in plant defense extends further, positively regulating defenses against soil-borne pathogens such as root-knot nematodes in tomato plants (Xu et al., 2019). In summary, the pivotal role of strigolactones in both plant growth regulation and defense against various biotic stresses underscores their significance in ensuring plant health and survival in diverse environmental conditions (Table 2).

5 | PHYTOHORMONAL CROSSTALK: GROWTH AND DEFENSE

5.1 | Phytohormonal cross-talk during plant growth

The importance of plant hormones in growth becomes evident through their influence on a range of parameters essential for assessing a plant's development. These parameters include morphological aspects such as height (Wang and Wang, 2022), leaf area (Davies, 2010), and flowering (Chandler, 2011), tracking changes in biomass and tissue (Ciura and Kruk, 2018), observing developmental stages like flowering senescence, and assessing nutrient uptake (Iqbal et al., 2017). Plant hormones play a central role in coordinating and fine-tuning these parameters to ensure optimal growth and adaptation to changing conditions, making them indispensable to the vitality and resilience of plants in their ever-evolving environments (EL Sabagh et al., 2022).

For instance, auxin plays a prominent role in plant regulation through the homeostasis of auxin levels. Antagonistically, both auxin and abscisic acid (ABA) regulate plant growth (Wang et al., 2011; He et al., 2012) (Figure 2). The ABA overly sensitive mutants (*abo6*) unable to encode the DEXH-box helicase showed root development and seed germination defects due to higher accumulation of ROS, which contributed to a reduction in the abundance of auxin transport proteins PIN1, PIN2 and AUX1 in the roots. Normal root growth phenotype was rescued via applying the exogenous reduced GSH and auxin, indicating the ROS-mediated crosstalk of ABA and Auxin (He et al., 2012). Similarly, in Arabidopsis, ABA treatments induced the transcript level of *AUXIN RECEPTOR FACTORS2 (ARF2)*, which directly regulates the *HOMEOBOX PROTEIN 33 (HB33)* expression level and

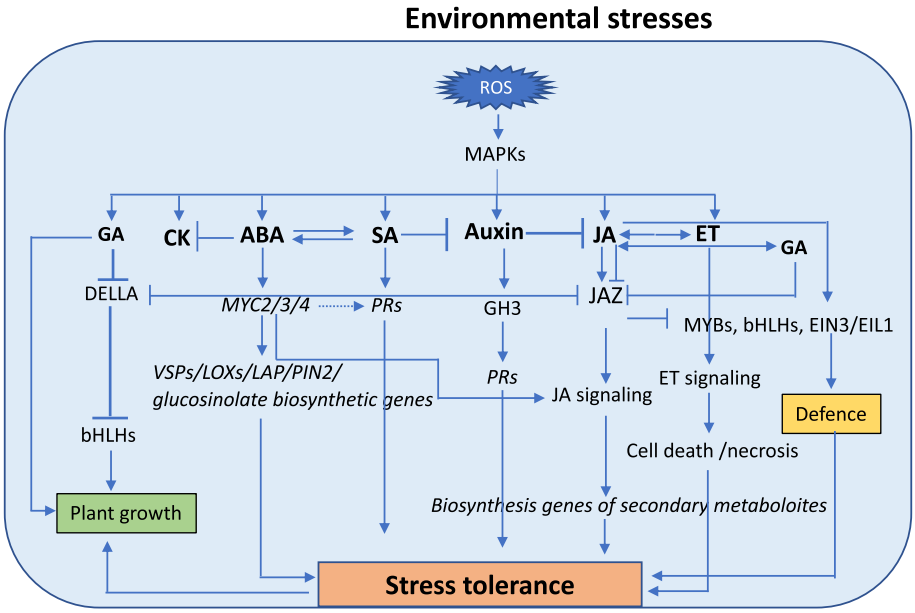


FIGURE 2 Phytohormonal crosstalk during environmental stress. When plants encounter environmental stress, reactive oxygen species (ROS) are produced, which activate phytohormonal crosstalk signalling pathways via mitogen-activated protein kinases (MAPKs). A dialogue between DELLA proteins and JASMONATE ZIM-domain (JAZ) proteins forms the basis for crosstalk between the gibberellin (GA) and jasmonic acid (JA) signalling pathways, helping to balance plant growth and defence in response to environmental stimuli. DELLA proteins interact with PIFs and ALC transcription factors, inhibiting GA-induced plant growth and development. Similarly, JA-mediated defence is interrupted by JAZs through direct interaction with bHLHs, MYBs, or EIN3/EIL1. In conclusion, JAZs are crucial in regulating a delicate balance between defence and growth via the JA and GA pathways under environmental signals. However, DELLA is degraded, leading to the liberation of a higher amount of JAZs, which suppresses JA signalling. This is important for defence against environmental stimuli. Under harsh conditions, plants receive signals to produce JA, which initiates the degradation of JAZs, enhancing the plant's defense system. This also leads to the release of the DELLA protein, which inhibits GA-mediated plant growth. Moreover, JA-ET crosstalk activates the ET signaling pathway to provide defense. SA and auxin activate the PR genes, which are components of the defence system that alleviate stress tolerance. Similarly, ABA activates the downstream signalling pathway by activating the VSPs, LOXs, LAP, PIN2 and glucosinolate biosynthetic genes, subsequently activating defence over growth. Abbreviations: GA; Gibberellic acids, CK; Cytokinin, JA; Jasmonic Acid, SA; Salicylic Acid, ET; Ethylene, ABA; abscisic acid, JAZ; Jasmonate-Zim Domain, GH3; Gretchen Hagen3, PR; Pathogenesis-related proteins, MYB; myeloblastosis, bHLHs; basic helix–loop–helix. Done with Biorender.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

mediates the root length. In *arf2* mutants, ABA application had a more pronounced effect on reducing cell division by altering the auxin homeostasis in mutant lines, leading to a lower root length compared to wild type (Wang et al., 2011). There are certain studies indicating that ABA and ethylene together regulate plant root growth via ETHYLENE-INSENSITIVE 2 (EIN2). For instance, *ein2* mutants exhibited normal root growth on ABA-containing media compared to Col-0 (Beaudoin et al., 2000; Ghassemian et al., 2000). Similarly, root length of ethylene-insensitive mutants such as *ethylene receptor1 (etr1)*, *etr 1–3*, *etr 1–2*, and *ethylene-insensitive 3* (*ein3*) were ABA-insensitive compared to Col-0, indicating an ethylene-dependent response of ABA in root growth (Beaudoin et al., 2000).

Moreover, *ethylene-overproducer1 (eto1-1)* mutants were also highly insensitive to ABA and able to grow normally as compared to Col-0 (Beaudoin et al., 2000), indicating that proper ET signalling and biosynthesis pathways are required to regulate the plant growth in response to ABA. Brassinosteroids (BRs) are also important regulators of plant growth through modulation of auxin hormone (Li et al., 2005). In model plants such as *Arabidopsis thaliana* and crop plants like *Brassica napus*, the application of BR brassinolide induces the polar transport of auxin and alters the endogenous level of auxin by upregulating the expression level of *PIN-FORMED (PIN)* and *RHO-RELATED PROTEIN FROM PLANTS 2 (ROP2)* genes (Li et al., 2005). Furthermore, the accumulation of PIN2 protein leads to the plant tropism response, indicating a synergistic crosstalk between auxin and BRs (Li et al., 2005). Transcriptomic data indicates the upregulation of ABA signaling and biosynthesis components in BRs-treated plants, showing a crosstalk between ABA-BRs (Divi et al., 2016). Overexpression of *DWF* and *BZR1* transcript level of BRs biosynthesis and signaling pathway enhanced the ABA level through the upregulation of *9-CIS-EPOXYCAROTENOID DIOXYGENASE 1* (*NCED1)* gene associated with ABA biosynthesis (Nambara and Marion-Poll, 2005).

5.2 | Phytohormonal cross-talk during plant defence

Within the domain of plant hormones, a remarkable transformation occurs when the plant faces environmental stressors, whether biotic or abiotic in nature (Iqbal et al., 2022). These chemical messengers, typically devoted to driving growth and development, shift their focus to fortify the plant's defense mechanisms (Pozo et al., 2015). For example, auxin, usually associated with plant growth, also steps into the arena of plant defense against biotic stress, regulating specific genes like ARFs during viral infection in tomato leaves. This highlights the dual role of auxin in both development and defense responses (Bouzroud et al., 2018).

Microarray analysis in rice plants has identified auxin-induced, auxin-suppressed, and members of auxin-related gene families in response to biotic stress. For instance, *GLYCOSIDE HJYDROLASE 3 (GH3)*, Auxin/Indole-3-Acetic Acid (*Aux/IAA)*, *SMALL AUXIN UP-REGULATED RNA* (*SAUR)* and *ARF* were reported up-regulated after infection of *M. grisea* and *S. hermonthica* compared to the non-infected plants (Ghanashyam and Jain, 2009). To know the importance of GH3 in defence against biotic stress, genetic approaches were employed to introduce *gh3.5* knockout and *GH3.5* overexpressing lines. In *gh3.5* knockout mutants of rice, the transcript level of *PATHOGENESIS-RELATED-1 (PR-1)* and the accumulation level of SA were lower, resulting in compromised resistance (Zhang et al., 2007; Ding et al., 2008). In contrast, GH3.5 overexpressed lines showed elevated defense against the *Xanthomonas oryzae* pv *oryzae* compared to the wild-type rice cultivars (Zhang et al., 2007; Ding et al., 2008). SA is a crucial phytohormone that acts as a defence mechanism against biotic stress. Wang et al. (2007) reported that SA constrains the auxin by suppressing not only the PIN protein but also the genes associated with TRANSPORT INHIBITOR RESPONSE 1 (TIR1) receptor. This enhances the stabilization of Aux/IAA repressor proteins, resulting in the inhibition of auxin (Wang et al., 2007). This inhibitory response against the auxin is a part of the plant's defence system, helping it survive against pathogen infections (Wang et al., 2007).

Furthermore, Auxin-JA crosstalk plays an important role in both development and defense. For instance, microarray expression data shows that exogenous application of auxin downregulates genes associated with JA biosynthesis pathway in *Arabidopsis thaliana* seedlings indicating crosstalk between JA and auxin (Liu and Wang, 2006). Moreover, besides the auxin-SA crosstalk, there is ample evidence that indicates a complex crosstalk between JA and auxin during the infection of the necrotrophic pathogen, which positively regulates plant necrotrophic resistance. Several studies indicate that auxin biosynthesis mutants, such as *anthranilate synthase* $\alpha 1$ (*asa1-1)* (Sun et al., 2009) and *cyp79b2 cyp79b3* (Zhao et al., 2002), show higher susceptibility to *Alternaria brassicicola* fungus compared to the wild type, possibly due to alterations in the auxin signalling pathway. Furthermore, it was observed that the wild-type plants exhibited elevated levels of IAA, whereas *asa1-1* mutant plants failed to produce this higher level of IAA, indicating ASA1-dependent auxin biosynthesis in response to *A. brassicicola* (Qi et al., 2012). The co-application of IAA and MeJA induces resistance against the necrotrophic pathogens *Alternaria brassicicola* by enhancing the expression level of *PLANT DEFENSIN 1.2* (*PDF1.2)* and *HEVEIN-LIKE (HEL)* or *PATHOGENESIS-RELATED PROTEIN 4 (PR4)*. These genes, known as defence marker genes, suggest synergistic crosstalk. The regulation occurs through the upregulation of auxin biosynthesis and subsequent auxin signaling via an ASA1-dependent pathway. This pathway is activated through crosstalk with JA in response to necrotrophic pathogens, particularly the *A. brassicicola* fungus (Sun et al., 2011).

Additionally, gibberellic acid (GA), a crucial plant hormone that regulates various aspects of growth and development, showcases its capacity to induce tolerance against both abiotic and biotic stresses. GA accomplishes this by modulating the antioxidant defense system, influencing the transcriptome, and suppressing the expression of nitrogen metabolic genes (Buhrow et al., 2016). Moreover, microarray experimental data revealed that, upon application of BTH, a synthetic chemical analogue of SA, several genes associated with GA biosynthesis and signalling were downregulated. This indicates a closed and dynamic cross-talk mechanism that regulates both growth and defence in plants (Wang et al., 2006).

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Besides the interaction of GA with SA, there is evidence indicating crosstalk between GA with JA through DELLAs, which act as negative regulators but alleviate biotic stress defence by positively regulating the JA-mediated pathway. In GA-deficient plants, the accumulation of DELLA increases. This competes with the negative regulator of the JA pathway, known as Jasmonate- Zinc-Finger Inflorescence Meristem (ZIM)-domain proteins (JAZ), subsequently activating the JA-GA signaling downstream pathway through the release of the basic helix–loop–helix (bHLH) transcription factor MYC2 (Nguyen et al., 2016) (Figure 2). When GA is present, JAZs are released to mask MYC2 by degrading DELLAs via 26S proteasome. This inhibits the GA-mediated JA signalling defence, leading to susceptibility (Hou et al., 2010; Wild et al., 2012; Nguyen et al., 2016).

Furthermore, the activation of JA signaling during insect or pathogen attacks triggers the degradation of JAZ repressors via the accumulation of DELLA repressors. These two repressors interact with each other, leading to deactivation. Consequently, more DELLA repressors inhibit PIF transcription factors, thereby slowing growth (Yang et al., 2012). The process results in the activation of defense genes, leading to the production of antimicrobial and anti-herbivore compounds and proteins, all aimed at safeguarding the plant against pests and pathogens (Mithöfer and Boland, 2012; Tiku, 2018). Thus, JA-GA synergistic crosstalk, involved in the initiation of trichome and the biosynthesis of sesquiterpene, provides assistance in defence against biotic stress, such as fungi and bacteria (Qi et al., 2014; Nguyen et al., 2016). Furthermore, studies elucidating the crosstalk between BRs, AUXs, and CKs with JA signaling showcased both positive and negative effects (Dervinis et al., 2010; Meldau, Baldwin and Wu, 2011; Yang et al., 2012; Shigenaga et al., 2017).

Similar to other phytohormones, ABA biosynthesis and downstream signaling system activate defense, which provides resistance to plants. For example, ABA-deficient mutant plants showed higher resistance against the bacterial speck disease through the higher accumulation level of salicylate, but became susceptible to the attack of *Spodoptera exigua* (Thaler and Bostock, 2004; Dinh et al., 2013; Lee et al., 2013; Nguyen et al., 2016). Plants exhibit SA-ABA crosstalk that is specific to the type of biotic stress. Furthermore, ABA, through MYC2 and its homologs MYC3 and MYC4 transcription factors, regulates the JA-signalling pathway at the synergistic level in *A. thaliana* plants (Schweizer et al., 2013; Nguyen et al., 2016). For example, ABA induces plant resistance against insects by upregulating *VEGETATIVE STORAGE PROTEIN (VSPs), LIPOXYGENASE (LOXs), LEUCINE AMINOPEPTIDASE (LAP), PIN-FORMED2 (PIN2)* and glucosinolate biosynthetic genes. These above-mentioned genes are regulated by the MYC2 transcription factor, which is directly dependent on the ABA-INDUCED CORONATINE INSENSITIVE1 (COI)-dependent pathway (Peña-Cortés et al.,1995; Boter et al., 2004; Nguyen et al., 2016) (Figure 2). Khatib et al. (2004) reported that *A. thaliana* plants activate three signalling pathways mediated by SA, JA, and ET in response to the Cellulose-Binding Elicitor Lectin (CBEL) elicitor of *Phytophthora parasitica* var. *nicotianae* (Khatib et al., 2004), indicating an intricate crosstalk between these phytohormones in response to biotic stress. To validate their hypothesis, the researchers used SA-deficient transgenic plants (NahG) and two mutants affected by the perception of JA (*coi1*) and ET (*ein2*). They found differential involvement of these hormones in necrosis induction and defence against CBEL in Arabidopsis plants. The researchers reported that CBEL-induced ethylene biosynthesis, hydroxyproline-rich glycoproteins (HRGP) accumulation, peroxidase activity, and transcript levels of *ACO1*, *ASA1*, *WALL-ASSOCIATED KINASES* (*WAK1*), and *PR-1* were higher in Col-0 than in mutant plants. However, necrosis was eliminated in the *ein2* and *coi1* mutant plants. Meanwhile, mRNA induction of *WAK1* and *PR*-1, as well as the accumulation of HRGP and peroxidase activity, were affected in *NahG* transgenic plants (Khatib et al., 2004). This suggests a significant interplay between SA-JA-ET in regulating and improving disease resistance in plants.

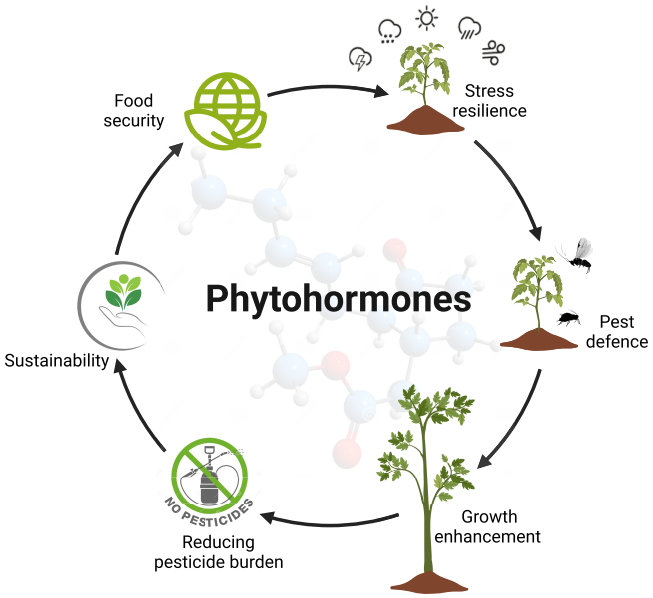


FIGURE 3 Potential Utilization Areas of Phytohormones as a Source in Sustainable Agriculture and Food Security. Done with Biorender.

6 | INTEGRATING PHYTOHORMONE FOR SUSTAINABLE AGRICULTURE

Phytohormones play a pivotal role in sustainable agriculture, offering avenues to enhance crop productivity and stress resilience while reducing reliance on conventional chemical interventions (Jan et al., 2020; Chen and Pang, 2023; Raza et al., 2023) (Figure 3). They promote growth, yield optimization, and stress tolerance in challenging environments (Nakashita et al., 2003; Bari and Jones, 2009; Kazan and Manners, 2009; Erb et al., 2012) and enhance plant immunity against pests and pathogens (Ali et al., 2021; Ali et al., 2023b). Various exogenous application methods, such as foliar spraying, seed priming and encapsulation demonstrate efficacy in promoting plant growth and stress resilience (Rhaman et al., 2020; Ahmad et al., 2021; Sampedro-Guerrero et al., 2022, 2023; Swain et al., 2023). Integrating phytohormone-based strategies with other sustainable practices, such

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

as crop rotation and diversification, biological control, and use of resistant cultivars, offers significant potential for synergistic effects. By further exploring and developing these integrated approaches, we can enhance their effectiveness in maximizing crop health and productivity while promoting long-term sustainable agriculture (Mouden et al., 2017; Divekar et al., 2022; Hirayama and Mochida, 2022; Doostkam et al., 2023) (Figure 3). Additionally, these strategies, with socio-economic and environmental implications, have the potential to enhance farmer livelihoods and promote eco-friendly agricultural practices (Ansari et al., 2017; Zheng et al., 2023), contributing to global food security goals (Yadav et al., 2021).

Field applications of phytohormones, such as jasmonic acid, salicylic acid, and brassinosteroids, show promise in modern agriculture, requiring precise timing and dosage to trigger effective defense responses (see Table S1 and Nakashita et al., 2003; Coll et al., 2015; Faize and Faize, 2018; Gondor et al., 2022; Vázquez-González et al., 2022; Rehman et al., 2023). Field trials with ABA and jasmonate applications demonstrate enhanced defense and reductions in pest populations, and the attraction of natural enemies (Thaler et al., 2001; Bayram and Tonğa, 2018b; Berggren et al., 2023). MeSA applications, including lures, effectively reduce pest populations and control nematode-borne diseases in diverse field conditions (Lee, 2010; Park et al., 2013; Regmi, et al., 2023).

Although there is immense potential for the utilization of phytohormones in agriculture for regulating plant growth and defense, as well as the development of new resistant cultivars to biotic and abiotic stressors using genetic tools (Bari and Jones, 2009; Asami and Nakagawa, 2018; Jiang and Asami, 2018; Mamta and Rajam, 2018; Kaur et al., 2021; Nowicka, 2022), integrating phytohormones to enhance crop growth, induce resistance, and improve productivity in agricultural practices encounters multifaceted challenges. Initially, the efficacy of exogenous applications of phytohormones remains a persistent issue, as variations in effectiveness among different plant species, cultivars, or environmental conditions often yield contradictory results across numerous studies. Formal procedures for the approval of phytohormones as plant protection products have not yet been settled. Regulatory constraints further complicate matters; for instance, the long-term effects on the environment, as well as human and animal health, remain uncertain and are among the factors impeding their widespread adoption (Chanclud and Lacombe, 2017). Accessibility and affordability present additional barriers, with discrepancies in the availability of phytohormone products and associated application technologies among farmers or regions exacerbating disparities in their usage. Moreover, a lack of knowledge and education among farmers regarding optimal application methods, dosages, and timing of phytohormone treatments can lead to suboptimal outcomes or misuse. Environmental and ecological considerations also loom large, as potential unintended effects such as off-target impacts on non-target organisms or ecosystem dynamics may undermine the sustainable implementation of phytohormones in agriculture. Lastly, integrating phytohormone treatments with other agricultural practices, such as crop rotation or pest control strategies, requires detailed studies, careful coordination, and optimization to achieve the desired synergistic effects.

6.1 | HARNESSING PHYTOHORMONES: NOVEL STRATEGIES USING GENETIC OR OTHER TECHNOLOGIES

Genetic manipulation techniques such as gene editing (e.g., CRISPR/Cas9), gene silencing (e.g., RNA interference), and gene overexpression are frequently used to modify the expression levels or activities of key genes involved in phytohormone biosynthesis, signaling pathways, or metabolism. The CRISPR/Cas9 system, a naturally occurring genome editing tool, has been extensively adopted and refined for precise editing, regulation, and monitoring of individual genes in plants, animals, and microbes (Song et al., 2016). This versatile tool serves a multitude of purposes, including enhancing crop growth, development, yield, and quality, while also bolstering tolerance to various environmental stresses, both biotic and abiotic. Leveraging CRISPR/Cas-based (Type I, II and III) genome editing offers a new frontier in crop improvement, providing a cutting-edge and powerful tool for precision breeding (Gaj et al., 2013; Chen et al., 2019; Rajput et al., 2021; Zhang et al., 2021; Shokat et al., 2023). CRISPR/Cas-based genome editing yielded many plant species with superior features in resistance to plant viruses, abiotic stress factors (drought, salinity, heat stress, cold tolerance, chilling stress tolerance and yield improvement and also speeding hybrid breeding (Chen et al., 2019; Lu et al., 2019; Rajput et al., 2021; Mandal et al., 2022). Among the phytohormones, CKs are one of the primary targets for yield improvement using CRISPR/Cas-based systems. Gene editing of cytokinin oxidase/dehydrogenase (CKO/CKX), encoded by the CKX gene, catalyses the irreversible degradation of cytokinins. The manipulation of CKX genes using CRISPR/Cas-based systems represents a promising approach for improving crop yield and performance by modulating cytokinin levels within plants (Mandal et al., 2022). Another recent paper targeted auxin using the CRISPR/Cas method via mutation of auxin efflux carriers, resulting in chilling tolerance by modulating ROS homeostasis in rice (Xu et al., 2022).

RNA interference (RNAi) is a gene regulatory mechanism naturally present in eukaryotic cells, conserved across evolutionary timescales. Its primary function is to safeguard cells against foreign DNA intrusion by silencing specific genes through the degradation of messenger RNA (Napoli et al., 1990; Fire et al., 1998; Saurabh et al., 2014; Mamta and Rajam, 2018; Muhammad et al., 2019; Kaur et al., 2021). Researchers have extensively investigated RNA interference (RNAi) to enhance various crop traits, such as stress tolerance, disease resistance, and yield improvement (Saurabh et al., 2014; Mamta and Rajam, 2018; Muhammad et al., 2019; Kaur et al., 2021; Rajput et al., 2021; Nowicka, 2022). RNAi (gene silencing) methodology yielded many improved and resistant plants to viruses, plant bacterial diseases, plant fungal diseases, insect and nematode pests in addition to drought and salt resistance (Rajput et al., 2021; Nowicka, 2022). Mutations or alterations of phytohormones (ethylene, auxin, ABA)-related genes by RNAi, resulted in shelf-life enhanced, seedless fruit development, virus resistance and drought tolerance (Pasin et al., 2020; Rajput et al., 2021; Poór et al., 2022; Nazir et al., 2024). In an earlier study, Yang et al. (2020)

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

reported that jasmonate signalling synergistically enhances RNA gene silencing and defence in rice.

Utilizing exogenous phytohormones or hormone analogues on plants serves as a valuable method to investigate their impacts on plant growth, development, and responses to environmental cues (Zhang et al., 2018). This approach aids in elucidating the specific roles and functions of individual phytohormones in various physiological processes. In such investigations, beyond merely conducting enzymatic reactions or volatile organic compound (VOC) profiling, employing transcriptomics and proteomics techniques allows for the analysis of alterations in gene expression or protein abundance resulting from phytohormone treatments or genetic modifications (Zhu et al., 2019; Yang et al., 2023; Gupta et al., 2024; Hu et al., 2024; Kumari et al., 2024; Xiao et al., 2024). Through this comprehensive approach, researchers can attain a deeper understanding of the molecular mechanisms governing hormone regulation (Liu et al., 2023). This knowledge can then be leveraged through techniques such as RNA interference (RNAi), CRISPR/Cas, overexpressions and/or their combination to engineer plants by altering the expression of enzymes or regulatory genes involved in phytohormone metabolism (Yang et al., 2008; Abe and Ichikawa, 2016; Liu et al., 2023). This modulation enables the adjustment of hormone levels within the plant, facilitating enhanced yield performance under different conditions such as salinity, drought, and cold while also conferring specific resistance to biotic stressors (Gosal and Wani, 2018; Singh et al., 2018). For such studies, hormone profiling and bioinformatics alongside systems biology approaches are essential.

Analytical techniques such as liquid chromatography-mass spectrometry (LC–MS–MS) and high-performance liquid chromatography (HPLC) are employed for quantifying endogenous phytohormone levels in plant tissues with and without stimuli. Such profiling studies enable researchers to monitor changes in hormone concentrations under different experimental conditions and correlate them with physiological responses. The results obtained from hormone profiling studies are analysed using bioinformatics approaches to unveil complex regulatory networks governing phytohormone biosynthesis, signaling, and crosstalk. This involves the integration of large-scale datasets to identify key genes, proteins, and pathways involved in hormone regulation. Moreover, modelling and simulation studies are employed to understand the dynamic interactions between phytohormones and other signaling molecules within the plant system (Shokat et al., 2021a). These computational approaches help in elucidating the intricate mechanisms underlying hormone-mediated responses and aid in predicting the outcomes of genetic and environmental perturbations on plant physiology.

7 | CHALLENGES AND FUTURE PROSPECTS

Phytohormones hold the potential to revolutionize agriculture by reducing reliance on synthetic chemicals and enhancing crop resilience. However, this path towards more sustainable agriculture presents challenges and opportunities. For instance, environmental impact assessment is crucial due to unpredictable effects on non-target organisms and ecosystems. Comprehensive phytohormone application on crops can impact human nutrition, gut microbiome, and metabolism (Mukherjee et al., 2022). Another challenge is developing stable phytohormone-engineered staple crops under multiple field stresses (Wani et al., 2016). Using incompatible insecticides can compromise phytohormones' effectiveness, requiring a robust regulatory framework (Bottrell and Schoenly, 2018). Educating farmers and consumers about these approaches is essential. In the future, commercialising phytohormones as potential agrochemicals offers promising avenues for economic profit, nutritional benefits, and environmental sustainability, making them key players in advancing sustainable agriculture (Chávez-Dulanto et al., 2021; Madaan et al., 2022; Rahman et al., 2023).

Future research in phytohormone engineering should prioritise fine-tuning gene modifications to ensure their controlled expression. This involves meticulous adjustments of regulatory elements to precisely regulate the timing and magnitude of phytohormone production. To avoid undesired negative effects on plant growth, exploring conditional, stress-induced, or senescence-induced promoters is crucial. These promoters allow for more nuanced control of gene expression, activating phytohormone production only under specific environmental conditions or developmental stages.

Additionally, understanding the intricate crosstalk between phytohormone signaling pathways is of paramount importance in genetic modifications. Investigating how different phytohormones interact and influence each other's expression can provide valuable insights into optimizing engineered plants for desired traits. Beyond controlled laboratory settings, it is imperative to investigate the effects of phytohormone engineering under real-world, fluctuating field conditions. Conducting studies over extended periods and across diverse agricultural environments ensures a comprehensive understanding of the practical implications of phytohormone modifications. This approach is essential for ensuring sustainable and predictable outcomes in agriculture and addressing challenges associated with variability in climate, soil conditions, and pest pressures.

AUTHOR CONTRIBUTIONS

JA conceived the idea. JA, AB, MM, JO, RR, and ND contributed to writing the initial draft, designing the tables, and preparing the figures. HAG, KAK, DK, and RC edited and reviewed the draft. All authors contributed significantly and approved the final version for publication.

ACKNOWLEDGMENTS

We would like to thank Biorender for their illustration creation services. The authors extend their appreciation to the Deanship of Scientific Research (RGP2/132/45) at King Khalid University, Saudi Arabia.

FUNDING INFORMATION

This work was supported by the project: Comprehensive research of mitigation and adaptation measures to diminish the negative impacts

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of climate changes on forest ecosystems in Slovakia (FORRES), ITMS: APVV-21-0224 supported by the Slovak Research and Development Agency and by Slovak Grant Agency for Science grant number VEGA 1/0392/22.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

ORCID

Jamin Ali https://orcid.org/0000-0001-7698-5000
Mohammad Mukarram https://orcid.org/0000-0002-9034-9366
James Ojo https://orcid.org/0000-0001-7476-4546
Nancy Dawam https://orcid.org/0000-0003-4054-7513
Riyazuddin Riyazuddin https://orcid.org/0000-0003-2580-2811
Hamed A. Ghramh https://orcid.org/0000-0001-7995-0663
Khalid Ali Khan https://orcid.org/0000-0002-4734-6338
Rizhao Chen https://orcid.org/0000-0001-8866-6648
Daniel Kurjak https://orcid.org/0000-0002-2489-8463
Ahmet Bayram https://orcid.org/0000-0003-4532-3527

REFERENCES

Abbas, M. et al. (2020) 'Gibberellic acid induced changes on growth, yield, superoxide dismutase, catalase and peroxidase in fruits of bitter gourd (Momordica charantia L.)', *Horticulturae*, 6(4), p. 72.

Abe, K. and Ichikawa, H. (2016) 'Gene overexpression resources in cereals for functional genomics and discovery of useful genes', *Frontiers in Plant Science*, 7, p. 210478.

Aboye, T. L. et al. (2015) 'A Cactus-Derived Toxin-Like Cystine Knot Peptide with Selective Antimicrobial Activity', *ChemBioChem*, 16(7), pp. 1068–1077.

Achard, P. et al. (2003) 'Ethylene regulates Arabidopsis development via the modulation of DELLA protein growth repressor function', *The Plant Cell*, 15(12), pp. 2816–2825.

Adie, B. et al. (2007) 'Modulation of plant defenses by ethylene', *Journal of plant growth regulation*, 26, pp. 160–177.

Agudelo-Morales, C. E. et al. (2021) 'Phytohormones and Plant Growth Regulators—A Review', *J. Sci. Technol. Appl*, 10, pp. 27–65.

Ahmad, S. et al. (2021) 'Ameliorative effect of melatonin improves drought tolerance by regulating growth, photosynthetic traits and leaf ultrastructure of maize seedlings', *BMC Plant Biology*, 21(1), pp. 1–14.

Akhtar, S. S. et al. (2020) 'Role of cytokinins for interactions of plants with microbial pathogens and pest insects', *Frontiers in Plant Science*, 10, p. 1777.

Al-Babili, S. and Bouwmeester, H. J. (2015) 'Strigolactones, a novel carotenoid-derived plant hormone', *Annual review of plant biology*, 66, pp. 161–186.

Ali, J. et al. (2021) 'Effects of cis-Jasmone Treatment of Brassicas on Interactions With Myzus persicae Aphids and Their Parasitoid Diaeretiella rapae', *Frontiers in Plant Science*, 12. doi: https://doi.org/10.3389/fpls.2021.711896.

Ali, J., Wei, D., et al. (2023a) 'Exogenous Application of Methyl Salicylate Induces Defence in Brassica against Peach Potato Aphid Myzus persicae', *Plants*, 12(9), p. 1770. https://doi.org/10.3390/plants12091770.

Ali, J., Bayram, A., et al. (2023b) 'Peach–Potato Aphid Myzus persicae: Current Management Strategies, Challenges, and Proposed Solutions', *Sustainability*, 15(14), p. 11150.

Ali, J. (2023) 'The Peach Potato Aphid (Myzus persicae): *Ecology and Management*', 1, p. 132. https://doi.org/10.1201/9781003400974.

Ali, J. et al. (2024) 'Defense Strategies and Associated Phytohormonal Regulation in Brassica Plants in Response to Chewing and Sap-sucking Insects', *Frontiers in Plant Science*, 15, p. 1376917.

Ament, K. et al. (2004) 'Jasmonic acid is a key regulator of spider mite-induced volatile terpenoid and methyl salicylate emission in tomato', *Plant Physiology*, 135(4), pp. 2025–2037. doi: https://doi.org/10.1104/pp.104.048694.

An, C. and Mou, Z. (2011) 'Salicylic acid and its function in plant immunity F', *Journal of integrative plant biology*, 53(6), pp. 412–428.

Anderson, J. A. et al. (2016) 'Emerging agricultural biotechnologies for sustainable agriculture and food security', *Journal of agricultural and food chemistry*, 64(2), pp. 383–393.

Anderson, J. P. et al. (2004) 'Antagonistic interaction between abscisic acid and jasmonate-ethylene signaling pathways modulates defense gene expression and disease resistance in Arabidopsis', *The Plant Cell*, 16(12), pp. 3460–3479.

Anfang, M. and Shani, E. (2021) 'Transport mechanisms of plant hormones', *Current Opinion in Plant Biology*, 63, p. 102055.

Ansari, R. A. et al. (2017) 'PGPR: current vogue in sustainable crop production', *Probiotics and plant health*, pp. 455–472.

Arimura, G. et al. (2000) 'Herbivory-induced volatiles elicit defence genes in lima bean leaves', *Nature*, 406(6795), pp. 512–515.

Asami, T. and Nakagawa, Y. (2018) 'Preface to the Special Issue: Brief review of plant hormones and their utilization in agriculture', *Journal of pesticide science*, 43(3), pp. 154–158.

Asghar, M. A. et al. (2019) 'Crosstalk between abscisic acid and auxin under osmotic stress', *Agronomy Journal*, 111(5), pp. 2157–2162.

Bari, R. and Jones, J. D. G. (2009) 'Role of plant hormones in plant defence responses', *Plant molecular biology*, 69, pp. 473–488.

Bayram, A. and Tonğa, A. (2018a) 'Methyl jasmonate affects population densities of phytophagous and entomophagous insects in wheat.', *Applied Ecology & Environmental Research*, 16(1).

Bayram, A. and Tonğa, A. (2018b) 'cis-Jasmone treatments affect pests and beneficial insects of wheat (Triticum aestivum L.): the influence of doses and plant growth stages', *Crop Protection*, 105, pp. 70–79.

Beaudoin, N. et al. (2000) 'Interactions between abscisic acid and ethylene signaling cascades', *The Plant Cell*, 12(7), pp. 1103–1115.

Belhadj, A. et al. (2006) 'Methyl jasmonate induces defense responses in grapevine and triggers protection against Erysiphe necator', *Journal of agricultural and food chemistry*, 54(24), pp. 9119–9125.

Benitez-Alfonso, Y. and Caño-Delgado, A. I. (2023) 'Brassinosteroids en route', *Nature Chemical Biology*, pp. 1–2.

Berggren, K. et al. (2023) 'Synergistic effects of methyl jasmonate treatment and propagation method on Norway spruce resistance against a bark-feeding insect', *Frontiers in Plant Science*, 14, p. 1165156.

Berrocal-Lobo, M., Molina, A. and Solano, R. (2002) 'Constitutive expression of ETHYLENE-RESPONSE-FACTOR1 in Arabidopsis confers resistance to several necrotrophic fungi', *The Plant Journal*, 29(1), pp. 23–32.

Beveridge, C. A. et al. (2003) 'Additional signalling compounds are required to orchestrate plant development', *Journal of plant growth regulation*, 22, pp. 15–24.

Bi, H. H. et al. (2007) 'Rice allelopathy induced by methyl jasmonate and methyl salicylate', *Journal of chemical ecology*, 33(5), pp. 1089–1103.

Birkett, M. A. et al. (2000) 'New roles for cis-jasmone as an insect semiochemical and in plant defense', *Proceedings of the National Academy of Sciences of the United States of America*, 97(16), pp. 9329–9334. doi: https://doi.org/10.1073/pnas.160241697.

Blassioli Moraes, M. C. et al. (2008) 'cis-Jasmone induces accumulation of defence compounds in wheat, Triticum aestivum', *Phytochemistry*, 69(1), pp. 9–17. doi: https://doi.org/10.1016/j.phytochem.2007.06.020.

Bodenhausen, N. and Reymond, P. (2007) 'Signaling pathways controlling induced resistance to insect herbivores in Arabidopsis', *Molecular Plant-Microbe Interactions*, 20(11), pp. 1406–1420.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Boter, M. et al. (2004) 'Conserved MYC transcription factors play a key role in jasmonate signaling both in tomato and Arabidopsis', *Genes & development*, 18(13), pp. 1577–1591.

Bottrell, D. G. and Schoenly, K. G. (2018) 'Integrated pest management for resource-limited farmers: challenges for achieving ecological, social and economic sustainability', *The Journal of Agricultural Science*, 156(3), pp. 408–426.

Bouzroud, S. et al. (2018) 'Auxin response factors (ARFs) are potential mediators of auxin action in tomato response to biotic and abiotic stress (Solanum lycopersicum)', *PloS one*, 13(2), p. e0193517.

Broekgaarden, C. et al. (2015) 'Ethylene: traffic controller on hormonal crossroads to defense', *Plant physiology*, 169(4), pp. 2371–2379.

Bruce, T. J. A. et al. (2008) 'cis-Jasmone induces Arabidopsis genes that affect the chemical ecology of multitrophic interactions with aphids and their parasitoids', *Proceedings of the National Academy of Sciences of the United States of America*, 105(12), pp. 4553–4558. doi: https://doi.org/10.1073/pnas.0710305105.

Bruce, T., Pickett, J. and Smart, L. (2003) 'cis-Jasmone switches on plant defence against insects', *Pesticide Outlook*, 14(3), pp. 96–98.

Bruinsma, M. et al. (2008) 'Differential effects of jasmonic acid treatment of Brassica nigra on the attraction of pollinators, parasitoids, and butterflies', *Entomologia Experimentalis Et Applicata*, 128(1), pp. 109–116. doi: https://doi.org/10.1111/j.1570-7458.2008.00695.x.

Bruinsma, M. et al. (2009) 'Jasmonic acid-induced volatiles of Brassica oleracea attract parasitoids: effects of time and dose, and comparison with induction by herbivores', *Journal of Experimental Botany*, 60(9), pp. 2575–2587. doi: https://doi.org/10.1093/jxb/erp101.

Buhrow, L. M. et al. (2016) 'Exogenous abscisic acid and gibberellic acid elicit opposing effects on Fusarium graminearum infection in wheat', *Phytopathology*, 106(9), pp. 986–996.

Chanclud, E. and Lacombe, B. (2017) 'Plant hormones: key players in gut microbiota and human diseases?', *Trends in plant science*, 22(9), pp. 754–758.

Chandler, J. W. (2011) 'The hormonal regulation of flower development', *Journal of Plant Growth Regulation*, 30(2), pp. 242–254.

Chávez-Dulanto, P. N. et al. (2021) 'Increasing the impact of science and technology to provide more people with healthier and safer food', *Food and Energy Security*, 10(1), p. e259.

Checker, V. G. et al. (2018) 'Role of phytohormones in plant defense: signaling and cross talk', *Molecular aspects of plant-pathogen interaction*, pp. 159–184.

Chen, J. and Pang, X. (2023) 'Phytohormones unlocking their potential role in tolerance of vegetable crops under drought and salinity stresses', *Frontiers in Plant Science*, 14, p. 1121780.

Chen, K. et al. (2019) 'CRISPR/Cas genome editing and precision plant breeding in agriculture', *Annual review of plant biology*, 70, pp. 667–697.

Chen, K. et al. (2020) 'Abscisic acid dynamics, signaling, and functions in plants', *Journal of integrative plant biology*, 62(1), pp. 25–54.

Choi, H. W. and Klessig, D. F. (2016) 'DAMPs, MAMPs, and NAMPs in plant innate immunity', *BMC plant biology*, 16, pp. 1–10.

Choudhary, P. et al. (2021) 'Hormonal crosstalk in regulating salinity stress tolerance in graminaceous crops', *Physiologia Plantarum*, 173(4), pp. 1587–1596.

Christmann, A. et al. (2006) 'Integration of abscisic acid signalling into plant responses', *Plant biology*, 8(03), pp. 314–325.

Ciura, J. and Kruk, J. (2018) 'Phytohormones as targets for improving plant productivity and stress tolerance', *Journal of plant physiology*, 229, pp. 32–40.

Coll, Y. et al. (2015) 'Brassinosteroids roles and applications: an up-date', *Biologia*, 70(6), pp. 726–732.

Cortleven, A. et al. (2019) 'Cytokinin action in response to abiotic and biotic stresses in plants', *Plant, Cell & Environment*, 42(3), pp. 998–1018.

D'Ovidio, R. et al. (2004) 'Characterization of the complex locus of bean encoding polygalacturonase-inhibiting proteins reveals subfunctionalization for defense against fungi and insects', *Plant Physiology*, 135(4), pp. 2424–2435.

Von Dahl, C. C. and Baldwin, I. T. (2007) 'Deciphering the role of ethylene in plant–herbivore interactions', *Journal of Plant Growth Regulation*, 26, pp. 201–209.

Davies, P. J. (2010) 'The plant hormones: their nature, occurrence, and functions', in *Plant hormones: biosynthesis, signal transduction, action*! Springer, pp. 1–15.

Demidchik, V., Maathuis, F. and Voitsekhovskaja, O. (2017) 'Unravelling the plant signalling machinery: An update on the cellular and genetic basis of plant signal transduction', *Functional Plant Biology*, 45(2), pp. 1–8.

Dervinis, C. et al. (2010) 'Cytokinin primes plant responses to wounding and reduces insect performance', *Journal of Plant Growth Regulation*, 29, pp. 289–296.

Dewhirst, S. Y. et al. (2012) 'Activation of defence in sweet pepper, Capsicum annum, by cis-jasmone, and its impact on aphid and aphid parasitoid behaviour', *Pest Management Science*, 68(10), pp. 1419–1429. doi: https://doi.org/10.1002/ps.3326.

Dharmasiri, S., Jayaweera, T. and Dharmasiri, N. (2013) 'Plant hormone signalling: current perspectives on perception and mechanisms of action'.

Ding, L.-N. et al. (2022) 'Plant disease resistance-related signaling pathways: recent progress and future prospects', *International Journal of Molecular Sciences*, 23(24), p. 16200.

Ding, P. and Ding, Y. (2020) 'Stories of salicylic acid: a plant defense hormone', *Trends in plant science*, 25(6), pp. 549–565.

Ding, X. et al. (2008) 'Activation of the indole-3-acetic acid–amido synthetase GH3-8 suppresses expansin expression and promotes salicylate- and jasmonate-independent basal immunity in rice', *The Plant Cell*, 20(1), pp. 228–240.

Dinh, S. T., Baldwin, I. T. and Galis, I. (2013) 'The HERBIVORE ELICITOR-REGULATED1 gene enhances abscisic acid levels and defenses against herbivores in Nicotiana attenuata plants', *Plant Physiology*, 162(4), pp. 2106–2124.

Divekar, P. A. et al. (2022) 'Plant secondary metabolites as defense tools against herbivores for sustainable crop protection', *International journal of molecular sciences*, 23(5), p. 2690.

Divi, U. K., Rahman, T. and Krishna, P. (2010) 'Brassinosteroid-mediated stress tolerance in Arabidopsis shows interactions with abscisic acid, ethylene and salicylic acid pathways', *BMC plant biology*, 10, pp. 1–14.

Divi, U. K., Rahman, T. and Krishna, P. (2016) 'Gene expression and functional analyses in brassinosteroid-mediated stress tolerance', *Plant Biotechnology Journal*, 14(1), pp. 419–432.

Dolan, L. et al. (1994) 'Clonal relationships and cell patterning in the root epidermis of Arabidopsis', *Development*, 120(9), pp. 2465–2474.

Doostkam, M. et al. (2023) 'Genetic variation of cucumber (Cucumis sativus L.) cultivars to exogenously applied jasmonic acid to induce resistance to Liriomyza sativae', *Arthropod-Plant Interactions*, pp. 1–11.

Erb, M, Meldau, S. and Howe, G. A. (2012) 'Role of phytohormones in insect-specific plant reactions', *Trends in plant science*, 17(5), pp. 250–9. doi: https://doi.org/10.1016/j.tplants.2012.01.003.

Erbilgin, N. et al. (2006) 'Exogenous application of methyl jasmonate elicits defenses in Norway spruce (Picea abies) and reduces host colonization by the bark beetle Ips typographus', *Oecologia*, 148(3), pp. 426–436.

Fahad, S. et al. (2015) 'Phytohormones and plant responses to salinity stress: a review', *Plant growth regulation*, 75, pp. 391–404.

Faize, L. and Faize, M. (2018) 'Functional analogues of salicylic acid and their use in crop protection', *Agronomy*, 8(1), p. 5.

Fan, L. et al. (2015) 'Factors affecting farmers' behaviour in pesticide use: Insights from a field study in northern China', *Science of the Total Environment*, 537, pp. 360–368.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Feng, G., Liu, G. and Xiao, J. (2015) 'The Arabidopsis EIN2 restricts organ growth by retarding cell expansion', *Plant signaling & behavior*, 10(5), p. e1017169.
Finkelstein, R. (2013) 'Abscisic acid synthesis and response', *The Arabidopsis book/American society of plant biologists*, 11.
Fire, A. et al. (1998) 'Potent and specific genetic interference by double-stranded RNA in Caenorhabditis elegans', *nature*, 391(6669), pp. 806–811.
Francis, B., Aravindakumar, C. T. and Simon, S. (2024) 'Regulatory role of strigolactones in biotic stress tolerance', in *Strigolactones*. Elsevier, pp. 189–200.
Fürstenberg-Hägg, J., Zagrobelny, M. and Bak, S. (2013) 'Plant defense against insect herbivores', *International journal of molecular sciences*, 14(5), pp. 10242–10297.
Gaffney, T. et al. (1993) 'Requirement of salicylic acid for the induction of systemic acquired resistance', *Science*, 261(August 1993), pp. 754–757.
Gaj, T., Gersbach, C. A. and Barbas, C. F. (2013) 'ZFN, TALEN, and CRISPR/Cas-based methods for genome engineering', *Trends in biotechnology*, 31(7), pp. 397–405.
Gehring, C. A., Irving, H. R. and Parish, R. W. (1990) 'Effects of auxin and abscisic acid on cytosolic calcium and pH in plant cells.', *Proceedings of the National Academy of Sciences*, 87(24), pp. 9645–9649.
Ghanashyam, C. and Jain, M. (2009) 'Role of auxin-responsive genes in biotic stress responses', *Plant signaling & behavior*, 4(9), pp. 846–848.
Ghassemian, M. et al. (2000) 'Regulation of abscisic acid signaling by the ethylene response pathway in Arabidopsis', *The Plant Cell*, 12(7), pp. 1117–1126.
Ghorbel, M. et al. (2021) 'Role of jasmonic acid in plants: the molecular point of view', *Plant Cell Reports*, 40, pp. 1471–1494.
Giron, D. et al. (2013) 'Cytokinins as key regulators in plant–microbe–insect interactions: connecting plant growth and defence', *Functional Ecology*, 27(3), pp. 599–609.
Gols, R. et al. (2003) 'Induction of direct and indirect plant responses by jasmonic acid, low spider mite densities, or a combination of jasmonic acid treatment and spider mite infestation', *Journal of Chemical Ecology*, 29(12), pp. 2651–2666.
Gondor, O. K. et al. (2022) 'The role of methyl salicylate in plant growth under stress conditions', *Journal of Plant Physiology*, p. 153809.
Gosal, S. S. and Wani, S. H. (2018) Biotechnologies of Crop Improvement, *Volume 2: Transgenic Approaches*. Springer.
Graham, M. A., Silverstein, K. A. T. and VandenBosch, K. A. (2008) 'Defensin-like genes: genomic perspectives on a diverse superfamily in plants', *Crop science*, 48, p. S-3.
Grant, M. and Lamb, C. (2006) 'Systemic immunity', *Current opinion in plant biology*, 9(4), pp. 414–420.
Guo, H. and Ecker, J. R. (2004) 'The ethylene signaling pathway: new insights', *Current opinion in plant biology*, 7(1), pp. 40–49.
Gupta, R. et al. (2024) 'Integrated "-omics" analysis highlights the role of brassinosteroid signaling and antioxidant machinery underlying improved rice seed longevity during artificial aging treatment', *Plant Physiology and Biochemistry*, 206, p. 108308.
Han, X. and Kahmann, R. (2019) 'Manipulation of phytohormone pathways by effectors of filamentous plant pathogens', *Frontiers in Plant Science*, 10, p. 464951.
Hare, P. D., Cress, W. A. and Van Staden, J. (1997) 'The involvement of cytokinins in plant responses to environmental stress', *Plant Growth Regulation*, 23, pp. 79–103.
Harfouche, A. L. et al. (2006) 'Ethylene signaling mediates a maize defense response to insect herbivory', *Molecular Plant-Microbe Interactions*, 19(2), pp. 189–199.
Hayat, S. et al. (2019) *Brassinosteroids: Plant growth and development*. Springer.
Hayat, S., Ali, B. and Ahmad, A. (2007) 'Salicylic acid: biosynthesis, metabolism and physiological role in plants', *Salicylic acid: A plant hormone*, pp. 1–14.
He, J. et al. (2012) 'DEXH box RNA helicase–mediated mitochondrial reactive oxygen species production in Arabidopsis mediates crosstalk between abscisic acid and auxin signaling', *The Plant Cell*, 24(5), pp. 1815–1833.
He, Z. et al. (2000) 'Perception of brassinosteroids by the extracellular domain of the receptor kinase BRI1', *Science*, 288(5475), pp. 2360–2363.
Hegde, M. et al. (2012) 'Aphid antixenosis in cotton is activated by the natural plant defence elicitor cis-jasmone', *Phytochemistry*, 78(2012), pp. 81–8. doi: https://doi.org/10.1016/j.phytochem.2012.03.004.
Heldt, H. W. and Piechulla, B. (2011) 'Multiple signals regulate the growth and development of plant organs and enable their adaptation to environmental conditions', *Plant biochemistry*. Elsevier, Amsterdam, pp. 451–485.
Hewedy, O. A. et al. (2023) 'Jasmonic acid regulates plant development and orchestrates stress response during tough times', *Environmental and Experimental Botany*, 208, p. 105260.
Hillwig, M. S. et al. (2016) 'Abscisic acid deficiency increases defence responses against M yzus persicae in A rabidopsis', *Molecular plant pathology*, 17(2), pp. 225–235.
Hirayama, T. and Mochida, K. (2022) 'Plant hormonomics: a key tool for deep physiological phenotyping to improve crop productivity', *Plant and Cell Physiology*, 63(12), pp. 1826–1839.
Hirsch, A. M. et al. (1997) 'The role of phytohormones in plant-microbe symbioses', *Plant and soil*, 194, pp. 171–184.
Hou, X. et al. (2010) 'DELLAs modulate jasmonate signaling via competitive binding to JAZs', *Developmental cell*, 19(6), pp. 884–894.
Howe, G. A. and Jander, G. (2008) 'Plant immunity to insect herbivores', *Annual review of plant biology*, 59, pp. 41–66. doi: https://doi.org/10.1146/annurev.arplant.59.032607.092825.
Hu, C. et al. (2021) 'Ethylene response factors 15 and 16 trigger jasmonate biosynthesis in tomato during herbivore resistance', *Plant Physiology*, 185(3), pp. 1182–1197.
Hu, X. et al. (2024) 'Transcriptomic and Phytohormone Metabolomics Provide Insight into the Changes in Citrus limon Infected by Citrus yellow vein clearing virus', *Horticulturae*, 10(3), p. 231.
Huang, L. et al. (2020) 'Brassinosteroid priming improves peanut drought tolerance via eliminating inhibition on genes in photosynthesis and hormone signaling', *Genes*, 11(8), p. 919.
Huang, R. et al. (2019) 'Noncanonical auxin signaling regulates cell division pattern during lateral root development', *Proceedings of the National Academy of Sciences*, 116(42), pp. 21285–21290.
Huang, W.-N. et al. (2013) 'Ethylene-induced changes in lignification and cell wall-degrading enzymes in the roots of mungbean (Vigna radiata) sprouts', *Plant physiology and biochemistry*, 73, pp. 412–419.
Hui, D. et al. (2003) 'Molecular interactions between the specialist herbivore Manduca sexta (Lepidoptera, Sphingidae) and its natural host Nicotiana attenuata: V. Microarray analysis and further characterization of large-scale changes in herbivore-induced mRNAs', *Plant physiology*, 131(4), pp. 1877–1893.
Hwang, J.-S. et al. (2010) 'Isolation and characterization of psacotheasin, a novel knottin-type antimicrobial peptide, from Psacothea hilaris', *Journal of microbiology and biotechnology*, 20(4), pp. 708–711.
Ibrahim, S. et al. (2018) 'Herbivore and phytohormone induced defensive response in kale against cabbage butterfly, Pieris brassicae Linn', *Journal of Asia-Pacific Entomology*, 21(1), pp. 367–373.
Iqbal, N. et al. (2017) 'Ethylene role in plant growth, development and senescence: interaction with other phytohormones', *Frontiers in plant science*, 8, p. 475.
Iqbal, S. et al. (2022) 'Phytohormones trigger drought tolerance in crop plants: outlook and future perspectives', *Frontiers in Plant Science*, 12, p. 3378.
Jan, S. et al. (2020) 'Plant growth regulators: a sustainable approach to combat pesticide toxicity', *3 Biotech*, 10, pp. 1–11.
Jiang, D. and Yan, S. (2018) 'MeJA is more effective than JA in inducing defense responses in Larix olgensis', *Arthropod-Plant Interactions*, 12(1), pp. 49–56.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Jiang, K. and Asami, T. (2018) 'Chemical regulators of plant hormones and their applications in basic research and agriculture', *Bioscience, biotechnology, and biochemistry*, 82(8), pp. 1265–1300.
Kahl, J. et al. (2000) 'Herbivore-induced ethylene suppresses a direct defense but not a putative indirect defense against an adapted herbivore', *Planta*, 210, pp. 336–342.
Kaur, R. et al. (2021) 'RNA interference and crop protection against biotic stresses', *Physiology and Molecular Biology of Plants*, 27(10), pp. 2357–2377.
Kazan, K. and Manners, J. M. (2009) 'Linking development to defense: auxin in plant-pathogen interactions', *Trends in Plant Science*, 14(7), pp. 373–382. doi: https://doi.org/10.1016/j.tplants.2009.04.005.
Khan, M. I. R. et al. (2015) 'Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants', *Frontiers in plant science*, 6, p. 462.
Khatib, M. et al. (2004) 'The CBEL elicitor of Phytophthora parasitica var. nicotianae activates defence in Arabidopsis thaliana via three different signalling pathways', *New Phytologist*, 162(2), pp. 501–510.
Koch, T., Bandemer, K. and Boland, W. (1997) 'Biosynthesis of cis-jasmone: a pathway for the inactivation and the disposal of the plant stress hormone jasmonic acid to the gas phase?', *Helvetica Chimica Acta*, 80(3), pp. 838–850.
Koepfli, J. B., Thimann, K. V and Went, F. W. (1938) 'Phytohormones: structure and physiological activity. I', *Journal of Biological Chemistry*, 122(3), pp. 763–780.
Krishna, P. (2003) 'Brassinosteroid-mediated stress responses', *Journal of Plant Growth Regulation*, 22, pp. 289–297.
Ku, Y.-S. et al. (2018) 'Plant hormone signaling crosstalks between biotic and abiotic stress responses', *International Journal of Molecular Sciences*, 19(10), p. 3206.
Kumari, M. et al. (2024) 'Metabolomics-driven investigation of plant defense response against pest and pathogen attack', *Physiologia Plantarum*, 176(2), p. e14270.
Kumari, S. et al. (2023) 'Plant hormones and secondary metabolites under environmental stresses: Shedding light on defense molecules', *Plant Physiology and Biochemistry*, p. 108238.
Kusajima, M. et al. (2022) 'Strigolactones modulate salicylic acid-mediated disease resistance in Arabidopsis thaliana', *International journal of molecular sciences*, 23(9), p. 5246.
Lahari, Z. et al. (2024) 'Strigolactone deficiency induces jasmonate, sugar and flavonoid phytoalexin accumulation enhancing rice defense against the blast fungus Pyricularia oryzae', *New Phytologist*, 241(2), pp. 827–844.
Leannec-Rialland, V. et al. (2022) 'Use of defensins to develop eco-friendly alternatives to synthetic fungicides to control phytopathogenic fungi and their mycotoxins', *Journal of Fungi*, 8(3), p. 229.
Lee, J. C. (2010) 'Effect of methyl salicylate-based lures on beneficial and pest arthropods in strawberry', *Environmental Entomology*, 39(2), pp. 653–660.
Lee, J. G. et al. (2013) 'Evaluation of glucosinolate variation in a collection of turnip (Brassica rapa) germplasm by the analysis of intact and desulfo glucosinolates', *Journal of agricultural and food chemistry*, 61(16), pp. 3984–3993.
Letham, D. S. (1969) 'Cytokinins and their relation to other phytohormones', *Bioscience*, 19(4), pp. 309–316.
Li, L. et al. (2005) 'Brassinosteroids stimulate plant tropisms through modulation of polar auxin transport in Brassica and Arabidopsis', *The Plant Cell*, 17(10), pp. 2738–2753.
Li, S.-J. et al. (2013) 'Root and shoot jasmonic acid induced plants differently affect the performance of Bemisia tabaci and its parasitoid Encarsia formosa', *Basic and Applied Ecology*, 14(8), pp. 670–679. doi: https://doi.org/10.1016/j.baae.2013.08.011.
Lin, Z., Zhong, S. and Grierson, D. (2009) 'Recent advances in ethylene research', *Journal of experimental botany*, 60(12), pp. 3311–3336.
Liu, J. and Wang, X. (2006) 'An integrative analysis of the effects of auxin on jasmonic acid biosynthesis in Arabidopsis thaliana', *Journal of Integrative Plant Biology*, 48(1), pp. 99–103.
Liu, S. et al. (2023) 'Metabolic pathways engineering for drought or/and heat tolerance in cereals', *Frontiers in Plant Science*, 14, p. 1111875.
Liu, Y. et al. (2005) 'Arabidopsis vegetative storage protein is an anti-insect acid phosphatase', *Plant Physiology*, 139(3), pp. 1545–1556.
Loake, G. and Grant, M. (2007) 'Salicylic acid in plant defence—the players and protagonists', *Current opinion in plant biology*, 10(5), pp. 466–472.
Lomate, P. R. and Hivrale, V. K. (2012) 'Wound and methyl jasmonate induced pigeon pea defensive proteinase inhibitor has potency to inhibit insect digestive proteinases', *Plant Physiology and Biochemistry*, 57, pp. 193–199.
Louis, J. et al. (2015) 'Ethylene contributes to maize insect resistance1-mediated maize defense against the phloem sap-sucking corn leaf aphid', *Plant Physiology*, 169(1), pp. 313–324.
Lu, P. et al. (2019) 'Overexpression of cotton a DTX/MATE gene enhances drought, salt, and cold stress tolerance in transgenic Arabidopsis', *Frontiers in plant science*, 10, p. 396232.
Lu, X. et al. (2020) 'Efficacy of binary combinations between methyl salicylate and carvacrol against thrips Anaphothrips obscurus: laboratory and field trials', *Pest management science*, 76(2), pp. 589–596.
Lymperopoulos, P., Msanne, J. and Rabara, R. (2018) 'Phytochrome and phytohormones: working in tandem for plant growth and development', *Frontiers in Plant Science*, 9, p. 1037.
Machado, R. A. R. et al. (2016) 'Auxin is rapidly induced by herbivore attack and regulates a subset of systemic, jasmonate-dependent defenses', *Plant Physiology*, 172(1), pp. 521–532.
Madaan, I. et al. (2022) 'Implications of Phytohormones as Agrochemicals in Dynamic Environmental Conditions', in *Agrochemicals in Soil and Environment: Impacts and Remediation*. Springer, pp. 535–563.
Mainali, R. P. and Nyaupane, S. (2023) 'Auxin in Plant Defense Reactions: New Insights and Potential Applications for Resistance Breeding Programmes', *Journal of the Institute of Agriculture and Animal Science*, pp. 102–112.
Malamy, J. et al. (1990) 'Salicylic acid : A likely endogenous signal in the resistance response of tobacco to viral infection', *Science*, 250(22), pp. 6–9.
Mamta, B. and Rajam, M. V (2018) 'RNA interference: a promising approach for crop improvement', *Biotechnologies of Crop Improvement, Volume 2: Transgenic Approaches*, pp. 41–65.
Mandal, S. et al. (2022) 'Cytokinins: A genetic target for increasing yield potential in the CRISPR era', *Frontiers in Genetics*, 13, p. 883930.
Manghwar, H. et al. (2022) 'Brassinosteroids (BRs) role in plant development and coping with different stresses', *International journal of molecular sciences*, 23(3), p. 1012.
Martin, D. M., Gershenzon, J. and Bohlmann, J. (2003) 'Induction of volatile terpene biosynthesis and diurnal emission by methyl jasmonate in foliage of norway spruce', *Plant Physiology*, 132, pp. 1586–1599. doi: https://doi.org/10.1104/pp.103.021196.some.
Martínez-de la Cruz, E. et al. (2015) 'Auxins differentially regulate root system architecture and cell cycle protein levels in maize seedlings', *Journal of plant physiology*, 176, pp. 147–156.
Matthes, M. C. et al. (2010) 'The transcriptome of cis-jasmone-induced resistance in Arabidopsis thaliana and its role in indirect defence', *Planta*, 232(5), pp. 1163–1180.
Mearaji, H. S. et al. (2021) 'Phytohormones and abiotic stresses: Roles of phytohormones in plants under abiotic stresses', in *Handbook of plant and crop physiology*. CRC Press, pp. 175–213.
Meldau, S., Baldwin, I. T. and Wu, J. (2011) 'SGT1 regulates wounding-and herbivory-induced jasmonic acid accumulation and Nicotiana attenuata's resistance to the specialist lepidopteran herbivore Manduca sexta', *New Phytologist*, 189(4), pp. 1143–1156.
Mithöfer, A. and Boland, W. (2012) 'Plant defense against herbivores: Chemical aspects', *Annual Review of Plant Biology*, 63, pp. 431–450. doi: https://doi.org/10.1146/annurev-arplant-042110-103854.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Mohamed, H. I., El-Shazly, H. H. and Badr, A. (2020) 'Role of salicylic acid in biotic and abiotic stress tolerance in plants', *Plant Phenolics in Sustainable Agriculture*: *Volume* 1, pp. 533–554.
Moubayidin, L., Di Mambro, R. and Sabatini, S. (2009) 'Cytokinin–auxin crosstalk', *Trends in plant science*, 14(10), pp. 557–562.
Mouden, S. et al. (2017) 'Integrated pest management in western flower thrips: past, present and future', *Pest management science*, 73(5), pp. 813–822.
Mouden, S. et al. (2020) 'Water dipping of auxin coated chrysanthemum cuttings confers protection against insect herbivores', *Insects*, 11(11), p. 790.
Muhammad Aslam, M. et al. (2022) 'Mechanisms of abscisic acid-mediated drought stress responses in plants', *International journal of molecular sciences*, 23(3), p. 1084.
Muhammad, T. et al. (2019) 'RNA interference: a natural immune system of plants to counteract biotic stressors', *Cells*, 8(1), p. 38.
Mukarram, M. et al. (2021) 'Drought: Sensing, signalling, effects and tolerance in higher plants', *Physiologia plantarum*, 172(2), pp. 1291–1300.
Mukherjee, A. et al. (2022) 'The bioactive potential of phytohormones: a review', *Biotechnology Reports*, 35, p. e00748.
Nadeem, S. M. et al. (2016) 'Role of phytohormones in stress tolerance of plants', *Plant, soil and microbes*: *volume 2: mechanisms and molecular interactions*, pp. 385–421.
Nakashita, H. et al. (2003) 'Brassinosteroid functions in a broad range of disease resistance in tobacco and rice', *Plant Journal*, 33(5), pp. 887–898. doi: https://doi.org/10.1046/j.1365-313X.2003.01675.x.
Nambara, E. and Marion-Poll, A. (2005) 'Abscisic acid biosynthesis and catabolism', *Annu. Rev. Plant Biol.*, 56, pp. 165–185.
Napoli, C., Lemieux, C. and Jorgensen, R. (1990) 'Introduction of a chimeric chalcone synthase gene into petunia results in reversible co-suppression of homologous genes in trans.', *The plant cell*, 2(4), pp. 279–289.
Nasir, F. et al. (2019) 'Strigolactones positively regulate defense against Magnaporthe oryzae in rice (Oryza sativa)', *Plant physiology and biochemistry*, 142, pp. 106–116.
Naveed, Z. A. et al. (2020) 'The PTI to ETI continuum in Phytophthora-plant interactions', *Frontiers in plant science*, 11, p. 593905.
Nazim, M. et al. (2021) 'Kaolin and Jasmonic acid improved cotton productivity under water stress conditions', *Saudi Journal of Biological Sciences*, 28(11), pp. 6606–6614.
Nazir, F. et al. (2024) 'Plant hormone ethylene: A leading edge in conferring drought stress tolerance', *Physiologia Plantarum*, 176(1), p. e14151.
Nguyen, D. et al. (2016) 'How plants handle multiple stresses: hormonal interactions underlying responses to abiotic stress and insect herbivory', *Plant Molecular Biology*, 91, pp. 727–740.
Nolan, T. M. et al. (2020) 'Brassinosteroids: multidimensional regulators of plant growth, development, and stress responses', *The Plant Cell*, 32(2), pp. 295–318.
Nowicka, B. (2022) 'Modifications of Phytohormone Metabolism Aimed at Stimulation of Plant Growth, Improving Their Productivity and Tolerance to Abiotic and Biotic Stress Factors', *Plants*, 11(24), p. 3430.
Odintsova, T. I. et al. (2019) 'Defensin-like peptides in wheat analyzed by whole-transcriptome sequencing: A focus on structural diversity and role in induced resistance', *PeerJ*, 7, p. e6125.
Park, H. W. et al. (2013) 'Infectivity of entomopathogenic nematode Steinernema carpocapsae Pocheon strain (Nematoda: Steinernematidae) on the green peach aphid Myzus persicae (Hemiptera: Aphididae) and its parasitoids', *Biocontrol Science and Technology*, 23(6), pp. 637–645.
Park, S.-W. et al. (2007) 'Methyl salicylate is a critical mobile signal for plant systemic acquired resistance', *Science*, 318(5847), pp. 113–116.
Pasin, F. et al. (2020) 'Abscisic acid connects phytohormone signaling with RNA metabolic pathways and promotes an antiviral response that is evaded by a self-controlled RNA virus', *Plant communications*, 1(5).
Peer, W. A. et al. (2011) 'Seven things we think we know about auxin transport', *Molecular plant*, 4(3), pp. 487–504.
Peña-Cortés, H., Fisahn, J. and Willmitzer, L. (1995) 'Signals involved in wound-induced proteinase inhibitor II gene expression in tomato and potato plants.', *Proceedings of the National Academy of Sciences*, 92(10), pp. 4106–4113.
Perez-Alonso, M. M. and Pollmann, S. (2018) 'How Auxin May Contribute to the Regulation of Plant Defense Responses against Herbivory. Austin J', *Plant Biol*, 4(1), pp. 2–5.
Pérez, A. C. and Goossens, A. (2013) 'Jasmonate signalling: a copycat of auxin signalling?', *Plant, cell & environment*, 36(12), pp. 2071–2084.
Perilli, S., Moubayidin, L. and Sabatini, S. (2010) 'The molecular basis of cytokinin function', *Current opinion in plant biology*, 13(1), pp. 21–26.
Perrot-Rechenmann, C. (2010) 'Cellular responses to auxin: division versus expansion', *Cold Spring Harbor perspectives in biology*, 2(5), p. a001446.
Pickett, J. A. et al. (2007) 'Developments in aspects of ecological phytochemistry: the role of cis-jasmone in inducible defence systems in plants', *Phytochemistry*, 68(22–24), pp. 2937–45. doi: https://doi.org/10.1016/j.phytochem.2007.09.025.
Pierre, S. P. et al. (2013) 'Belowground induction by Delia radicum or phytohormones affect aboveground herbivore communities on field-grown broccoli', *Frontiers in Plant Science*, 4(AUG), p. 305. doi: https://doi.org/10.3389/fpls.2013.00305.
Pieterse, C. M. J. et al. (2009) 'Networking by small-molecule hormones in plant immunity', *Nature Chemical Biology*, 5(5), pp. 308–316. doi: https://doi.org/10.1038/nchembio.164.
Poór, P. et al. (2022) 'Ethylene involvement in the regulation of heat stress tolerance in plants', *Plant cell reports*, 41(3), pp. 675–698.
Pozo, M. J. et al. (2015) 'Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses', *New Phytologist*, 205(4), pp. 1431–1436.
Qi, L. et al. (2012) 'Arabidopsis thaliana plants differentially modulate auxin biosynthesis and transport during defense responses to the necrotrophic pathogen Alternaria brassicicola', *New Phytologist*, 195(4), pp. 872–882.
Qi, T. et al. (2014) 'Arabidopsis DELLA and JAZ proteins bind the WD-repeat/bHLH/MYB complex to modulate gibberellin and jasmonate signaling synergy', *The Plant Cell*, 26(3), pp. 1118–1133.
Rahman, S. U. et al. (2023) 'Role of phytohormones in heavy metal tolerance in plants: A review', *Ecological Indicators*, 146, p. 109844.
Rajput, M. et al. (2021) 'RNA interference and CRISPR/Cas gene editing for crop improvement: Paradigm shift towards sustainable agriculture', *Plants*, 10(9), p. 1914.
Raskin, I. (1992) 'Role of salicylic acid in plants', *Annual review of plant biology*, 43(1), pp. 439–463.
Raza, A. et al. (2023) 'Role of phytohormones in regulating cold stress tolerance: physiological and molecular approaches for developing cold-smart crop plants', *Plant Stress*, p. 100152.
Razo-Belman, R. and Ozuna, C. (2023) 'Volatile organic compounds: A review of their current applications as pest biocontrol and disease management', *Horticulturae*, 9(4), p. 441.
Regmi, P., Leskey, T. C. and Piñero, J. C. (2023) 'Methyl salicylate improves the effectiveness of the odor-baited trap tree approach for adult plum curculio, Conotrachelus nenuphar (Coleoptera: Curculionidae), monitoring and attract-and-kill', *Journal of Economic Entomology*, p. toad110.
Rehman, M. et al. (2023) 'The multifaceted role of jasmonic acid in plant stress mitigation: An overview', *Plants*, 12(23), p. 3982.
Rhaman, M. S. et al. (2020) 'Seed priming with phytohormones: An effective approach for the mitigation of abiotic stress', *Plants*, 10(1), p. 37.
Rivas-San Vicente, M. and Plasencia, J. (2011) 'Salicylic acid beyond defence: its role in plant growth and development', *Journal of experimental botany*, 62(10), pp. 3321–3338.
Rizza, A. et al. (2017) 'In vivo gibberellin gradients visualized in rapidly elongating tissues', *Nature Plants*, 3(10), pp. 803–813.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Rodriguez-Saona, C. et al. (2001) 'Exogenous methyl jasmonate induces volatile emissions in cotton plants', *Journal of Chemical Ecology*, 27(4), pp. 679–695.

Rodriguez-Saona, C., Blaauw, B. R. and Isaacs, R. (2012) 'Manipulation of natural enemies in agroecosystems: habitat and semiochemicals for sustainable insect pest control', *Integrated pest management and pest control–current and future tactics*, pp. 89–126.

Ruan, J. et al. (2019) 'Jasmonic acid signaling pathway in plants', *International Journal of Molecular Sciences*, 20(10), p. 2479. doi: https://doi.org/10.3390/ijms20102479.

Ryan, C. A. (2000) 'The systemin signaling pathway: differential activation of plant defensive genes', *Biochimica et Biophysica Acta (BBA)-Protein Structure and Molecular Enzymology*, 1477(1–2), pp. 112–121.

Ryan, C. A. and Pearce, G. (2003) 'Systemins: a functionally defined family of peptide signals that regulate defensive genes in Solanaceae species', *Proceedings of the National Academy of Sciences*, 100(suppl_2), pp. 14577–14580.

EL Sabagh, A. et al. (2022) 'Phytohormones as growth regulators during abiotic stress tolerance in plants', *Frontiers in Agronomy*, 4, p. 765068.

Sampedro-Guerrero, J. et al. (2022) 'Encapsulation reduces the deleterious effects of salicylic acid treatments on root growth and gravitropic response', *International Journal of Molecular Sciences*, 23(22), p. 14019.

Sampedro-Guerrero, J. et al. (2023) 'Efficient strategies for controlled release of nanoencapsulated phytohormones to improve plant stress tolerance', *Plant Methods*, 19(1), p. 47.

Santner, A. and Estelle, M. (2009) 'Recent advances and emerging trends in plant hormone signalling', *Nature*, 459(7250), pp. 1071–1078. doi: https://doi.org/10.1038/nature08122.

Saurabh, S., Vidyarthi, A. S. and Prasad, D. (2014) 'RNA interference: concept to reality in crop improvement', *Planta*, 239, pp. 543–564.

Schäfer, M. et al. (2015) 'Cytokinin levels and signaling respond to wounding and the perception of herbivore elicitors in Nicotiana attenuata', *Journal of integrative plant biology*, 57(2), pp. 198–212.

Schweiger, R. et al. (2014) 'Interactions between the jasmonic and salicylic acid pathway modulate the plant metabolome and affect herbivores of different feeding types', *Plant, cell & environment*, 37(7), pp. 1574–1585. doi: https://doi.org/10.1111/pce.12257.

Schweizer, F. et al. (2013) 'Arabidopsis basic helix-loop-helix transcription factors MYC2, MYC3, and MYC4 regulate glucosinolate biosynthesis, insect performance, and feeding behavior', *The Plant Cell*, 25(8), pp. 3117–3132.

Senaratna, T. et al. (2000) 'Acetyl salicylic acid (Aspirin) and salicylic acid induce multiple stress tolerance in bean and tomato plants', *Plant Growth Regulation*, 30(2), pp. 157–161.

Seng, S. et al. (2023) 'Abscisic Acid: A Potential Secreted Effector Synthesized by Phytophagous Insects for Host-Plant Manipulation', *Insects*, 14(6), p. 489.

Seo, H. S. et al. (2001) 'Jasmonic acid carboxyl methyltransferase: A key enzyme for jasmonate-regulated plant responses', *Proceedings of the National Academy of Sciences of the United States of America*, 98(8), pp. 4788–4793. doi: https://doi.org/10.1073/pnas.081557298.

Sharma, R. R. and Singh, R. (2009) 'Gibberellic acid influences the production of malformed and button berries, and fruit yield and quality in strawberry (Fragaria× ananassa Duch.)', *Scientia Horticulturae*, 119(4), pp. 430–433.

Sheteiwy, M. S. et al. (2021) 'Seed priming and foliar application with jasmonic acid enhance salinity stress tolerance of soybean (Glycine max L.) seedlings', *Journal of the Science of Food and Agriculture*, 101(5), pp. 2027–2041.

Shigenaga, A. M. et al. (2017) 'Towards engineering of hormonal crosstalk in plant immunity', *Current opinion in plant biology*, 38, pp. 164–172.

Shokat, S. et al. (2021b) 'Elevated CO2 modulates the effect of heat stress responses in Triticum aestivum by differential expression of an isoflavone reductase-like gene', *Journal of Experimental Botany*, 72(21), pp. 7594–7609.

Shokat, S. et al. (2023) 'The role of genetic diversity and pre-breeding traits to improve drought and heat tolerance of bread wheat at the reproductive stage', *Food and Energy Security*, 12(6), p. e478.

Shokat, S., Großkinsky, D. K. and Liu, F. (2021a) 'Impact of elevated CO2 on two contrasting wheat genotypes exposed to intermediate drought stress at anthesis', *Journal of Agronomy and Crop Science*, 207(1), pp. 20–33.

Singh, A. K. et al. (2018) 'RNAi approach: A powerful technique for gene function studies and enhancing abiotic stress tolerance in crop plants', *Biotechnologies of Crop Improvement, Volume 2: Transgenic Approaches*, pp. 113–127.

Skalák, J. et al. (2019) 'Multifaceted activity of cytokinin in leaf development shapes its size and structure in Arabidopsis', *The Plant Journal*, 97(5), pp. 805–824.

Smigocki, A. C. (1995) 'Phenotype modification and enhanced tolerance to insect pests by regulated expression of a cytokinin biosynthesis gene', *HortScience*, 30(5), pp. 967–969.

Smith, S. M. (2014) 'Q&A: What are strigolactones and why are they important to plants and soil microbes?', *BMC biology*, 12, pp. 1–7.

Sobhy, I. S. et al. (2017) 'cis-Jasmone elicits aphid-induced stress signalling in Potatoes', *Journal of Chemical Ecology*, 43(1), pp. 39–42. doi: https://doi.org/10.1007/s10886-016-0805-9.

Sobhy, I. S., Lou, Y. and Bruce, T. J. A. (2022) *Inducing Plant Resistance Against Insects Using Exogenous Bioactive Chemicals: Key Advances and Future Perspectives*. Frontiers Media SA.

Song, G. et al. (2016) 'CRISPR/Cas9: a powerful tool for crop genome editing', *The crop journal*, 4(2), pp. 75–82.

Song, S. et al. (2022) 'A molecular framework for signaling crosstalk between jasmonate and ethylene in anthocyanin biosynthesis, trichome development, and defenses against insect herbivores in Arabidopsis', *Journal of Integrative Plant Biology*, 64(9), pp. 1770–1788.

Stotz, H. U., Thomson, J. and Wang, Y. (2009) 'Plant defensins: defense, development and application', *Plant signaling & behavior*, 4(11), pp. 1010–1012.

Sun, J. et al. (2009) 'Arabidopsis ASA1 is important for jasmonate-mediated regulation of auxin biosynthesis and transport during lateral root formation', *The Plant Cell*, 21(5), pp. 1495–1511.

Sun, J. et al. (2011) 'Jasmonate modulates endocytosis and plasma membrane accumulation of the Arabidopsis PIN2 protein', *New Phytologist*, 191(2), pp. 360–375.

Sun, T. (2004) 'Gibberellin signal transduction in stem elongation & leaf growth', in *Plant hormones: biosynthesis, signal transduction, action*! Springer, pp. 308–328.

Swain, R. et al. (2023) 'Instigating prevalent abiotic stress resilience in crop by exogenous application of phytohormones and nutrient', *Frontiers in Plant Science*, 14, p. 1104874.

Tanaka, K. et al. (2009) 'Highly selective tuning of a silkworm olfactory receptor to a key mulberry leaf volatile', *Current Biology*, 19(11), pp. 881–90. doi: https://doi.org/10.1016/j.cub.2009.04.035.

Tanimoto, E. (2005) 'Regulation of root growth by plant hormones—roles for auxin and gibberellin', *Critical reviews in plant sciences*, 24(4), pp. 249–265.

Thaler, J. S. et al. (2001) 'Jasmonate-mediated induced plant resistance affects a community of herbivores', *Ecological Entomology*, 26(3), pp. 312–324.

Thaler, J. S. et al. (2002) 'Jasmonate-deficient plants have reduced direct and indirect defences against herbivores', *Ecology Letters*, 5, pp. 764–774.

Thaler, J. S. and Bostock, R. M. (2004) 'Interactions between abscisic-acid-mediated responses and plant resistance to pathogens and insects', *Ecology*, 85(1), pp. 48–58.

Tian, D. et al. (2014) 'Roles of ethylene and jasmonic acid in systemic induced defense in tomato (Solanum lycopersicum) against Helicoverpa zea', *Planta*, 239, pp. 577–589.

Tiku, A. R. (2018) 'Antimicrobial compounds and their role in plant defense', *Molecular aspects of plant-pathogen interaction*, pp. 283–307.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Tonğa, A. et al. (2020) 'cis-Jasmone treatments affect multiple sucking insect pests and associated predators in cotton', *Entomologia Generalis*, pp. 49–61.

Tonğa, A. et al. (2022) 'Cotton treatment with methyl jasmonate at different growth stages reduces the population of sucking insect pests and marginally increases their associated predators', *Entomologia Experimentalis et Applicata*, 170(3), pp. 207–221.

Torres-Vera, R. et al. (2014) 'Do strigolactones contribute to plant defence?', *Molecular Plant Pathology*, 15(2), pp. 211–216.

Torrey, J. G. (1985) 'The Development of Plant Biotechnology: Building on early discoveries about plant nutrition, researchers have produced an array of techniques for exploiting the genetic potential of plants', *American Scientist*, 73(4), pp. 354–363.

Tripathi, D., Raikhy, G. and Kumar, D. (2019) 'Chemical elicitors of systemic acquired resistance—Salicylic acid and its functional analogs', *Current Plant Biology*, 17, pp. 48–59.

Tuteja, N. and Sopory, S. K. (2008) 'Chemical signaling under abiotic stress environment in plants', *Plant signaling & behavior*, 3(8), pp. 525–536.

Uefune, M., Ozawa, R. and Takabayashi, J. (2014) 'Prohydrojasmon treatment of lima bean plants reduces the performance of two-spotted spider mites and induces volatiles', *Journal of Plant Interactions*, 9(1), pp. 69–73.

Vaishnav, D. and Chowdhury, P. (2023) 'Types and Function of Phytohormone and Their Role in Stress'.

Vardhini, B. V. et al. (2010) 'Role of brassinosteroids in alleviating various abiotic and biotic stresses-a review', *Plant Stress*, 4(1), pp. 55–61.

Vázquez-González, C. et al. (2022) 'Inducibility of chemical defences by exogenous application of methyl jasmonate is long-lasting and conserved among populations in mature Pinus pinaster trees', *Forest Ecology and Management*, 518, p. 120280.

Verma, V., Ravindran, P. and Kumar, P. P. (2016) 'Plant hormone-mediated regulation of stress responses', *BMC plant biology*, 16, pp. 1–10.

Vijayan, P. et al. (1998) 'A role for jasmonate in pathogen defense of Arabidopsis', *Proceedings of the National Academy of Sciences*, 95(12), pp. 7209–7214.

Vincent, D., Rafiqi, M. and Job, D. (2020) 'The multiple facets of plant–fungal interactions revealed through plant and fungal secretomics', *Frontiers in Plant Science*, 10, p. 1626.

Vos, I. A. et al. (2013) 'Onset of herbivore-induced resistance in systemic tissue primed for jasmonate-dependent defenses is activated by abscisic acid', *Frontiers in Plant Science*, 4, p. 539.

Vos, I. A. et al. (2019) 'Abscisic acid is essential for rewiring of jasmonic acid-dependent defenses during herbivory', *BioRxiv*, p. 747345.

Waadt, R. et al. (2022) 'Plant hormone regulation of abiotic stress responses', *Nature Reviews Molecular Cell Biology*, 23(10), pp. 680–694.

Wang, D. et al. (2007) 'Salicylic acid inhibits pathogen growth in plants through repression of the auxin signaling pathway', *Current Biology*, 17(20), pp. 1784–1790.

Wang, D., Amornsiripanitch, N. and Dong, X. (2006) 'A genomic approach to identify regulatory nodes in the transcriptional network of systemic acquired resistance in plants', *PLoS pathogens*, 2(11), p. e123.

Wang, L. et al. (2011) 'Auxin Response Factor2 (ARF2) and its regulated homeodomain gene HB33 mediate abscisic acid response in Arabidopsis', *PLoS genetics*, 7(7), p. e1002172.

Wang, S. and Wang, Y. (2022) 'Harnessing hormone gibberellin knowledge for plant height regulation', *Plant Cell Reports*, 41(10), pp. 1945–1953.

Wang, Z. et al. (2012) 'Defense to Sclerotinia sclerotiorum in oilseed rape is associated with the sequential activations of salicylic acid signaling and jasmonic acid signaling', *Plant Science*, 184, pp. 75–82.

Wani, S. H. et al. (2016) 'Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants', *The crop journal*, 4(3), pp. 162–176.

War, A. R. et al. (2012) 'Mechanisms of plant defense against insect herbivores', *Plant Signaling and Behavior*, 7(10). doi: https://doi.org/10.4161/psb.21663.

Wasternack, C. (2007) 'Jasmonates: an update on biosynthesis, signal transduction and action in plant stress response, growth and development', *Annals of Botany*, 100, pp. 681–697. doi: https://doi.org/10.1093/aob/mcm079.

Wasternack, C. (2014) 'Action of jasmonates in plant stress responses and development - Applied aspects', *Biotechnology Advances*, 32(1), pp. 31–39. doi: https://doi.org/10.1016/j.biotechadv.2013.09.009.

Wei, X. et al. (2021) 'Application of methyl jasmonate and salicylic acid lead to contrasting effects on the plant's metabolome and herbivory', *Plant Science*, 303, p. 110784.

Weyers, J. D. B. and Paterson, N. W. (2001) 'Plant hormones and the control of physiological processes', *New Phytologist*, 152(3), pp. 375–407.

White, R. F. (1979) 'Acetylsalicylic acid (aspirin) induces resistance to tobacco mosaic virus in tobacco', *Virology*, 99(2), pp. 410–412. doi: https://doi.org/10.1016/0042-6822(79)90019-9.

Wild, M. et al. (2012) 'The Arabidopsis DELLA RGA-LIKE3 is a direct target of MYC2 and modulates jasmonate signaling responses', *The Plant Cell*, 24(8), pp. 3307–3319.

Wyckhuys, K. A. G., Tang, F. H. M. and Hadi, B. A. R. (2023) 'Pest management science often disregards farming system complexities', *Communications Earth & Environment*, 4(1), p. 223.

Xia, X.-J. et al. (2009) 'Reactive oxygen species are involved in brassinosteroid-induced stress tolerance in cucumber', *Plant physiology*, 150(2), pp. 801–814.

Xiao, F. et al. (2024) 'Physiological responses to drought stress of three pine species and comparative transcriptome analysis of Pinus yunnanensis var. pygmaea', *BMC genomics*, 25(1), p. 281.

Xie, X., Yoneyama, Kaori and Yoneyama, Koichi (2010) 'The strigolactone story', *Annual review of phytopathology*, 48, pp. 93–117.

Xu, H. et al. (2022) 'CRISPR/Cas9-mediated mutation in auxin efflux carrier OsPIN9 confers chilling tolerance by modulating reactive oxygen species homeostasis in rice', *Frontiers in Plant Science*, 13, p. 967031.

Xu, X. et al. (2019) 'Strigolactones positively regulate defense against root-knot nematodes in tomato', *Journal of Experimental Botany*, 70(4), pp. 1325–1337.

Yadav, B. et al. (2021) 'An overview of recent advancement in phytohormones-mediated stress management and drought tolerance in crop plants', *Plant Gene*, 25, p. 100264.

Yamaguchi, S. and Kamiya, Y. (2000) 'Gibberellin biosynthesis: its regulation by endogenous and environmental signals', *Plant and cell physiology*, 41(3), pp. 251–257.

Yamaguchi, Y., Pearce, G. and Huffaker, A. (2013) 'Defense signal peptides', *Handbook of Biologically Active Peptides*, pp. 5–14.

Yang, D.-L. et al. (2012) 'Plant hormone jasmonate prioritizes defense over growth by interfering with gibberellin signaling cascade', *Proceedings of the National Academy of Sciences*, 109(19), pp. E1192–E1200.

Yang, J. et al. (2019) 'The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses', *Frontiers in plant science*, 10, p. 1349.

Yang, J. H. et al. (2008) 'Phytohormone abscisic acid control RNA-dependent RNA polymerase 6 gene expression and post-transcriptional gene silencing in rice cells', *Nucleic Acids Research*, 36(4), pp. 1220–1226.

Yang, Y.-X. et al. (2015) 'Crosstalk among jasmonate, salicylate and ethylene signaling pathways in plant disease and immune responses', *Current Protein and Peptide Science*, 16(5), pp. 450–461.

Yang, Z. et al. (2020) 'Jasmonate signaling enhances RNA silencing and antiviral defense in rice', *Cell Host & Microbe*, 28(1), pp. 89–103.

Yang, Z. et al. (2023) 'Aphid-repellent, ladybug-attraction activities, and binding mechanism of methyl salicylate derivatives containing geraniol moiety', *Pest Management Science*, 79(2), pp. 760–770.

Yu, M.-H., Zhao, Z.-Z. and He, J.-X. (2018) 'Brassinosteroid signaling in plant–microbe interactions', *International Journal of Molecular Sciences*, 19(12), p. 4091.

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

de Zélicourt, A. et al. (2007) 'Ha-DEF1, a sunflower defensin, induces cell death in Orobanche parasitic plants', *Planta*, 226, pp. 591–600.
Zhang, D. et al. (2021) 'CRISPR/Cas: A powerful tool for gene function study and crop improvement', *Journal of Advanced Research*, 29, pp. 207–221.
Zhang, L. et al. (2018) 'Exogenous brassinosteroid enhances plant defense against Colletotrichum gloeosporioides by activating phenylpropanoid pathway in Camellia sinensis L.', *Journal of plant growth regulation*, 37, pp. 1235–1243.
Zhang, S. et al. (2007) 'Seed priming with brassinolide improves lucerne (Medicago sativa L.) seed germination and seedling growth in relation to physiological changes under salinity stress', *Australian Journal of Agricultural Research*, 58(8), pp. 811–815.
Zhang, X. et al. (2022) 'Cytokinin confers brown planthopper resistance by elevating jasmonic acid pathway in rice', *International Journal of Molecular Sciences*, 23(11), p. 5946.
Zhang, Y. et al. (2022) 'Molecular mechanisms of diverse auxin responses during plant growth and development', *International Journal of Molecular Sciences*, 23(20), p. 12495.
Zhang, Z. et al. (2007) 'Dual regulation role of GH3. 5 in salicylic acid and auxin signaling during Arabidopsis-Pseudomonas syringae interaction', *Plant physiology*, 145(2), pp. 450–464.
Zhang, Z. et al. (2020) 'A WOX/auxin biosynthesis module controls growth to shape leaf form', *Current biology*, 30(24), pp. 4857–4868.
Zhao, B. et al. (2021) 'Roles of phytohormones and their signaling pathways in leaf development and stress responses', *Journal of Agricultural and Food Chemistry*, 69(12), pp. 3566–3584.
Zhao, Y. et al. (2002) 'Trp-dependent auxin biosynthesis in Arabidopsis: involvement of cytochrome P450s CYP79B2 and CYP79B3', *Genes & development*, 16(23), pp. 3100–3112.
Zheng, Y. et al. (2023) 'Phytohormones regulate the abiotic stress: An overview of physiological, biochemical, and molecular responses in horticultural crops', *Frontiers in Plant Science*, 13, p. 1095363.
Zhu, C. et al. (2019) 'Transcriptome and phytochemical analyses provide new insights into long non-coding RNAs modulating characteristic secondary metabolites of oolong tea (Camellia sinensis) in solar-withering', *Frontiers in plant science*, 10, p. 1638.
Zhu, F. et al. (2014) 'Salicylic acid and jasmonic acid are essential for systemic resistance against tobacco mosaic virus in Nicotiana benthamiana', *Molecular plant-microbe interactions*, 27(6), pp. 567–577.
Zipfel, C. (2009) 'Early molecular events in PAMP-triggered immunity', *Current Opinion in Plant Biology*, 12(4), pp. 414–420. doi: https://doi.org/10.1016/j.pbi.2009.06.003.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Ali, J., Mukarram, M., Ojo, J., Dawam, N., Riyazuddin, R., Ghramh, H.A. et al. (2024) Harnessing Phytohormones: Advancing Plant Growth and Defence Strategies for Sustainable Agriculture. *Physiologia Plantarum*, 176(3), e14307. Available from: https://doi.org/10.1111/ppl.14307

13993054, 2024, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ppl.14307 by JAMIN ALI - Keele University , Wiley Online Library on [05/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License