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TECHNICAL REVIEW — PLANT PHYSIOLOGY

Phytohormones in Crop Production

Mechanisms, Physiological Functions and Agricultural Applications

A review of the nine major plant hormone groups, from auxins and cytokinins to strigolactones and salicylic acid: how they regulate growth and stress responses, and how they are applied in agriculture.

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1. Introduction

Phytohormones are endogenous signalling molecules that regulate plant growth, development and responses to environmental conditions at very low concentrations. Rather than acting simply as growth promoters or inhibitors, they coordinate processes throughout the plant life cycle, including cell division and expansion, root and shoot development, seed germination, flowering, fruit development, senescence and responses to biotic and abiotic stresses. Their activity depends not only on their biosynthesis but also on metabolism, transport, tissue-specific distribution, perception and downstream signalling (Zhang et al., 2023).

The major phytohormones considered in this review are auxins, cytokinins, gibberellins (GAs), abscisic acid (ABA), ethylene, brassinosteroids (BRs), jasmonates (JAs), strigolactones (SLs) and salicylic acid (SA). Their functions can be seen in Table 1.

Table 1. Main physiological functions of the major phytohormones.

Phytohormone	Main physiological functions
Auxins	Cell expansion and elongation; root initiation and development; apical dominance; vascular differentiation; tropic responses; organ formation; fruit development and fruit set
Cytokinins	Cell division; shoot initiation and development; regulation of root growth; release of lateral buds; nutrient mobilisation; chloroplast development; delay of leaf senescence; reproductive development
Gibberellins (GAs)	Seed germination; stem and internode elongation; leaf expansion; transition to flowering; flower development; fruit growth and development
Abscisic acid (ABA)	Seed maturation and dormancy; regulation of germination; stomatal closure and water relations; growth adjustment under stress; responses to drought, salinity and other abiotic stresses

Phytohormone	Main physiological functions
Ethylene	Seedling development; regulation of cell expansion and elongation; root development; flower and leaf senescence; organ abscission; fruit ripening; biotic and abiotic stress responses
Brassinosteroids (BRs)	Cell expansion and division; vascular differentiation; root and shoot growth; reproductive development; modulation of stress responses
Jasmonates (JAs)	Defence against herbivores and pathogens; wound responses; regulation of growth–defence balance; reproductive development; senescence; responses to abiotic stress
Strigolactones (SLs)	Suppression of shoot branching; regulation of root architecture; nutrient-responsive growth; interactions with arbuscular mycorrhizal fungi; adaptation to phosphate and nitrogen availability
Salicylic acid (SA)	Plant immunity and defence signalling; systemic acquired resistance; responses to biotrophic pathogens; modulation of growth and abiotic stress responses

Importantly, plant responses cannot generally be attributed to the concentration of a single hormone. Hormonal pathways form interconnected regulatory networks in which one hormone can modify the availability, perception, sensitivity or signalling of another (Vanstraelen and Benková, 2012). These interactions may be synergistic, additive or antagonistic, and their outcome is strongly dependent on developmental and physiological context (Vanstraelen and Benková, 2012). Consequently, hormonal balance and spatial distribution can be as important as absolute hormone concentration. Hormone transport creates differences in hormone concentration between cells and tissues, including local hormone maxima and gradients, contributing to the spatial regulation of plant growth and development (Zhang et al., 2023).

This complexity is particularly relevant when phytohormones are manipulated in agriculture. Exogenous hormone application can modify a wide range of crop responses, but the outcome can vary considerably with hormone concentration, application method, developmental stage and the physiological context of the plant (Koprna et al., 2016). This dependence on concentration and developmental context is one of the major considerations when translating phytohormone physiology into practical crop management.

This review therefore examines the principal phytohormones from a functional and agricultural perspective, focusing on how they are produced and transported, how they are perceived by plant cells, the physiological responses they regulate, their interactions with other hormonal pathways, and the concentration-dependent effects observed following endogenous or exogenous manipulation. Particular emphasis is placed on translating these mechanisms into crop-relevant responses and practical agricultural applications.

2. Major Phytohormones: Mechanisms and Functions

The physiological effects summarised in Table 1 depend on how each hormone is produced, metabolised, transported and perceived by the plant. These processes determine not only the amount of a hormone present but also where and when it is active and how strongly individual tissues respond. Hormone distribution is particularly important, as transport combined with local production and metabolism creates differences in hormone concentration between cells and tissues, allowing specific developmental responses to occur at particular locations within the plant (Zhang et al., 2023).

The following sections examine each major phytohormone individually, focusing on its main active forms, production and transport, how it is perceived by the plant, and the mechanisms underlying its principal physiological effects. Particular attention is also given to concentration-dependent responses and the effects of exogenous applications in agricultural crops.

2.1 Auxins

Auxins are major regulators of plant growth and development. Indole-3-acetic acid (IAA) is the most abundant and widespread endogenous auxin, although plants also contain other naturally occurring auxins, including indole-3-butyric acid (IBA), phenylacetic acid (PAA) and, in some species, 4-chloroindole-3-acetic acid (4-Cl-IAA) (Hammes and Pedersen, 2024). IAA is produced in many parts of the plant, but its synthesis is particularly associated with actively growing and developing tissues. Once produced, the amount of active IAA available in a tissue is carefully regulated. Plants can convert IAA into inactive or storage forms, release it again when required, degrade excess IAA, or transport it to other tissues. Together, these processes allow plants to maintain different auxin concentrations in

different organs and at different stages of development (Cohen and Strader, 2024; Gao et al., 2024).

The distribution of auxin within the plant is particularly important for its activity. Auxin can move over longer distances through the vascular system and can also be transported directionally from cell to cell. This directional movement, known as polar auxin transport, allows the plant to establish areas with different auxin concentrations. These differences help regulate processes such as organ formation, vascular development, lateral root formation and responses to light and gravity (Zhang et al., 2023; Hammes and Pedersen, 2024).

At the cellular level, auxin is perceived through specific receptor systems that ultimately modify gene expression and cellular activity. In the main signalling pathway, increasing auxin concentrations remove proteins that normally repress the auxin response, allowing auxin-responsive genes to become active. This mechanism enables relatively small changes in auxin concentration to produce changes in plant growth and development (Du et al., 2020; Cohen and Strader, 2024).

One important response is auxin-induced cell expansion. Auxin stimulates proton transport across the plasma membrane, resulting in acidification of the apoplast. This promotes cell-wall loosening and allows turgor-driven cell expansion, providing the basis for the classical acid-growth response associated with auxin-promoted shoot elongation (Du et al., 2020).

Auxin responses depend strongly on both concentration and the tissue involved. For example, auxin can promote cell expansion and elongation in shoots, while increased auxin concentrations can inhibit elongation in roots (Du et al., 2020).

The effect also depends on the developmental stage and sensitivity of the target tissue, as well as interactions with other hormones (Gao et al., 2024). These factors are particularly important when auxins are applied externally in agriculture.

Auxins and auxin-related compounds are widely used to manipulate plant development, particularly rooting, fruit set and fruit development. Their effectiveness depends on the type of auxin or analogue, concentration, application method, crop and developmental stage (Gao et al., 2024). For this reason, agricultural responses to auxins are best considered quantitatively rather than simply describing auxin as beneficial or inhibitory.

2.2 Cytokinins

Cytokinins are a group of plant hormones derived primarily from adenine. The major naturally occurring forms include trans-zeatin (tZ), cis-zeatin (cZ), isopentenyladenine (iP) and dihydrozeatin (DHZ), although their abundance and biological activity vary among plant species. The free-base forms are generally considered the biologically active cytokinins, while plants also contain ribosides, ribotides and conjugated forms that participate in cytokinin metabolism and transport (Kieber and Schaller, 2018; Argueso and Kieber, 2024).

Cytokinins are produced in several plant tissues, including both roots and shoots, particularly in actively growing regions. Their concentration is controlled through biosynthesis, conversion between different cytokinin forms and irreversible degradation by cytokinin oxidase/dehydrogenase (CKX). This regulation allows plants to adjust cytokinin availability according to developmental stage and environmental conditions, including nutrient availability (Sakakibara, 2006; Kieber and Schaller, 2018).

Cytokinins can act locally where they are produced but can also move between different parts of the plant. Long-distance transport occurs through both the xylem and phloem, helping coordinate development and nutrient status between roots and shoots (Zhang et al., 2023; Argueso and Kieber, 2024).

Cytokinins are perceived by specific receptors, mainly located in cellular membranes. Once cytokinin binds to these receptors, the signal is transferred through a series of steps that ultimately changes gene expression and cellular activity. This signalling system allows changes in cytokinin concentration to regulate processes such as cell division, shoot and root development, nutrient responses and senescence (Kieber and Schaller, 2018; Argueso and Kieber, 2024).

An important characteristic of cytokinin activity is its close interaction with other hormones, particularly auxin. Their relationship is highly dependent on the tissue and developmental process, and the two hormones can act either cooperatively or antagonistically. In roots, auxin generally promotes lateral root initiation, while cytokinin can oppose auxin activity and restrict root development. In shoots, cytokinin promotes meristem activity and lateral bud growth, whereas auxin contributes to apical dominance and the suppression of lateral branching. Consequently, it is often the balance between auxin and cytokinin activity, rather

than the concentration of either hormone alone, that determines the developmental response (Argueso and Kieber, 2024; Koprna et al., 2016).

From an agricultural perspective, cytokinins have been investigated for their ability to influence branching, delay senescence, improve nutrient mobilisation and modify flower, seed and fruit development. Exogenous cytokinin applications have been evaluated in crops including wheat, rice, maize, barley, soybean, cotton, vegetables and fruit trees. However, responses are highly dependent on cytokinin type, concentration and particularly the developmental stage at which treatment is applied, which has limited the consistency of their use as agricultural growth regulators (Koprna et al., 2016).

2.3 Gibberellins

Gibberellins (GAs) are a large family of plant hormones involved in the regulation of plant growth and development. More than one hundred different GAs have been identified, but only a small number are biologically active (Richards et al., 2001; Xue et al., 2021).

Gibberellins are produced in several actively growing and developing tissues, including young shoots, developing seeds and reproductive tissues. Their levels are tightly regulated through biosynthesis and inactivation, allowing the plant to adjust the amount of active GA according to its developmental stage and environmental conditions. GA metabolism is also subject to feedback regulation, helping maintain appropriate levels of active hormone within individual tissues (Richards et al., 2001; Xue et al., 2021).

Gibberellins can move between plant tissues, although their transport is less strongly directional than the polar transport characteristic of auxin. Both short- and long-distance movement contribute to GA distribution, while local biosynthesis and inactivation are important in determining where biologically active GA accumulates. Consequently, GA activity can differ substantially between organs and developmental stages (Zhang et al., 2023).

The basic mechanism of GA action can be understood as the removal of a growth restraint. In the absence of sufficient active GA, proteins known as DELLAs suppress several GA-dependent growth responses. When GA binds to its receptor, DELLA proteins are targeted for degradation, removing this restraint and allowing GA-responsive growth and developmental processes to proceed (Xue et al., 2021). This mechanism helps explain why

increasing GA activity is strongly associated with processes such as stem elongation, seed germination and reproductive development (Richards et al., 2001).

GA activity is also closely connected with other hormonal pathways. DELLA proteins interact with components of several other hormone signalling systems, allowing GA responses to be adjusted according to the overall physiological state of the plant. This crosstalk contributes to the balance between growth and other processes, including responses to environmental stress (Xue et al., 2021).

From an agricultural perspective, manipulation of GA activity can strongly influence plant height, germination, flowering and fruit development. The importance of GA regulation is particularly evident in cereal crops: reduced GA signalling associated with DELLA proteins contributed to the semi-dwarf growth habit of important wheat varieties, demonstrating how modification of GA responses can alter plant architecture and agronomic performance (Richards et al., 2001; Xue et al., 2021).

2.4 Abscisic Acid (ABA)

Abscisic acid (ABA) is an important regulator of plant development and environmental stress responses. In contrast to auxin, cytokinin and gibberellin, which are strongly associated with growth and developmental progression, ABA has a particularly important role in coordinating growth with environmental conditions, especially water availability. It also regulates seed maturation, dormancy and germination (Zhang et al., 2023; Mo et al., 2024).

ABA is produced in both roots and shoots, and its synthesis can increase rapidly when plants experience environmental stresses such as water deficit. Its concentration is controlled through a balance between biosynthesis, degradation and conversion into inactive or stored forms, allowing ABA levels to change according to the physiological requirements of the plant (Mo et al., 2024; Zhang et al., 2023).

ABA can act close to where it is produced or be transported to other parts of the plant. Long-distance transport allows ABA produced in one tissue to regulate responses elsewhere. For example, ABA produced in aerial tissues can influence root development, while movement of ABA within leaves contributes to the regulation of stomatal opening and closing. ABA transport therefore contributes to communication between tissues during both normal development and water stress (Zhang et al., 2023).

At the cellular level, ABA is perceived by specific receptors that activate a signalling pathway leading to changes in cellular activity and gene expression. One of the most important rapid responses occurs in the guard cells surrounding stomata. Under water deficit, increased ABA signalling promotes stomatal closure, reducing water loss through transpiration. ABA also activates longer-term responses that help the plant adjust its growth and physiology to stressful conditions (Mo et al., 2024).

ABA also provides a good example of hormonal antagonism. During seed germination, ABA and gibberellins generally have opposing roles: ABA promotes and maintains dormancy, whereas GA promotes germination and subsequent growth. The balance between the two hormonal pathways therefore contributes to determining whether a seed remains dormant or begins germination (Vanstraelen and Benková, 2012).

From an agricultural perspective, ABA is particularly relevant to crop responses to drought and other environmental stresses because of its effects on stomatal regulation, water use and stress-responsive metabolism. Manipulating ABA concentration or signalling can therefore influence crop water relations and stress tolerance, although these responses involve an important trade-off: restricting water loss can improve survival under water deficit, but excessive or prolonged growth restriction may also reduce productivity. The crop-specific effects of ABA application, including concentration and application timing, will be considered quantitatively in Section 4.

2.5 Ethylene

Ethylene is a gaseous plant hormone involved in the regulation of plant growth, development and responses to environmental conditions. Its gaseous nature distinguishes it from the other major phytohormones and allows it to diffuse readily through plant tissues and into the surrounding atmosphere. Ethylene is particularly associated with fruit ripening, senescence and organ abscission, but it also regulates seedling development, root growth and responses to biotic and abiotic stresses (Wang et al., 2025; Vanstraelen and Benková, 2012).

Ethylene can be produced in most plant tissues, although production varies considerably with developmental stage and environmental conditions. Its synthesis commonly increases during processes such as fruit ripening and senescence and in response to stresses including

wounding, flooding and pathogen attack. Because ethylene is a gas, it cannot be stored or transported in the same way as many other hormones. Plants therefore regulate ethylene activity largely by controlling how much is produced and how sensitive individual tissues are to it (Wang et al., 2025).

Once produced, ethylene diffuses relatively freely between cells and tissues. This means that its distribution does not depend on specialised directional transport systems comparable to the polar transport of auxin. However, ethylene can also influence longer-distance plant responses indirectly by modifying the production and transport of other hormones, particularly auxin (Vanstraelen and Benková, 2012; Zhang et al., 2023).

Ethylene is perceived by specific receptors located mainly on membranes of the endoplasmic reticulum. An interesting feature of this system is that, in the absence of ethylene, the receptors actively suppress the ethylene response. When ethylene binds to the receptors, this suppression is removed, allowing ethylene-responsive genes and physiological processes to become active (Wang et al., 2025).

Ethylene also interacts strongly with other hormones, particularly auxin. In roots, increased ethylene activity can stimulate auxin production and alter its transport, resulting in greater auxin activity in the root elongation zone. Because root cells are highly sensitive to auxin, this increase can inhibit cell elongation and consequently reduce root elongation. Thus, some of the effects of ethylene on root growth are mediated through changes in auxin synthesis and distribution rather than through ethylene acting independently (Vanstraelen and Benková, 2012).

From an agricultural perspective, ethylene is particularly important because of its strong influence on fruit ripening, senescence and abscission. Its activity can be manipulated either by supplying ethylene or ethylene-releasing compounds, or by inhibiting ethylene production or perception when ripening and senescence need to be delayed. This makes ethylene regulation particularly relevant to crop maturation and postharvest management (Wang et al., 2025). Specific compounds, concentrations, application stages and crop responses will be considered in Section 4.

2.6 Brassinosteroids (BRs)

Brassinosteroids (BRs) are plant steroid hormones that regulate growth and development, particularly cell expansion and division, vascular differentiation and reproductive development. More than 40 naturally occurring BRs were already identified in the earlier literature, with brassinolide and castasterone among the most biologically active forms. BRs occur at very low concentrations and are generally more abundant in young, actively growing tissues, pollen and developing seeds than in mature vegetative tissues (Clouse and Sasse, 1998).

Brassinosteroids are produced naturally by plants from sterols, compounds that form part of plant cell membranes. Through a series of biochemical reactions, these sterols are converted into biologically active brassinosteroids. Their production varies among tissues and developmental stages, allowing plants to regulate BR activity according to their growth requirements (Clouse and Sasse, 1998).

Unlike auxin, BRs are not characterised by a specialised long-distance or polar transport system. Their effects depend strongly on local production and local perception, with BR levels varying substantially among plant tissues. This makes the regulation of BR biosynthesis and metabolism within individual tissues particularly important for controlling their physiological effects (Clouse and Sasse, 1998; Wang et al., 2012).

Brassinosteroids are detected by receptors located on the plasma membrane. When a BR binds to its receptor, it initiates a signal that is transmitted inside the cell and ultimately changes the activity of genes involved in growth and development. In this way, the presence of BR allows the cell to activate the processes responsible for BR-regulated growth responses (Wang et al., 2012).

One of the most characteristic effects of BRs is the promotion of cell expansion. Plants deficient in BR production or unable to perceive BR normally show pronounced dwarfism, demonstrating that endogenous BRs are required for normal plant growth. However, BRs also influence cell division, vascular development, seed germination, plant architecture, flowering, male fertility and senescence (Clouse and Sasse, 1998; Wang et al., 2012).

BRs also interact closely with auxin and gibberellins rather than regulating growth independently. BR and auxin signalling can converge on common growth processes, while BRs can influence GA metabolism and signalling. This interaction is particularly relevant to

cell elongation: BR and GA pathways can converge on common regulatory mechanisms, allowing plant growth to reflect the combined activity of both hormonal systems (Wang et al., 2012; Xue et al., 2021).

From an agricultural perspective, exogenous BR applications have been investigated for their effects on crop growth, yield and tolerance to unfavourable environmental conditions. Responses have been reported in crops including wheat, rice and sugar beet, although the effects depend strongly on BR type, concentration, crop and growing conditions (Clouse and Sasse, 1998). The specific concentrations, application methods and crop responses will be considered in Section 4.

2.7 Jasmonates (JAs)

Jasmonates (JAs) are a group of plant hormones particularly important in coordinating plant defence and responses to environmental stress. They also participate in normal growth and development, including reproductive development and senescence. Jasmonic acid (JA) is one of the main compounds in this group, while jasmonoyl-isoleucine (JA-Ile) is the principal biologically active form responsible for activating jasmonate signalling in higher plants (Browse, 2009; Howe et al., 2018).

Jasmonates are produced from fatty acids that are naturally present in plant cell membranes. Their production can increase rapidly when plant tissues are damaged, for example following mechanical injury or herbivore attack. This provides the plant with a mechanism to rapidly convert information about tissue damage into a hormonal signal that activates defensive responses (Browse, 2009; Howe et al., 2018).

Jasmonate signals are not restricted to the tissue where they are initially produced. Wounding can generate signals that move to other parts of the plant, allowing undamaged tissues to prepare defensive responses before they are directly attacked. Jasmonates and related compounds therefore contribute to communication between damaged and undamaged tissues and to the development of broader plant defence responses (Zhang et al., 2023).

The way jasmonates are perceived follows a mechanism somewhat similar to what we discussed for gibberellins. When jasmonate activity is low, specific proteins suppress the expression of jasmonate-responsive genes. When the active jasmonate signal is detected,

these suppressor proteins are removed, allowing genes involved in defence, stress responses and development to become active (Browse, 2009; Howe et al., 2018). An important characteristic of jasmonate activity is the balance between defence and growth. Increasing jasmonate signalling can strengthen defensive responses against herbivores and some pathogens, but these responses require resources that might otherwise be used for plant growth. Jasmonates therefore contribute to the adjustment of plant growth when defence becomes a priority, rather than acting simply as growth-promoting or growth-inhibiting hormones (Howe et al., 2018).

Jasmonates also interact strongly with other hormonal pathways. Their interaction with salicylic acid is particularly important in plant defence, as the two pathways can act antagonistically depending on the type of threat encountered. Jasmonates also interact with ethylene and auxin, helping integrate defence responses with plant growth and development (Howe et al., 2018).

From an agricultural perspective, jasmonates are of particular interest because of their ability to activate plant defence and stress-response mechanisms. Exogenous application of jasmonic acid or methyl jasmonate has therefore been investigated as a means of influencing crop resistance, stress tolerance, secondary metabolism and postharvest responses. However, because stronger jasmonate signalling can also restrict growth, the final response depends strongly on concentration, timing, crop and physiological condition. Specific agricultural applications and concentrations will be considered in Section 4 (Howe et al., 2018).

2.8 Strigolactones (SLs)

Strigolactones (SLs) are a group of plant hormones with an important role in controlling plant architecture, particularly shoot branching and root development. They also have a distinctive function below ground, where compounds released from roots participate in communication with arbuscular mycorrhizal fungi. SL activity is also closely linked to plant nutrient status, particularly the availability of phosphorus and nitrogen (Seto, 2024; Barbier et al., 2023).

Strigolactones are produced naturally by plants from carotenoids, the same broad group of compounds that includes many plant pigments. Their production occurs through a series of

biochemical reactions that convert carotenoid-derived compounds into different forms of SLs. Production is strongly influenced by the nutritional condition of the plant and commonly increases when important nutrients, particularly phosphorus or nitrogen, become limited (Seto, 2024; Barbier et al., 2023).

SLs can act within the plant but can also be released from roots into the surrounding soil. Within the plant, they contribute to communication between roots and shoots and to the regulation of shoot and root architecture. In the rhizosphere, SLs act as signals that stimulate interactions with arbuscular mycorrhizal fungi, which can improve the plant's access to mineral nutrients, particularly phosphorus (Seto, 2024; Barbier et al., 2023).

The way strigolactones are perceived follows a mechanism somewhat similar to what we discussed for gibberellins and jasmonates. When an SL signal is detected, proteins that normally suppress the SL response are removed. This allows changes in gene activity that regulate processes such as shoot branching and root development. Although the complete signalling pathway involves several proteins, the important point is that SL perception removes an existing restriction and allows the plant to modify its growth in response to the hormonal signal (Seto, 2024).

One of the most characteristic effects of SLs is the suppression of shoot branching. When SL activity is high, the growth of lateral buds is restricted, resulting in fewer branches or tillers. SLs also influence root architecture, including root elongation and lateral root formation, particularly when nutrient availability changes. In this way, SLs help coordinate above- and below-ground growth according to the nutritional conditions experienced by the plant (Barbier et al., 2023; Sun et al., 2022).

Strigolactones interact particularly closely with auxin and cytokinin in the regulation of plant architecture. In shoots, auxin contributes to SL production and transport-related responses, while SLs can influence auxin transport and restrict lateral bud growth. Cytokinin generally has the opposite effect on lateral buds, promoting their growth. Consequently, shoot branching reflects the combined activity of auxin, cytokinin and strigolactones rather than the action of any one hormone independently (Vanstraelen and Benková, 2012).

From an agricultural perspective, SLs are particularly interesting because their effects on branching, tillering, root architecture and nutrient acquisition could potentially be used to

modify crop architecture and improve nutrient-use efficiency. Their role in plant responses to phosphorus and nitrogen availability makes them especially relevant to crop nutrition. However, manipulating SL activity is complex because the same hormonal pathway affects several processes simultaneously, including shoot development, root growth and interactions with soil microorganisms (Barbier et al., 2023; Sun et al., 2022).

2.9 Salicylic Acid (SA)

Salicylic acid (SA) is a plant hormone particularly important in the regulation of plant defence and immunity. Unlike hormones such as auxin, gibberellins or brassinosteroids, whose major roles are strongly associated with growth and development, SA is primarily associated with the plant's response to pathogen attack, particularly pathogens that obtain nutrients from living plant tissues. SA also participates in the coordination of defence responses between infected and non-infected parts of the plant (Browse, 2009; Hwang et al., 2012).

SA is produced naturally by plants, and its concentration can increase considerably following recognition of a pathogen. This increase acts as a signal that activates defence responses in the affected tissue and contributes to the establishment of resistance in other parts of the plant. In this way, SA helps the plant move from a normal physiological state towards a defence-oriented state when infection is detected (Browse, 2009).

One of the most important characteristics of SA is its involvement in systemic acquired resistance (SAR). Following a local infection, defence signalling can extend to tissues that have not yet been infected, preparing them to respond more effectively to subsequent pathogen attack. SA is an important component of this process and contributes to the activation of defence-related genes in both local and systemic responses (Browse, 2009).

The way SA produces its effects is based largely on changes in gene activity. When SA levels increase during a defence response, the hormone activates signalling that ultimately allows defence-related genes to become active. These genes lead to the production of proteins and other defensive responses that help restrict pathogen development. Therefore, SA does not attack the pathogen directly; instead, it acts as an internal signal that activates the plant's own defence mechanisms (Hwang et al., 2014).

An important characteristic of SA signalling is its interaction with jasmonates. The two pathways often regulate different types of defence responses. SA is particularly associated with defence against biotrophic pathogens, which depend on living plant tissue, whereas jasmonate signalling is particularly important against necrotrophic pathogens, which obtain nutrients from damaged or dead tissue, and against herbivores. SA and JA pathways can act antagonistically, meaning that strong activation of one pathway can reduce the activity of the other. This allows the plant to adjust its defence strategy according to the type of threat encountered (Browse, 2009; Howe et al., 2018).

SA also interacts with hormones involved in plant growth. Increased SA activity can influence auxin-related processes and other growth pathways, illustrating the trade-off that can occur between investment in growth and investment in defence. Consequently, the final response to SA depends not only on its concentration but also on the physiological condition of the plant and its interaction with other hormonal pathways.

From an agricultural perspective, SA is of interest because activation of SA-related signalling can influence crop resistance to disease and responses to environmental stress. Exogenous SA and related compounds have therefore been investigated as treatments for stimulating plant defence responses. However, because defence activation can also affect growth and resource allocation, the outcome depends on concentration, timing, crop and physiological condition. Specific agricultural applications will be considered in Section 4.

3. Hormonal Crosstalk and Balance

Phytohormones do not act independently. Instead, their signalling pathways interact with one another, a process known as hormonal crosstalk. Through these interactions, one hormone can enhance, reduce or modify the response produced by another, allowing plants to coordinate growth, development and responses to environmental conditions. Consequently, the final physiological response often depends on the balance and interaction between several hormones rather than on the concentration of a single hormone alone (Vanstraelen and Benková, 2012).

The following sections examine why this hormonal balance is important and how interactions between specific hormones influence plant responses. Particular attention is given to the relationships between:

- Auxin and Cytokinin

- Gibberellins and ABA

- Brassinosteroids and Gibberellins

- Jasmonates and Salicylic acid,

- Combined effects of Strigolactones, Auxin and Cytokinin.

These examples illustrate how hormonal interactions can be synergistic, antagonistic or dependent on the tissue and developmental stage, and how their combined activity ultimately determines the physiological response of the plant (Vanstraelen and Benková, 2012).

3.1 Auxin–Cytokinin Interaction

Auxin and cytokinin provide one of the clearest examples of hormonal crosstalk. Although both regulate plant growth and development, their effects can be different or even opposing depending on the tissue. Their relative activity helps determine whether cells continue dividing, begin to differentiate, or whether particular organs and buds continue to develop (Vanstraelen and Benková, 2012).

In roots, auxin generally supports meristem activity and root development, whereas cytokinin promotes the transition of cells from division towards differentiation. Cytokinin can also modify the distribution of auxin within the root. Their interaction therefore helps control the balance between the production of new cells and their subsequent differentiation as the root develops (Vanstraelen and Benková, 2012).

The relationship is also important in shoots. Auxin produced near the shoot apex contributes to apical dominance and the suppression of lateral bud growth, whereas cytokinin promotes bud activation and branching. Changes in the relative activity of these two hormones can therefore alter plant architecture. This illustrates why auxin and cytokinin should not be considered independently: their balance and interaction can be more important than the concentration of either hormone alone (Vanstraelen and Benková, 2012; Kieber and Schaller, 2018).

3.2 Gibberellin–ABA Interaction

Gibberellins (GAs) and abscisic acid (ABA) provide one of the clearest examples of antagonistic hormonal crosstalk. This relationship is particularly important during seed dormancy and germination. ABA promotes the establishment and maintenance of dormancy, whereas GA promotes the breaking of dormancy and the initiation of germination. The relative activity of the two hormones therefore contributes to determining whether a seed remains dormant or begins to germinate (Richards et al., 2001; Vanstraelen and Benková, 2012).

The interaction involves changes in both hormone production and signalling. Conditions favourable for germination can increase GA activity while reducing ABA activity. Increased GA signalling also promotes the degradation of DELLA proteins, removing their restriction on growth and allowing germination to proceed. Conversely, stronger ABA activity favours dormancy and restricts germination (Vanstraelen and Benková, 2012; Xue et al., 2021).

The GA–ABA relationship therefore functions as a regulatory balance between maintaining dormancy and allowing growth to resume when conditions are favourable. Importantly, the two hormones do not simply operate as independent opposing signals; their production and signalling pathways can influence one another. This interaction allows environmental information, such as light and other conditions affecting germination, to be integrated into the decision of whether the seed remains dormant or begins development (Vanstraelen and Benková, 2012).

3.3 Brassinosteroid–Gibberellin Interaction

Brassinosteroids (BRs) and gibberellins (GAs) are both strongly associated with plant growth, particularly cell elongation. However, they act through different signalling pathways that interact with each other. Their combined activity allows the plant to coordinate the extent of cell and stem elongation rather than each hormone regulating these processes independently (Wang et al., 2012; Xue et al., 2021).

An important point of interaction involves the DELLA proteins discussed previously. When GA levels are low, DELLA proteins accumulate and restrict growth. These proteins can also interfere with BR signalling, reducing the ability of BRs to activate genes involved in cell elongation. When GA levels increase, DELLAs are degraded, removing this restriction and

allowing BR signalling to promote growth more effectively (Wang et al., 2012; Xue et al., 2021).

The relationship can also operate in the other direction, as BR activity can influence GA production and thereby contribute to increased cell elongation. The interaction between BR and GA therefore illustrates how two growth-promoting hormones can act cooperatively: GA removes restrictions on growth while BR signalling contributes to activating the cellular responses required for elongation. The strength of this interaction can vary between tissues and plant species (Wang et al., 2012; Xue et al., 2021).

3.4 Jasmonate–Salicylic Acid Interaction

Jasmonates (JAs) and salicylic acid (SA) are both important in plant defence, but they are generally associated with responses to different types of threats. SA is particularly important in defence against biotrophic pathogens (pathogens that feed on and depend on living plant cells, including many viruses, some bacteria, and fungi such as rusts and powdery mildews), whereas JA is strongly associated with defence against necrotrophic pathogens (pathogens that kill plant cells and obtain nutrients from dead or damaged tissues, including fungi such as *Botrytis* and *Alternaria*) and herbivores, particularly insects (Browse, 2009; Howe et al., 2018).

The two pathways often interact antagonistically. Increased SA signalling can suppress JA-dependent responses, while JA can also reduce SA responses, although the effect of SA on JA is generally stronger. This interaction allows the plant to adjust its defence response according to the type of attack rather than activating all defence mechanisms simultaneously (Browse, 2009).

This balance is important because activating defence requires resources and can interfere with normal growth and reproduction. Crosstalk between JA and SA therefore helps the plant prioritise an appropriate defence strategy while limiting unnecessary physiological costs. However, the relationship is not always strictly antagonistic and can vary according to the pathogen, tissue and physiological conditions of the plant (Howe et al., 2018).

3.5 Strigolactone–Auxin–Cytokinin Interaction

Strigolactones (SLs), auxin and cytokinins interact closely in the regulation of shoot branching. Auxin produced near the shoot apex contributes to apical dominance and

indirectly suppresses the growth of lateral buds. Cytokinins generally have the opposite effect, promoting the activation and growth of these buds, while SLs contribute to maintaining bud dormancy and restricting branching (Vanstraelen and Benková, 2012).

Auxin helps coordinate the other two hormonal signals. It can stimulate SL production while reducing cytokinin availability. Consequently, high auxin activity from the main shoot favours conditions that restrict lateral bud growth. When the shoot apex is removed, the auxin supply decreases, SL production is reduced and cytokinin levels can increase, creating conditions that favour bud growth and branching (Vanstraelen and Benková, 2012).

The interaction is therefore not simply a competition between three hormones. Auxin acts partly by influencing the other hormonal pathways, while cytokinin and SLs have opposing effects directly associated with bud growth. Their combined activity provides a good example of how hormonal balance controls plant architecture and allows branching to respond to changes in the plant's developmental and physiological conditions (Vanstraelen and Benková, 2012).

The interactions described in the previous sections show that hormonal crosstalk can involve antagonistic, cooperative or more complex relationships between different phytohormones. Table 2 summarises the main hormonal interactions discussed in this section, their general relationship and the principal physiological processes influenced by their combined activity.

Table 2. Main phytohormone interactions, general relationships and associated physiological responses

Interaction	**General relationship**	**Main outcome**
Auxin–cytokinin	Context-dependent / often opposing	Root and shoot development, branching
GA–ABA	Mainly antagonistic	Dormancy vs germination
BR–GA	Mainly cooperative	Cell and stem elongation
JA–SA	Often antagonistic	Selection of defence responses
SL–auxin–cytokinin	Integrated/opposing	Shoot branching and architecture

4. Phytohormones in Agricultural Practice

The ability of phytohormones to regulate plant growth, development and stress responses has led to their use, or the use of synthetic compounds with similar activity, as plant growth regulators in agriculture. However, the response to an exogenous hormone application depends strongly on the compound applied, concentration, crop, application method and developmental stage of the plant. Consequently, the same hormone can produce beneficial, negligible or even undesirable effects depending on how and when it is applied (Koprna et al., 2016).

Concentration is particularly important because hormonal responses are not necessarily proportional to the amount applied. Increasing the concentration does not always increase the desired response, and some hormones can promote a process at low concentrations while inhibiting it at higher concentrations. Brassinosteroids, for example, can inhibit primary root extension when applied externally, while very low concentrations have sometimes promoted elongation or adventitious rooting (Clouse and Sasse, 1998).

Application timing is equally important. Hormonal sensitivity changes throughout plant development, meaning that treatment at germination, vegetative growth, flowering or fruit development can produce very different responses. Cytokinin studies in cereal crops, for example, have shown that effects on tillering, grain formation, grain filling and final yield depend strongly on the developmental stage at which treatment occurs (Koprna et al., 2016).

For this reason, agricultural use of phytohormones should be considered in terms of the complete treatment rather than the hormone alone. Table 3 presents selected examples of exogenous phytohormone applications, including the compound applied, crop, concentration or rate, application method, developmental stage and observed plant response. These examples illustrate both the potential agricultural value of phytohormones and the importance of selecting an appropriate concentration and application timing.

Table 3. Selected examples of exogenous phytohormone applications in agricultural crops

Auxins

Auxin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
IAA (indole-3-acetic acid)	Bean	Applied to excised stem sections	Increased tissue IAA and produced a corresponding growth response	Bialek et al., 1983
IAA	Maize/oat	Applied to auxin-depleted coleoptile segments	Rapidly stimulated elongation following a short lag period, associated with apoplastic acidification	Classical experiments reviewed by Du et al., 2020
IAA	Pea/soybean	Applied to auxin-depleted epicotyl/hypocotyl segments	Stimulated tissue elongation and acidification	Classical experiments reviewed by Du et al., 2020
IAA	*Arabidopsis thaliana*	Exogenous treatment; roots	Nanomolar IAA inhibited root elongation rapidly; inhibition began within ~30 s and was reversible after IAA removal	Fendrych et al., 2018*
IAA	*Arabidopsis thaliana*	10 µM IAA pulse; root hairs	Rapid plasma-membrane depolarisation and increased cytosolic Ca^{2+}	Dindas et al., 2018*
IBA (indole-3-butyric acid)	Plant cuttings	Applied during vegetative propagation	Promoted adventitious rooting; widely adopted as a rooting treatment	Historical studies reviewed by Cohen & Strader, 2024
NAA (1-naphthaleneacetic acid)	Cucumber	Exogenous treatment; 72 h after flooding	Enhanced adventitious-root formation under flooding	Qi et al., 2023
NAA + BA	Spinach	Foliar spray; 20, 40 and 60 days after germination	Increased shoot biomass	Durrani et al., 2010
NAA + BA + carbaryl	Apple	Foliar spray; fruit ~11 mm	Promoted fruit thinning and affected fruit weight	Elfving & Cline, 1993
BA, NAA and carbaryl	Apple	Foliar spray; 22 days after full bloom	Increased fruit weight without increasing yield	Wismer et al., 1995

Auxin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
NAA/IBA + BA/CPPU/GA	Pear	Foliar spray; young-fruit development	Increased fruit size	Chen et al., 2012

Cytokinins

Cytokinin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
BA (6-benzyladenine)	Wheat	Irrigation; ear emergence	Increased flag-leaf area, grain-filling period and yield	Alizadeh, 2010
BA	Wheat	Irrigation; 17 days after sowing	Modified sink activity, chlorophyll and carbohydrate status	Criado et al., 2009
BA	Wheat	Injection; anthesis	Increased seed weight	Gupta et al., 2003
BA	Wheat	Injection into young ears	Increased grain size	Warrier et al., 1987
BA + putrescine	Wheat	Foliar spray; anthesis	Improved stress-related metabolism and yield under water stress	Gupta et al., 2012
BAP or moringa leaf extract	Wheat	Foliar spray; tillering, jointing, booting and heading	Increased grain weight and yield	Yasmeen et al., 2013
BA + kinetin	Wheat	Seed priming; before sowing	Improved plant growth and grain yield under salinity	Iqbal et al., 2006
Kinetin	Wheat	Irrigation; 22-day-old seedlings	Improved growth, chlorophyll content, grain yield and salt tolerance	Gadallah, 1999
Kinetin, SA or ascorbate	Wheat	Seed priming; before sowing	Improved plant growth and grain yield under salinity	Afzal et al., 2013
Kinetin, SA or ascorbate	Wheat	Seed priming; before sowing	Increased fertility, grain yield and harvest index	Jafar et al., 2012
Zeatin + ABA + IAA + GA_3	Wheat	Injection into sheath surrounding young ear; after ear formation	Modified fertility, floret development and grain number	Wang et al., 2001

Cytokinin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
BA + ABA	Wheat / triticale	Injection; after anthesis	Modified grain weight, grain number and yield	Sivakumar et al., 2001
BA	Barley	Foliar spray; anthesis	Increased ear weight, grain yield and photosynthesis	Hosseini et al., 2008
BA + kinetin + ABA	Barley	Seed priming and foliar spray	Increased grain and straw yield under salinity	Sarwat & El-Sherif, 2007
BA, kinetin, kinetin riboside, zeatin, zeatin riboside, iP or PBA	Barley	Root immersion and irrigation	Promoted/modified shoot growth	Sharif & Dale, 1980
BA	Barley	Irrigation; until ear emergence	Increased grain yield in secondary shoots	Williams & Cartwright, 1980
BA	Oat	Foliar spray + nitrogen; booting	Increased total spikelet number, but not fertile spikelet number	Peltonen-Sainio, 1997
Kinetin, IAA, GA_3 and ABA treatments	Oat	Irrigation; 35–42 days after germination	Modified tillering	Harrison & Kaufman, 1980
BA	Spinach	Foliar spray; 20, 40 and 60 days after germination	Increased shoot biomass	Durrani et al., 2010
BA	Cotton	Foliar spray; 2–4 leaf stage	Increased yield and improved response to water stress	Burke, 2011
TDZ (thidiazuron)	Cotton	Foliar spray; open-boll stage	Promoted defoliation and boll opening and affected yield/quality	Malik et al., 2002
BA	Apple	Foliar spray; fruit approximately 10 mm	Increased fruit weight	Yuan & Greene, 2000
BA	Apple	Foliar spray; full bloom/end of bloom	Fruit thinning and increased fruit weight	Original studies reviewed by Koprna et al., 2016
BA	Apple	Foliar spray; young nursery trees	Increased lateral branching	Original studies reviewed by Koprna et al., 2016

Cytokinin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
BA + GA_3/GA_{4+7}	Apple	Foliar spray; nursery trees approximately 70–75 cm	Increased branching	Gąstoł et al., 2012
BA	Pear	Foliar spray; 100 mg L^{-1}, 2 weeks after full bloom	Increased fruit size and yield; thinning response depended on cultivar	Stern & Flaishman, 2003
BA/CPPU + auxin/GA	Pear	Foliar spray; young-fruit development	Increased fruit size	Chen et al., 2012
BA/kinetin + GA	Mandarin	Foliar spray; flowering and fruit set	Improved fruit characteristics	Khalid et al., 2012
BA	Olive	Foliar spray; bud swelling and again six weeks later	Modified leaf biomass, photosynthesis, yield and oil content	Aziz et al., 2011
CPPU	Kiwifruit	Foliar spray; petal fall and subsequent fruit development	Increased fruit weight and size, although fruit quality was reduced	Kim et al., 2006
2-Cl-3-MeOBAP	Spring barley	Foliar spray; tillering	Increased biological yield (7%) and ears/m^2 (5%)	Koprna et al., 2016
2-Cl-3-MeOBAP	Spring barley	Foliar spray; stem elongation	Increased biological yield (4%) and ears/m^2 (7%)	Koprna et al., 2016
2-Cl-3-MeOBAP	Winter wheat	Foliar spray; tillering/stem elongation	No significant positive treatment effect detected	Koprna et al., 2016

Gibberellins (Gas)

Gibberellin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
GA	*Arabidopsis thaliana*	Exogenous application; short-day conditions	Promoted earlier flowering	Langridge, 1957
GA	GA-deficient *Arabidopsis* (ga1-3)	Exogenous application; during vegetative/reproductive development	Restored delayed flowering and abnormalities in petal and stamen development	Studies reviewed by Richards et al., 2001

Gibberellin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
GA_3	Barley	Applied to aleurone tissue	Stimulated α-amylase-related responses associated with mobilisation of seed reserves	Heimovaara-Dijkstra et al., 1994
GA_3 + kinetin	Rice	Seed priming; before germination	Improved germination under aerobic but not anaerobic conditions	Miyoshi & Sato, 2011
GA_3, kinetin or IAA	Rice	Foliar spray; early tillering	Delayed senescence and increased grain weight and yield	Kariali & Mohapatra, 2007
GA_3 + kinetin + IAA	Rice	Injection; booting stage	Promoted more homogeneous branch development and increased grain yield	Patel & Mohapatra, 1992
GA_3, kinetin or IAA	Rice	Foliar spray; reproductive stage	Modified grain yield and mobilisation index	Ray & Choudhuri, 1981
GA_3 + kinetin	Maize and soybean	Seed priming; before germination	Improved germination capacity at low temperature	Wang et al., 1996
GA_3	Cowpea	Foliar application; 30, 60 and 90 mg L^{-1}	Modified vegetative growth, nodulation and yield; responses depended on GA_3 concentration	Emongor, 2007
GA_3 + kinetin + IAA	Lentil	Foliar spray; after germination	Increased/modified shoot length, leaf number and flowering	Naeem et al., 2004
GA_3, BA or IAA	Faba bean	Foliar spray; 35 and 50 days after sowing	Modified pod set, seed yield and seed quality	Ibrahim et al., 2007
BA + GA_{4+7}	Hot pepper	Foliar spray; anthesis	Increased/modified fruit weight and yield	Batlang, 2008
GA_3/GA_{4+7} + BA	Apple	Foliar spray; nursery trees at 70–75 cm height	Promoted lateral branching	Gąstoł et al., 2012
GA_3 + BA	Pear	Foliar spray; full bloom and 3 weeks later	Modified fruit set and yield	Yehia & Hassan, 2005

Gibberellin / compound	Crop / plant	Method / timing	Main reported effect	Original reference
GA_3/GA_{4+7} + BA/CPPU/NAA/IBA	Pear	Foliar spray; young-fruit period	Increased fruit size	Chen et al., 2012
GA + BA/kinetin	Mandarin	Foliar spray; flowering and fruit set	Improved fruit quality in young trees	Khalid et al., 2012
GA + BA	Sweet cherry	Foliar spray; flowering and fruit set	Increased branching in one-year-old trees	Moghadam & Zamanipour, 2013

Abscisic acid(ABA)

Hormone / treatment	Crop / plant	Method / timing	Main reported effect	Original reference
ABA	*Arabidopsis thaliana*	3 µM ABA during seed germination	Suppressed germination of wild-type seeds; used to demonstrate the role of ABA in maintaining dormancy	Steber et al., 1998*
ABA	*Arabidopsis thaliana*	Exogenous ABA treatment	Induced stomatal closure and activation of slow anion channels	Kwak et al., 2002
ABA	*Arabidopsis thaliana*	Exogenous ABA treatment	Rapid activation of ABA-responsive SnRK2 signalling involved in osmotic-stress responses	Boudsocq et al., 2004
ABA	Tomato	Foliar ABA spray; leaves exposed to high relative humidity	Counteracted the increase in stomatal conductance associated with transfer to high relative humidity	Arve & Torre, 2015
ABA + zeatin + IAA + GA_3	Wheat	Injection into sheath surrounding young ear after ear formation; field	Affected fertility, floret development and grain number	Wang et al., 2001
ABA + BA	Wheat and triticale	Injection after anthesis; pot experiment	Affected grain weight, grain number and yield	Sivakumar et al., 2001
ABA + BA + kinetin	Barley	Seed priming followed by foliar application; field under salinity	Increased grain and straw yield under salinity	Sarwat & El-Sherif, 2007

Ethylene

Ethylene / compound	Crop / plant	Concentration / rate	Method / timing	Main reported effect	Reference
Ethephon	Mustard (*Brassica juncea*)	Not reported in review	Exogenous treatment under high N	Increased growth, photosynthesis and N accumulation	Khan et al., 2008
Ethephon	Mustard (*Brassica juncea*)	Not reported in review	Exogenous treatment	Increased photosynthesis; response depended on cultivar and ethylene sensitivity	Khan, 2004
Ethylene	Mustard (*Brassica juncea*)	Not reported in review	Following defoliation	Modified growth and photosynthetic response after defoliation	Khan, 2005
Ethylene	*Poa* spp.	Not reported in review	Exogenous treatment	Altered leaf elongation, with species-dependent responses	Fiorani et al., 2002
Ethephon	Apple (*Starkrimson*)	500 mg L^{-1}	Postharvest treatment before cold storage	Accelerated senescence and altered cuticular-wax composition during storage	Li et al., 2017
Ethephon	Apple	0.2 mmol L^{-1}	Postharvest; fruit subsequently ripened at 20 ± 1°C	Accelerated ripening-related changes, including weight loss, respiration and changes in sugars, acidity and firmness	Cao et al., 2024
Ethephon	Apple (*Northern Spy*)	Concentration-dependent treatments	Early-summer application to young trees	Increased flowering in the following year; stronger response at higher concentration or with a second application	Duyvelshoff and Cline, 2013
Ethylene	Banana	100 ppm	Treatment of fruit tissue	Exogenous 100 ppm ethylene induced preclimacteric banana ripening and increased respiration and endogenous ethylene production	Domínguez & Vendrell, 1994
Ethephon	Banana (*Musa acuminata*, AAB)	1000 ppm	Fully green fruit; postharvest treatment	Induced ripening and significantly altered several physicochemical characteristics	Maduwanthi & Marapana, 2021

Ethylene / compound	Crop / plant	Concentration / rate	Method / timing	Main reported effect	Reference
Ethephon	Orange (*Citrus nobilis*)	700 ppm	Postharvest degreening combined with cool storage	Promoted orange peel colour while maintaining postharvest life	Prabowo et al., 2020
Ethephon	Selayar orange	500 or 1000 ppm	Postharvest degreening	Both concentrations promoted peel colour development compared with untreated fruit	Arzam et al., 2021
Ethephon	Mango (*Tainong No. 1*)	1200 mg L^{-1}	Postharvest ripening treatment	Used to induce postharvest mango ripening	Lin et al., 2026
Ethephon + urea + $CaCO_3$	Pineapple	25 ppm ethephon + 2% urea + 0.04% $CaCO_3$	Flower-induction treatment	Induced >90% flowering within 50 days and produced more uniform ripening and harvesting	Dass et al., 1975
Ethephon + urea	Pineapple	10 ppm ethephon + 2% urea; pH 9	Flower-induction treatment	Induced >90% flowering within 50–60 days	Dass et al., 1976
Ethephon	Pineapple (*Sugarloaf*)	Multiple concentrations	Applied as a flowering inducer	Accelerated and synchronised flowering and fruit maturity and produced more uniform ripening	Norman, 1977

Brassinosteroid

Brassinosteroid / compound	Crop / plant	Concentration / rate	Method / conditions	Main reported effect	Original reference
24-Epibrassinolide	Rice	Not reported in review	Seedlings exposed to chilling at 1–5°C	Reduced electrolyte leakage and malondialdehyde, maintained superoxide dismutase activity and improved chilling resistance	Wang & Zeng, 1993

Brassinosteroid / compound	Crop / plant	Concentration / rate	Method / conditions	Main reported effect	Original reference
Brassinosteroid	Rice	Not reported in review	Plants exposed to unfavourable growth conditions	Reduced growth inhibition caused by adverse conditions	Takematsu et al., 1986
Brassinosteroid	Rice	Not reported in review	Salt-stress conditions	Improved salt tolerance	Takeuchi, 1992; Takeuchi et al., 1992
Synthetic BR	Sugar beet	Not reported in review	Plants subjected to mild drought stress	Ameliorated the effects of drought stress	Schilling et al., 1991
Epibrassinolide	Chickpea (*Cicer arietinum*)	Not reported in review	Juvenile plants under water stress	Improved plant response to water stress	Singh et al., 1993
24-Epibrassinolide	Barley	Not reported in review	Leaves exposed to 500 mM NaCl for 24 h	Protective effect on leaf ultrastructure under severe salt stress	Study reviewed by Clouse & Sasse, 1998
24-Epibrassinolide	*Eucalyptus camaldulensis*	10 µM	Seed germination in 150 mM NaCl	Increased both germination rate and final germination percentage	Sasse et al., 1995
Brassinosteroid	Pak choi (*Brassica chinensis*)	Not reported in review	Hypocotyl treatment	Stimulated hypocotyl elongation and cell-wall relaxation	Wang et al., 1993
Brassinolide	Squash (*Cucurbita maxima*)	Not reported in review	Hypocotyl segments	Stimulated elongation of internal hypocotyl tissues	Tominaga et al., 1994
Brassinosteroid	Carrot (*Daucus carota*)	Not reported in review	Cultured cells	Stimulated cell division and cell enlargement	Sala & Sala, 1985
Brassinosteroids	Potato	Very low concentrations; exact rate not reported in review	Plants challenged with *Phytophthora infestans*	Increased susceptibility to potato late blight; effect was long-lasting	Vasyukova et al., 1994

Jasmonate

Jasmonate / compound	Crop / plant	Concentration / rate	Method / timing	Main reported effect	Original reference
Methyl jasmonate (MeJA)	Banana fruit	Not reported in review	Postharvest treatment under chilling conditions	Induced chilling tolerance and activated jasmonate-related responses	Zhao et al., 2013
Methyl jasmonate (MeJA)	'Hamlin' and 'Valencia' orange	Not reported in review	Applied to mature fruit	Induced fruit abscission, associated with increased ethylene production	Hartmond et al., 2000
Jasmonic acid (JA)	*Arabidopsis thaliana*	Not reported in review	Exogenous application following infection with *Pythium*	Substantially reduced disease incidence in JA-deficient plants, restoring resistance towards wild-type levels	Vijayan et al., 1998
Methyl jasmonate (MeJA)	Tomato	Not reported in review	Plants exposed to airborne MeJA	Induced accumulation of proteinase inhibitors in leaves, demonstrating volatile signalling associated with plant defence	Farmer & Ryan, 1990
Methyl jasmonate (MeJA) + ethylene	Plant experimental systems	Not reported in review	Combined exogenous treatment	Synergistically induced expression of defence-related genes	Xu et al., 1994
JA-Ile macrolactone derivatives	*Nicotiana attenuata*	Not reported in review	Exogenous treatment	Activated jasmonate-mediated defence while reducing the usual negative effects of defence activation on growth and fitness	Study discussed by Howe et al., 2018

Strigolactone

Strigolactone / compound	Crop / plant	Concentration / rate	Method / timing	Main reported effect	Original reference
GR24	Tomato	5 µM	Exogenous treatment under phosphate deficiency	Promoted root-hair elongation	Santoro et al., 2020
GR24	Rice	Not reported in review	Exogenous application to SL-deficient plants	Suppressed excessive tillering/shoot branching	Umehara et al., 2008
GR24	Rice	Not reported in review	Exogenous treatment of roots	Inhibited crown-root elongation	Arite et al., 2012
GR24	Rice	Not reported in review	Exogenous treatment under phosphate- and nitrogen-deficient conditions	Modified root development and root responses to nutrient deficiency	Sun et al., 2014
GR24	Rice	Not reported in review	Exogenous treatment	Inhibited adventitious-root formation	Sun et al., 2015
GR24	Pea	Not reported in review	Applied to SL-deficient plants	Suppressed axillary-bud growth and shoot branching	Studies reviewed by Seto, 2024
GR24	*Arabidopsis thaliana*	50 µM	Treatment under phosphate deficiency	Increased root-hair density in the SL-deficient *max4* mutant	Kapulnik et al., 2011
GR24	*Arabidopsis thaliana*	Not reported in review	Exogenous root treatment	Modified lateral-root formation and root-system architecture	Kapulnik et al., 2011
GR24	*Arabidopsis thaliana* / pea	Not reported in review	Exogenous treatment	Modified adventitious-root formation	Rasmussen et al., 2012

Salicylic acid

Salicylic acid / treatment	Crop / plant	Concentration / rate	Method / timing	Main reported effect	Reference
SA	Apple 'Orin'	1.0 mM	Postharvest immersion for 15 min	Maintained firmness, reduced weight loss and delayed ripening-related changes	Li et al., 2023
SA	Apple	2.5 mM	Postharvest treatment; fruit challenged with Penicillium expansum	Reduced blue mould development and maintained fruit physicochemical quality	da Rocha Neto et al., 2016
SA / methyl salicylate	Apple 'Topaz'	2 mM SA or 2 mM MeSA	Preharvest sprays during fruit maturation	Increased several phenolic compounds but reduced red peel coloration	Gacnik et al., 2021
SA	Satsuma mandarin	2 mM	Postharvest dip for 2 min	Reduced postharvest decay, maintained firmness and enhanced defence-associated responses	Zhu et al., 2016
SA	'Kinnow' mandarin	2–12 mM; 4 mM gave the strongest overall response	Postharvest treatment followed by cold storage	Reduced decay and helped maintain fruit quality during storage	Haider et al., 2020
SA	'Lane Late' sweet orange	2, 4, 6 and 8 mM	Preharvest spray 10 days before harvest	Reduced fruit rot and chilling injury and maintained firmness during cold storage; strongest response at 8 mM	Ahmad et al., 2013
SA	Pineapple 'Comte de Paris'	Not specified here	Preharvest spray and/or postharvest immersion	Reduced internal browning; combined pre- and postharvest treatment produced the strongest response	Lu et al., 2011
SA	Wax apple 'Taaptimjaan'	0.5 and 1.0 mM	Preharvest spray 24 h before harvest	Delayed postharvest deterioration and softening; 0.5 mM gave the more favourable response	Supapvanich et al., 2017

Salicylic acid / treatment	*Crop / plant*	*Concentration / rate*	*Method / timing*	*Main reported effect*	*Reference*
SA, kinetin, ascorbate	*Wheat*	*Not reported in review*	*Seed priming; field conditions under salinity*	*Increased plant growth and grain yield under salinity*	*Afzal et al., 2013*
SA, kinetin, ascorbate	*Wheat*	*Not reported in review*	*Seed priming; field conditions*	*Increased fertility, grain yield and ha*rvest index	Jafar et al., 2012

5. Conclusions

Phytohormones form an integrated regulatory network that coordinates plant growth, development and responses to environmental conditions. Although each hormone has characteristic physiological functions, their effects cannot be understood completely when considered in isolation. Auxins, cytokinins, gibberellins, abscisic acid, ethylene, brassinosteroids, jasmonates, strigolactones and salicylic acid interact at multiple levels, including their biosynthesis, transport, perception and signalling. These interactions allow plants to coordinate processes as diverse as cell division and expansion, root and shoot development, flowering, fruit development, dormancy, senescence and responses to biotic and abiotic stresses.

A central aspect of phytohormone activity is that the physiological response depends not simply on the presence or absolute concentration of a hormone, but also on its spatial distribution, the sensitivity of the responding tissue, the developmental stage of the plant and its interaction with other hormonal pathways. The same hormone can therefore produce different, and sometimes opposing, responses depending on the tissue or physiological context. Hormonal balance is consequently a fundamental component of plant regulation, as illustrated by interactions such as auxin–cytokinin in root and shoot development, GA–ABA in dormancy and germination, BR–GA in growth, JA–SA in defence, and SL–auxin–cytokinin in shoot branching.

These characteristics are particularly important when phytohormones are manipulated in agriculture. Exogenous applications of natural hormones, synthetic analogues or other plant growth regulators can influence propagation, plant architecture, flowering, fruit set and

development, ripening, senescence, postharvest quality and responses to environmental stress. However, the examples examined in this review demonstrate that these responses are strongly dependent on concentration, application method, timing, crop species and developmental stage. Increasing the applied concentration does not necessarily increase the desired response, and inappropriate concentrations or timing may produce negligible or undesirable effects. Agricultural use of phytohormones therefore requires treatments to be considered within the physiological context of the crop rather than assuming a universally beneficial concentration or response.

Understanding phytohormone function and, particularly, the balance between different hormonal pathways provides a physiological basis for more precise manipulation of crop growth and development. Future agricultural applications should therefore focus not only on individual hormones but also on how their concentration, timing and interactions influence the overall hormonal status of the plant. Such an approach can improve the rational use of plant growth regulators and help translate knowledge of phytohormone physiology into more consistent and targeted crop-management strategies.

6. References

Afzal I, Basra SMA, Cheema MA, Farooq M, Jafar MZ, Shahid M, Yasmeen A. 2013. Seed priming: A shotgun approach for alleviation of salt stress in wheat. *International Journal of Agriculture and Biology.* 15: 1199–1203.

Ahmad S, Singh Z, Khan AS, Iqbal Z. 2013. Preharvest application of salicylic acid maintain the rind textural properties and reduce fruit rot and chilling injury of sweet orange during cold storage. *Pakistan Journal of Agricultural Sciences.* 50: 559–569.

Alizadeh O, Haghighi BJ, Ordookhani K. 2010. The effects of exogenous cytokinin application on sink size in bread wheat (Triticum aestivum). *African Journal of Agricultural Research.* 5: 2893–2898.

Argueso CT, Kieber JJ. 2024. Cytokinin: From autoclaved DNA to two-component signaling. *The Plant Cell.* 36: 1429–1450.

Arite T, Kameoka H, Kyozuka J. 2012. Strigolactone positively controls crown root elongation in rice. *Journal of Plant Growth Regulation.* 31: 165–172.

Arve LE, Torre S. 2015. Ethylene is involved in high air humidity promoted stomatal opening of tomato (*Lycopersicon esculentum*) leaves. *Functional Plant Biology.* 42: 376–386.

Arzam TS, Baba B, Supriyadi S. 2021. Effect of ethephon concentration on degreening process of Selayar orange (Citrus reticulata L.). *IOP Conference Series: Earth and Environmental Science.* 807: 042054.

Aziz ABA, Hegazi ES, Yehia TA, Kassim NE, Mahmoud TSM. 2011. Growth, flowering and fruiting of Manzanillo olive trees as affected by benzyladenine. *Journal of Horticultural Science & Ornamental Plants.* 3: 244–251.

Barbier FF, Dun EA, Kerr SC, Chabikwa TG, Beveridge CA. 2023. An update on the signals controlling shoot branching. *Trends in Plant Science.* 28: 100–112.

Batlang U. 2008. Benzyladenine plus gibberellins (GA4+7) increase fruit size and yield in greenhouse-grown hot pepper (Capsicum annuum L.). *Journal of Biological Sciences.* 8: 659–662.

Bialek K, Meudt WJ, Cohen JD. 1983. Indole-3-acetic acid (IAA) and IAA conjugates applied to bean stem sections. IAA content and the growth response. *Plant Physiology.* 73: 130–134.

Boudsocq M, Barbier-Brygoo H, Laurière C. 2004. Identification of nine sucrose nonfermenting 1-related protein kinases 2 activated by hyperosmotic and saline stresses in Arabidopsis thaliana. *Journal of Biological Chemistry.* 279: 41758–41766.

Browse J. 2009. Jasmonate passes muster: A receptor and targets for the defense hormone. *Annual Review of Plant Biology.* 60: 183–205.

Burke JJ. 2011. 6-Benzyladenine enhancement of cotton. *Journal of Cotton Science.* 15: 206–214.

Cao Y, Lv J, Tai R, Tang W, Ge Y. 2024. Impacts of 1-methylcyclopropene (1-MCP) and ethephon treatments on expression of aquaporin (AQP) genes during apple fruit ripening. *Scientia Horticulturae.* 331: 113126.

Chen X, Bao J, Chen Y, Chen T, Zhang C, Huang X. 2012. Effect of hormone treatments on deformed fruit development in pear. *African Journal of Biotechnology.* 11: 10207–10214.

Clouse SD, Sasse JM. 1998. Brassinosteroids: Essential regulators of plant growth and development. *Annual Review of Plant Physiology and Plant Molecular Biology.* 49: 427–451.

Cohen JD, Strader LC. 2024. An auxin research odyssey: 1989–2023. *Plant Physiology.* 195: 164–178.

Criado MV, Caputo C, Roberts IN, Castro MA, Barneix AJ. 2009. Cytokinin-induced changes of nitrogen remobilization and chloroplast ultrastructure in wheat (Triticum aestivum). *Journal of Plant Physiology.* 166: 1775–1785.

da Rocha Neto AC, Maraschin M, Di Piero RM. 2016. Antifungal activity of salicylic acid against *Penicillium expansum* and its possible mechanisms of action. *International Journal of Food Microbiology.* 215: 64–70.

Dass HC, Randhawa GS, Negi SP. 1975. Flowering in pineapple as influenced by ethephon and its combinations with urea and calcium carbonate. *Scientia Horticulturae.* 3: 231–238.

Dass HC, Randhawa GS, Negi SP. 1976. Effect of pH and urea on the efficacy of ethephon for induction of flowering in pineapple. *Scientia Horticulturae.* 5: 265–268.

Dindas J, Scherzer S, Roelfsema MRG, von Meyer K, Müller HM, Al-Rasheid KAS, Palme K, Dietrich P, Becker D, Bennett MJ, Hedrich R. 2018. AUX1-mediated root hair auxin influx governs SCF^TIR1/AFB-type Ca^{2+} signaling. *Nature Communications.* 9: 1174.

Domínguez M, Vendrell M. 1994. Effect of ethylene treatment on ethylene production, EFE activity and ACC levels in peel and pulp of banana fruit. *Postharvest Biology and Technology.* 4: 167–177.

Du M, Spalding EP, Gray WM. 2020. Rapid auxin-mediated cell expansion. *Annual Review of Plant Biology.* 71: 379–402.

Durrani F, Subhan M, Mehmood S, Abbas S. 2010. Effect of NAA and benzyladenine on growth and yield of spinach. *Pakistan Journal of Agricultural Research.* 23: 126–130.

Duyvelshoff C, Cline JA. 2013. Ethephon and prohexadione-calcium influence the flowering, early yield, and vegetative growth of young 'Northern Spy' apple trees. *Scientia Horticulturae.* 151: 128–134.

Elfving DC, Cline RA. 1993. Benzyladenine and other chemicals for thinning 'Empire' apple trees. *Journal of the American Society for Horticultural Science.* 118: 593–598.

Emongor VE. 2007. Gibberellic acid (GA_3) influence on vegetative growth, nodulation and yield of cowpea (*Vigna unguiculata* L. Walp.). *Journal of Agronomy.* 6: 509–517.

Farmer EE, Ryan CA. 1990. Interplant communication: Airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. *Proceedings of the National Academy of Sciences of the United States of America.* 87: 7713–7716.

Fendrych M, Akhmanova M, Merrin J, Glanc M, Hagihara S, Takahashi K, Uchida N, Torii KU, Friml J. 2018. Rapid and reversible root growth inhibition by TIR1 auxin signalling. *Nature Plants.* 4: 453–459.

Fiorani F, Bögemann GM, Visser EJW, Lambers H, Voesenek LACJ. 2002. Ethylene emission and responsiveness to applied ethylene vary among *Poa* species that inherently differ in leaf elongation rates. *Plant Physiology.* 129: 1382–1390.

Gacnik S, Veberič R, Hudina M, Marinovic S, Halbwirth H, Mikulič-Petkovšek M. 2021. Salicylic and methyl salicylic acid affect quality and phenolic profile of apple fruits three weeks before the harvest. *Plants.* 10: 1807.

Gadallah MAA. 1999. Effects of kinetin on growth, grain yield and some mineral elements in wheat plants growing under excess salinity and oxygen deficiency. *Plant Growth Regulation.* 27: 63–74.

Gao J, Zhuang S, Zhang W. 2024. Advances in plant auxin biology: Synthesis, metabolism, signaling, interaction with other hormones, and roles under abiotic stress. *Plants.* 13: 2523.

Gąstoł M, Domagała-Świątkiewicz I, Bijak M. 2012. The effect of different bioregulators on lateral shoot formation in maiden apple trees. *Folia Horticulturae.* 24: 147–152.

Gupta NK, Gupta S, Shukla DS, Deshmukh PS. 2003. Differential responses of BA injection on yield and specific grain growth in contrasting genotypes of wheat (*Triticum aestivum* L.). *Plant Growth Regulation.* 40: 201–205.

Gupta S, Agarwal VP, Gupta NK. 2012. Efficacy of putrescine and benzyladenine on photosynthesis and productivity in relation to drought tolerance in wheat (*Triticum aestivum*). *Physiology and Molecular Biology of Plants.* 18: 331–336.

Haider ST, Ahmad S, Khan AS, Anjum MA, Nasir M, Naz S. 2020. Effects of salicylic acid on postharvest fruit quality of 'Kinnow' mandarin under cold storage. *Scientia Horticulturae.* 259: 108843.

Hammes UZ, Pedersen BP. 2024. Auxin transporters: The biochemical view. *Cold Spring Harbor Perspectives in Biology.* 16: a040061.

Harrison MA, Kaufman PB. 1980. Hormonal regulation of lateral bud (tiller) release in oats (*Avena sativa* L.). *Plant Physiology.* 66: 1123–1127.

Hartmond U, Yuan R, Burns JK, Grant A, Kender WJ. 2000. Citrus fruit abscission induced by methyl-jasmonate. *Journal of the American Society for Horticultural Science.* 125: 547–552.

Heimovaara-Dijkstra S, Heistek JC, Wang M. 1994. Counteractive effects of ABA and GA_3 on extracellular Ca^{2+} in barley aleurone protoplasts. *New Phytologist.* 127: 333–340.

Hosseini SM, Poustini K, Ahmadi A. 2008. Effects of foliar application of BAP on source and sink strength in four six-rowed barley cultivars. *Plant Growth Regulation.* 54: 231–239.

Howe GA, Major IT, Koo AJ. 2018. Modularity in jasmonate signaling for multistress resilience. *Annual Review of Plant Biology.* 69: 387–415.

Hwang IS, Choi DS, Kim NH, Kim DS, Hwang BK. 2014. Pathogenesis-related protein 4b interacts with leucine-rich repeat protein 1 to suppress PR4b-triggered cell death and defense response in pepper. *The Plant Journal.* 77: 521–533.

Ibrahim ME, Bekheta MA, El-Moursi A, Gaafar NA. 2007. Improvement of growth and seed yield quality of *Vicia faba* L. plants as affected by application of some bioregulators. *Australian Journal of Basic and Applied Sciences.* 1: 657–666.

Iqbal M, Ashraf M, Jamil A. 2006. Seed enhancement with cytokinins: Changes in growth and grain yield in salt stressed wheat plants. *Plant Growth Regulation.* 50: 29–39.

Jafar MZ, Farooq M, Cheema MA, Afzal I, Basra SMA, Wahid MA, Aziz T, Shahid M. 2012. Improving the performance of wheat by seed priming under saline conditions. *Journal of Agronomy and Crop Science.* 198: 38–45.

Kapulnik Y, Delaux PM, Resnick N, Mayzlish-Gati E, Wininger S, Bhattacharya C, Séjalon-Delmas N, Combier JP, Bécard G, Belausov E, Beeckman T, Dor E, Hershenhorn J, Koltai H. 2011. Strigolactones affect lateral root formation and root-hair elongation in *Arabidopsis*. *Planta.* 233: 209–216.

Kariali E, Mohapatra PK. 2007. Hormonal regulation of tiller dynamics in differentially-tillering rice cultivars. *Plant Growth Regulation.* 53: 215–223.

Khalid S, Malik AU, Khan AS, Jamil A. 2012. Influence of exogenous applications of plant growth regulators on fruit quality of young 'Kinnow' mandarin (*Citrus nobilis × C. deliciosa*) trees. *International Journal of Agriculture and Biology.* 14: 229–234.

Khan NA. 2004. An evaluation of the effects of exogenous ethephon, an ethylene releasing compound, on photosynthesis of mustard (*Brassica juncea*) cultivars that differ in photosynthetic capacity. *BMC Plant Biology.* 4: 21.

Khan NA. 2005. The influence of exogenous ethylene on growth and photosynthesis of mustard (*Brassica juncea*) following defoliation. *Scientia Horticulturae.* 105: 499–505.

Khan NA, Mir MR, Nazar R, Singh S. 2008. The application of ethephon (an ethylene releaser) increases growth, photosynthesis and nitrogen accumulation in mustard (*Brassica juncea* L.) under high nitrogen levels. *Plant Biology.* 10: 534–538.

Kieber JJ, Schaller GE. 2018. Cytokinin signaling in plant development. *Development.* 145: dev149344.

Kim JG, Takami Y, Mizugami T, Beppu K, Fukuda T, Kataoka I. 2006. CPPU application on size and quality of hardy kiwifruit. *Scientia Horticulturae.* 110: 219–222.

Koprna R, De Diego N, Dundálková L, Spíchal L. 2016. Use of cytokinins as agrochemicals. *Bioorganic & Medicinal Chemistry.* 24: 484–492.

Kwak JM, Moon JH, Murata Y, Kuchitsu K, Leonhardt N, DeLong A, Schroeder JI. 2002. Disruption of a guard cell-expressed protein phosphatase 2A regulatory subunit, RCN1, confers abscisic acid insensitivity in Arabidopsis. *The Plant Cell.* 14: 2849–2861.

Langridge J. 1957. Effect of day-length and gibberellic acid on the flowering of *Arabidopsis*. *Nature.* 180: 36–37.

Li J, Yan J, Li Y, Wang Y, Wang H, Liu Z. 2017. Effects of ethephon on cuticular wax composition and fruit quality of 'Starkrimson' apples during cold storage. *Scientia Horticulturae.* 225: 250–256.

Li L, Li C, Sun J, Xin M, Yi P, He X, Sheng J, Zhou Z, Ling D, Zheng F. 2023. Salicylic acid treatment maintains postharvest quality of apple fruit by regulating antioxidant capacity and ethylene metabolism. *Scientia Horticulturae.* 307: 111500.

Lin Q, Li L, Sun J, Wang R, Ji N, Yang X, Xin Q, Zhou X, Zhang M, Zhao S, Liu B, Hao G. 2026. Effects of combined treatment of ethephon and red light irradiation on post-harvest mango ripening. *Scientia Horticulturae.* 365: 114944.

Lu X, Sun D, Li Y, Shi W, Sun G. 2011. Pre- and post-harvest salicylic acid treatments alleviate internal browning and maintain quality of winter pineapple fruit. *Scientia Horticulturae.* 130: 97–101.

Maduwanthi SDT, Marapana RAUJ. 2021. Induced ripening agents and their effect on fruit quality of banana. *International Journal of Food Science.* 2021: 2520179.

Malik MNA, Din SU, Makhdum MI. 2002. Effects of thidiazuron on growth and yield of cotton. *Asian Journal of Plant Sciences.* 1: 42–43.

Miyoshi K, Sato T. 2011. The effects of kinetin and gibberellin on the germination of dehusked seeds of indica and japonica rice (*Oryza sativa* L.) under anaerobic and aerobic conditions. *Annals of Botany.* 107: 1159–1167.

Mo W, Tang W, Du Y, Jing Y, Bu Q, Lin R. 2024. Abscisic acid: A conserved hormone in plants and humans and a promising aid to combat diseases. *Frontiers in Plant Science.* 15: 1437184.

Moghadam EG, Zamanipour M. 2013. Induction of lateral branching in sweet cherry (*Prunus avium* L. cvs. Siah Mashhad & Dovomras) trees in nursery. *Journal of Agricultural Science.* 5: 23–30.

Naeem M, Bhatti I, Ahmad RH, Ashraf MY. 2004. Effect of some growth hormones (GA_3, IAA and kinetin) on the morphology and early or delayed initiation of bud of lentil (*Lens culinaris* Medik.). *Pakistan Journal of Botany.* 36: 801–809.

Norman JC. 1977. Effect of ethephon on flowering, fruit development and yield of pineapple. *Scientia Horticulturae.* 7: 257–267.

Patel RZ, Mohapatra PK. 1992. Regulation of spikelet development in rice by hormones. *Journal of Experimental Botany.* 43: 257–262.

Peltonen-Sainio P. 1997. Nitrogen fertilizer and foliar application of cytokinin affect spikelet and floret set and survival in oat. *Field Crops Research.* 49: 169–176.

Prabowo A, Yulianingsih R, Maharani DM, Sugiarto Y. 2020. Effect of ethephon and storage temperature on degreening of citrus fruit. *International Journal of Food Science.* 2020: 6853627.

Qi X, Li Q, Ma X, Qian C, Wang H, Ren N, Shen C, Huang S, Xu X, Xu Q, Chen X. 2023. Naphthaleneacetic acid promotes adventitious root development in cucumber under waterlogging stress by regulating auxin transport and signalling. *Plant Physiology and Biochemistry.* 196: 333–344.

Rasmussen A, Mason MG, De Cuyper C, Brewer PB, Herold S, Agusti J, Geelen D, Greb T, Goormachtig S, Beeckman T, Beveridge CA. 2012. Strigolactones suppress adventitious rooting in *Arabidopsis* and pea. *Plant Physiology.* 158: 1976–1987.

Ray S, Choudhuri MA. 1981. Effects of plant growth regulators on grain-filling and yield of rice. *Annals of Botany.* 47: 755–758.

Richards DE, King KE, Ait-ali T, Harberd NP. 2001. How gibberellin regulates plant growth and development: A molecular genetic analysis of gibberellin signaling. *Annual Review of Plant Physiology and Plant Molecular Biology.* 52: 67–88.

Sakakibara H. 2006. Cytokinins: Activity, biosynthesis, and translocation. *Annual Review of Plant Biology.* 57: 431–449.

Sala C, Sala F. 1985. Effect of brassinosteroid on cell division and enlargement in cultured carrot (*Daucus carota* L.) cells. *Plant Cell Reports.* 4: 144–147.

Santoro V, Schiavon M, Gresta F, Ertani A, Cardinale F, Sturrock CJ, Celi L, Schubert A. 2020. Strigolactones control root system architecture and tip anatomy in *Solanum lycopersicum* L. plants under P starvation. *Plants.* 9: 612.

Sarwat MI, El-Sherif MH. 2007. Increasing salt tolerance in some barley genotypes (*Hordeum vulgare*) by using kinetin and benzyladenine. *World Journal of Agricultural Sciences.* 3: 617–629.

Sasse JM, Smith R, Hudson I. 1995. Effect of 24-epibrassinolide on germination of seeds of *Eucalyptus camaldulensis* in saline conditions. *Proceedings of the Plant Growth Regulation Society of America.* 22: 136–141.

Schilling G, Schiller C, Otto S. 1991. Influence of brassinosteroids on organ relations and enzyme activities of sugar-beet plants. In: Cutler HG, Yokota T, Adam G, editors. *Brassinosteroids: Chemistry, Bioactivity, and Applications.* ACS Symposium Series 474. Washington, DC: American Chemical Society. pp. 208–219.

Seto Y. 2024. Latest knowledge on strigolactone biosynthesis and perception. *Bioscience, Biotechnology, and Biochemistry.* 88: 1–7

Sharif R, Dale JE. 1980. Growth-regulating substances and the growth of tiller buds in barley; effects of IAA and cytokinins. *Journal of Experimental Botany.* 31: 921–930.

Singh J, Nakamura S, Ota Y. 1993. Effect of epibrassinolide on gram (*Cicer arietinum*) plants grown under water stress in the juvenile stage. *Indian Journal of Agricultural Sciences.* 63: 395–397.

Sivakumar T, Virendranath, Srivastava GC. 2001. Effects of benzyl adenine and abscisic acid on grain yield and yield components in triticale and wheat. *Journal of Agronomy and Crop Science.* 186: 43–46.

Steber CM, Cooney SE, McCourt P. 1998. Isolation of the GA-response mutant sly1 as a suppressor of ABI1-1 in Arabidopsis thaliana. *Genetics.* 149: 509–521.

Stern RA, Flaishman MA. 2003. Benzyladenine effects on fruit size, fruit thinning and return yield of 'Spadona' and 'Coscia' pear. *Scientia Horticulturae.* 98: 499–504.

Sun H, Tao J, Liu S, Huang S, Chen S, Xie X, Yoneyama K, Zhang Y, Xu G. 2014. Strigolactones are involved in phosphate- and nitrate-deficiency-induced root development and auxin transport in rice. *Journal of Experimental Botany.* 65: 6735–6746.

Sun H, Tao J, Hou M, Huang S, Chen S, Liang Z, Xie T, Wei Y, Xie X, Yoneyama K, Xu G, Zhang Y. 2015. A strigolactone signal is required for adventitious root formation in rice. *Annals of Botany.* 115: 1155–1162.

Sun Y, Wang C, Wang N, Jiang X, Mao H, Zhu C, Wen F, Wang X, Lu Z, Yue G, et al. 2022. Manipulation of auxin transport in the Arabidopsis inflorescence stem by strigolactones. *Plant Physiology.* 189: 1032–1045.

Supapvanich S, Mitsang P, Youryon P. 2017. Preharvest salicylic acid application maintains physicochemical quality of 'Taaptimjaan' wax apple fruit during short-term storage. *Scientia Horticulturae.* 215: 178–183.

Takematsu T, Takeuchi Y, Choi CD. 1986. Overcoming effects of brassinosteroids on growth inhibition of rice caused by unfavourable growth conditions. *Shokucho.* 20: 2–12.

Takeuchi Y. 1992. Studies on physiology and applications of brassinosteroids. *Shokubutsu no Kagaku Chosetsu.* 27: 1–10.

Takeuchi Y, Ogasawara M, Konnai M, Takematsu T. 1992. Application of brassinosteroids in agriculture in Japan. *Proceedings of the Plant Growth Regulation Society of America.* 19: 343–352.

Tominaga R, Sakurai N, Kuraishi S. 1994. Brassinolide-induced elongation of inner tissues of segments of squash (*Cucurbita maxima* Duch.) hypocotyls. *Plant and Cell Physiology.* 35: 1103–1106.

Umehara M, Hanada A, Yoshida S, Akiyama K, Arite T, Takeda-Kamiya N, Magome H, Kamiya Y, Shirasu K, Yoneyama K, Kyozuka J, Yamaguchi S. 2008. Inhibition of shoot branching by new terpenoid plant hormones. *Nature.* 455: 195–200.

Vanstraelen M, Benková E. 2012. Hormonal interactions in the regulation of plant development. *Annual Review of Cell and Developmental Biology.* 28: 463–487.

Vasyukova NI, Chalenko GI, Kaneva IM, Khripach VA. 1994. Brassinosteroids and potato blight. *Applied Biochemistry and Microbiology.* 30: 464–470.

Vijayan P, Shockey J, Lévesque CA, Cook RJ, Browse J. 1998. A role for jasmonate in pathogen defense of Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America.* 95: 7209–7214.

Wang B, Zeng G. 1993. Effect of epibrassinolide on the resistance of rice seedlings to chilling injury. *Zhongguo Shuidao Kexue.* 7: 53–55.

Wang Q, Zhang F, Smith DL. 1996. Application of GA_3 and kinetin to improve corn and soybean seedling emergence at low temperature. *Environmental and Experimental Botany.* 36: 377–383.

Wang TW, Cosgrove DJ, Arteca RN. 1993. Brassinosteroid stimulation of hypocotyl elongation and wall relaxation in pakchoi (*Brassica chinensis* cv Lei-Choi). *Plant Physiology.* 101: 965–968.

Wang X, Wen H, Suprun A, Zhu H. 2025. Ethylene signaling in regulating plant growth, development, and stress responses. *Plants.* 14: 309.

Wang Z, Cao W, Dai T, Zhou Q. 2001. Effects of exogenous hormones on floret development and grain set in wheat. *Plant Growth Regulation.* 35: 225–231.

Wang ZY, Bai MY, Oh E, Zhu JY. 2012. Brassinosteroid signaling network and regulation of photomorphogenesis. *Annual Review of Genetics.* 46: 701–724.

Warrier A, Bhardwaj SN, Pande PC. 1987. Effect of kinetin on water status and yield in wheat under water stress. *Plant and Cell Physiology.* 28: 735–739.

Williams RH, Cartwright PM. 1980. The effect of applications of a synthetic cytokinin on shoot dominance and grain yield in spring barley. *Annals of Botany.* 46: 445–452.

Wismer PT, Proctor JTA, Elfving DC. 1995. Benzyladenine affects cell division and cell size during apple fruit thinning. *Journal of the American Society for Horticultural Science.* 120: 802–807.

Xu Y, Chang PFL, Liu D, Narasimhan ML, Raghothama KG, Hasegawa PM, Bressan RA. 1994. Plant defense genes are synergistically induced by ethylene and methyl jasmonate. *The Plant Cell.* 6: 1077–1085

Xue L, Zhang JJ, Xue HW. 2021. Characterization of the complex roles of brassinosteroids in plant growth and development. *International Journal of Molecular Sciences.* 22: 12822.

Yasmeen A, Basra SMA, Farooq M, Rehman HU, Hussain N, Athar HR. 2013. Exogenous application of moringa leaf extract modulates the antioxidant enzyme system to improve wheat performance under saline conditions. *Plant Growth Regulation.* 69: 225–233.

Yehia TA, Hassan HSA. 2005. Effect of some chemical treatments on fruiting of 'Le Conte' pear trees. *Journal of Applied Sciences Research.* 1: 35–42.

Yuan R, Greene DW. 2000. Benzyladenine as a chemical thinner for 'McIntosh' apples. I. Fruit thinning effects and associated relationships with photosynthesis, assimilate translocation, and nonstructural carbohydrates. *Journal of the American Society for Horticultural Science.* 125: 169–176.

Zhang Y, Berman A, Shani E. 2023. Plant hormone transport and localization: Signaling molecules on the move. *Annual Review of Plant Biology.* 74: 453–479.

Zhao ML, Wang JN, Shan W, Fan JG, Kuang JF, Wu KQ, Li XP, Chen WX, He FY, Chen JY, Lu WJ. 2013. Induction of jasmonate signalling regulators MaMYC2s and their physical interactions with MaICE1 in methyl jasmonate-induced chilling tolerance in banana fruit. *Plant, Cell & Environment.* 36: 30–51.

Zhu F, Chen J, Xiao X, Zhang M, Yun Z, Zeng Y, Xu J, Cheng Y, Deng X. 2016. Salicylic acid treatment reduces the rot of postharvest citrus fruit by inducing the accumulation of H_2O_2, primary metabolites and lipophilic polymethoxylated flavones. *Food Chemistry.* 207: 68–74.