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REVIEW

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

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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.

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 defence 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 defences 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 defences 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 defence 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 defence 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 defence (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 defence 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 defence 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).

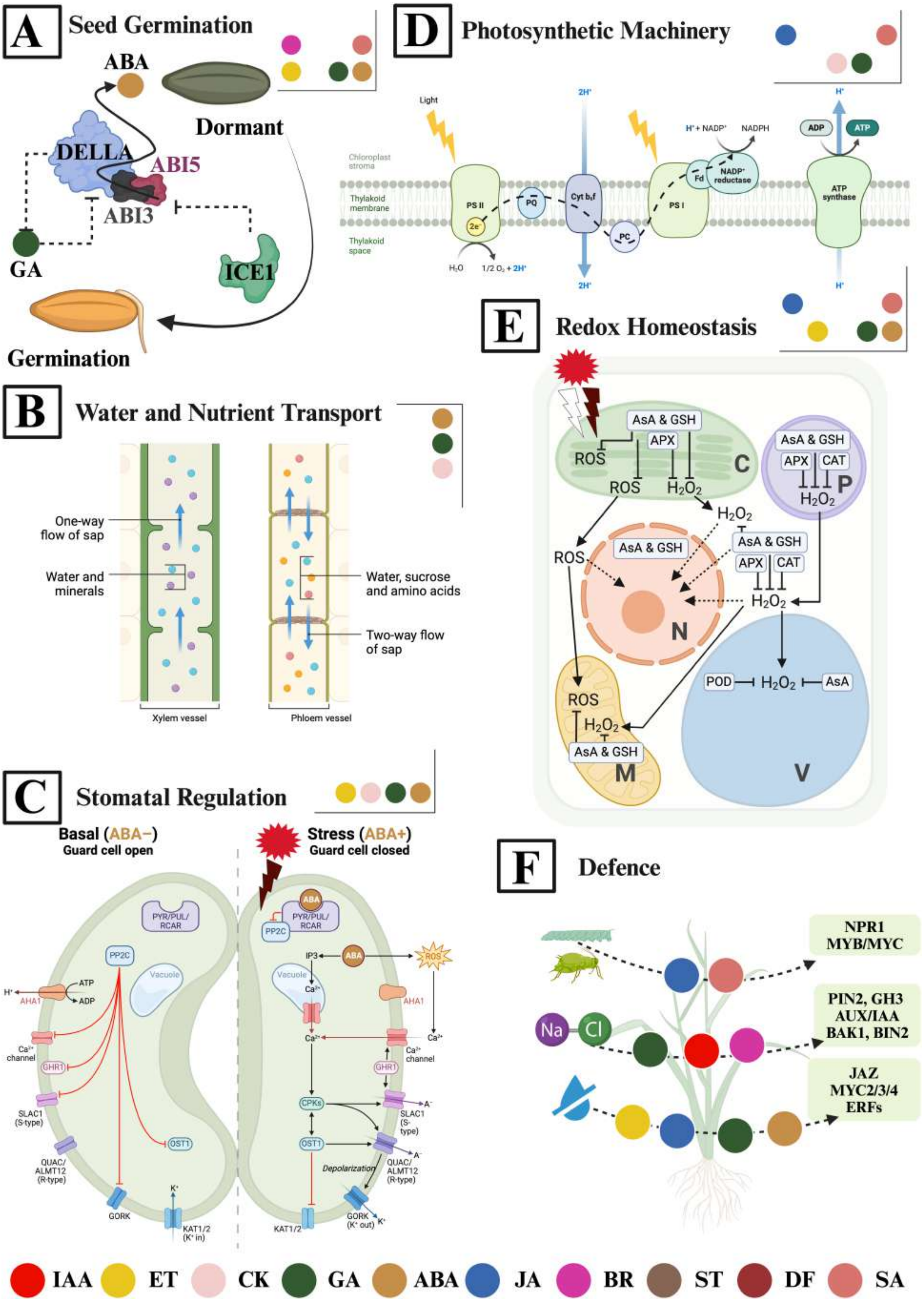

FIGURE 1 Legend on next page.

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 defence 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 defence 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 defence 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 defence (Anfang and Shani, 2021). In conclusion, phytohormone signaling pathways intricately regulate plant growth and defence, 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.

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)

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).

TABLE 2 Role of Phytohormones in Plant Defence.

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 defence 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)

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 defence 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 defence 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 defence related-gene expression and activated systemic acquired resistance against *Alternaria solani*	(Spletzer and Enyedi, 1999)
	Cicer arietinum	Induced plant defences 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 defence 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)

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 defence genes and resistance against *Erysiphe graminis*	(Stadnik and Buchenauer, 2000)
Brassinosteroids	*S. tuberosum* and *S. lycopersicum*	Enhanced plant defences 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 defence 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 defence 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)

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 defence 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 defence 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 defence against *M. sexta*	(Machado et al., 2016)
	O. sativa	2,4-D, an auxin analogue widely used in monocot crops, boosts rice defences 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 defence 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).

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 defence 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 defence 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 defence 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 defence 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 defence 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 defence-related hormones JA and SA	(Torres-Vera et al., 2014)
	O. sativa	Enhances rice defence against *Pyricularia oryzae* by inducing the accumulation of jasmonate, sugar, and flavonoid phytoalexins	(Lahari et al., 2024)
	S. lycopersicum	Regulate defence 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 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 defence 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 defence (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 defence responses against insect attacks (Birkett et al., 2000; Thaler et al., 2001; Uefune et al.,2014). Jasmonates activate defence-related genes and secondary metabolites, enhancing plant defence (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 defences 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 defence 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 defence signaling network (Jiang and Yan, 2018). MeJA activates defence 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).

Salicylic acid (SA), a key phytohormone, plays a central role in a plant's immune system, acting as a defence mechanism against biotrophic pathogens (Raskin, 1992; Ding and Ding, 2020). Synthesized through the phenylpropanoid pathway, SA rapidly increases in response to pathogen invasion, activating defence-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 defence 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 defence responses. MeSA, released by plants during pathogen attacks, acts as a mobile signal, inducing defence 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 defence 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 defences against both abiotic and biotic stress (Krishna, 2003; Vardhini et al., 2010). In the context of biotic stress, BRs orchestrate plant defence 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 defence-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 defence 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 defence 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 defence 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 defence-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 defence 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 defences (Von Dahl and Baldwin, 2007). Furthermore, it enhances jasmonic acid accumulation and regulates the expression of defence-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 defence against various biotic stresses (Adie et al., 2007). Moreover, ethylene modulates defence pathways by activating specific defences, 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 defence against insect herbivores (Louis et al., 2015). Recent studies also highlight ethylene's role in anthocyanin accumulation, trichome development, and defences 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 defence, 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 defence 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 defence 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 defence pathways (Dinh et al., 2013). ABA primes JA-regulated defence 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 defences (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 defence (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 defence 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 defence mechanisms. ABA initiates defence 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 defence 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 defence, 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 defence by stimulating ethylene production, which is crucial in defence responses (Perez-Alonso and Pollmann, 2018). Auxin also facilitates plant defence by interacting with microbial biocontrol agents. Microbial agents produce auxins like IAA, influencing plant physiology and triggering defence responses such as enhanced root growth and basal defence 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 defence strategies.

Cytokinins (CKs) (Table 2) play a crucial role in regulating plant defence 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 defence 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 defence against herbivory by reducing weight gain in insect larvae and altering the expression of defence-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 defence 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 defence 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 defence 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 defence and their potential applications in pest management strategies.

Strigolactones emerge as crucial players in bolstering plant defence against biotic stresses (Al-Babili and Bouwmeester, 2015; Francis et al., 2024). Research indicates that strigolactones actively participate in plant defence 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 defence 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 defence-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 induces the accumulation of phytoalexins, sugars, and flavonoids, thereby enhancing rice defence mechanisms against the blast fungus *Pyricularia oryzae* (Lahari et al., 2024). This multifaceted role of strigolactones in plant defence extends further, positively regulating defences 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 defence against various biotic stresses underscores their significance in ensuring plant health and survival in diverse environmental conditions (Table 2).

5 | PHYTOHORMONAL CROSSTALK: GROWTH AND DEFENCE

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

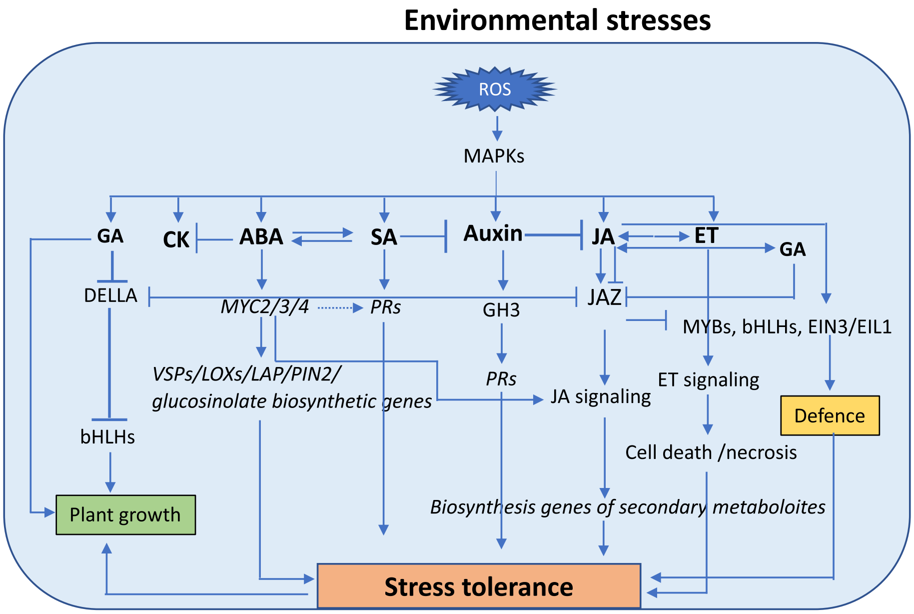

FIGURE 2 Phytohormonal crosstalk during environmental stress. When plants encounter environmental stress, reactive oxygen species (ROS) are produced, which activate phytohormonal crosstalk signalling pathways via mitogen-activated protein kinases (MAPKs). A dialogue between DELLA proteins and JASMONATE 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 defence 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 defence. 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.

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 defence mechanisms (Pozo et al., 2015). For example, auxin, usually associated with plant growth, also steps into the arena of plant defence 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 defence 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 defence 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 defence. 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* α*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 defence 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).

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 defence 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 defence, 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.

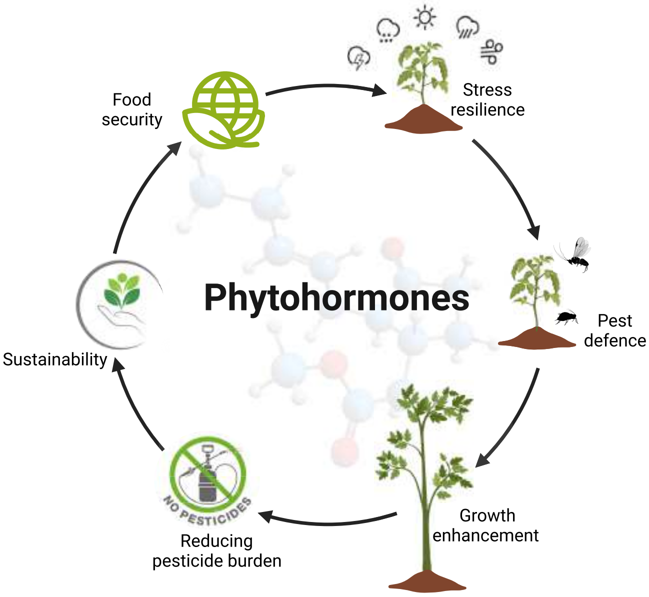

FIGURE 3 Potential utilization areas of phytohormones as a source in sustainable agriculture and food security. Done with Biorender.

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 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 defence 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 defence 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 defence, 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)

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.

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DATA AVAILABILITY STATEMENT

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