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REVIEW

Phytohormones: Structure, Physiological Effects, and Hormone Interactions of Classical and Newly Discovered Plant Growth Regulators

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ABSTRACT: Plants utilize a complex network of phytohormones to adapt to environmental stressors and coordinate their growth and development. Along with the classic five hormones (auxin, cytokinin, gibberellin, abscisic acid, and ethylene), newly discovered classes of hormones such as brassinosteroids, salicylic acid, jasmonic acid, strigolactones, karrikins, and peptide hormones regulate almost all aspects of plant physiology. This review article has been prepared with the needs of researchers and practitioners involved in plant production in mind. Phytohormones are systematically discussed in terms of their discovery history, chemical structures, fundamental roles in plant physiology, and interhormone interactions. Each hormone class is examined under four main headings: discovery and historical development, chemical structure and types, physiological effects, and interactions with other hormones. This study aims to provide a practical, up-to-date reference for decision-making in agricultural applications, without getting bogged down in complex molecular mechanisms. Emphasis is placed on stress tolerance, growth-defense balance, and hormone crosstalk.

KEYWORDS: Abscisic acid; auxin; brassinosteroid; cytokinin; ethylene; gibberellin; jasmonic acid; karrikin; peptide hormones; plant physiology; salicylic acid; stress tolerance; strigolactone

1 Introduction

Plants utilize an extremely complex hormonal communication network to respond to environmental stimuli, regulate their growth and development, and adapt to stressful conditions. The fundamental elements of this network, phytohormones, are organic compounds synthesized by plant metabolism, effective at low concentrations, and generally transported to tissues far from the site of synthesis.

Although phytohormones differ significantly in their chemical structure (terpenoid, phenolic, fatty acid derivative, gas, and peptide), the regions where they are synthesized (apical meristem, root, leaf, etc.), and their transport mechanisms (polar transport, phloem, xylem, diffusion), they all play a coordinated role in almost every stage of the plant's life cycle (germination, growth, flowering, fruit ripening, senescence, and stress response). In addition to the classic five hormones (auxin, cytokinin, gibberellin, abscisic acid, and ethylene), new classes such as brassinosteroids, salicylic acid, jasmonic acid, strigolactones, karrikins, and peptide hormones have been added.

This review article has been prepared with the needs of agricultural engineers and practicing researchers working in plant breeding and propagation in mind. The discovery history of phytohormones, their chemical structure, fundamental physiological effects, and interactions with other hormones have been systematically examined. Each hormone class has been studied under four main headings:

- Discovery and Historical Development
- Chemical Structure and Types
- Role in Plant Physiology
- Interactions with Other Hormones

The aim of this study is to create a practical and up-to-date reference that can be used in decision-making processes in agricultural applications, without getting bogged down in complex hormone signaling mechanisms. Table 1 summarizes a general comparison of phytohormone classes.

Table 1: A general overview of phytohormone classes: chemical structure, synthesis site, transport, and basic physiological function.

Hormone Class	Chemical Structure Group	Main Synthesis Site	Transportation Route	Basic Physiological Function	Discovery
Auxin (IAA)	Indole derivative organic acid	Apical meristem, young leaves	Polar Auxin transport (PAT) + phloem	Cell elongation, tropism, root formation, branch pruning.	1926
Cytokinin (CK)	Adenine derivative/Phenylurea derivative	Root apical meristem	Xylem (upwards)	Cell division, shoot formation, chlorophyll maintenance, aging delay.	1955
Giberellin (GA)	Diterpenoid (terpenoid)	Young leaf, embryo, seed, cambium	Phloem + xylem (bidirectional)	Stem elongation, seed germination, flowering, parthenocarpy.	1926–1938
Abscisic Acid (ABA)	Sesquiterpenoid	Leaf mesophyll cells, root	Phloem + xylem (bidirectional)	Stomatal closure, seed dormancy, stress response, storage organ dormancy.	1963
Ethylene (C_2H_4)	Simple gas alkene	All mature and stressed tissues	Diffusion (gas)	Fruit ripening, senescence, organ drop, stress response.	1934
Brassinosteroid (BR)	Polycyclic steroid	Young leaves, pollen, shoot tips	Short distance (paracrine)	Cell elongation/division, vascular development, stress tolerance, pollen tube growth.	1979
Salicylic Acid (SA)	Phenolic acid	Leaf (infection area and distant tissues)	Phloem (as methyl SA)	Systemic acquired resistance (SAR), pathogen defense, flowering, abiotic stress.	1990s
Jasmonic Acid (JA)	Oxylipin (fatty acid derivative)	Wound area, leaf, flower	Phloem (JA-Ile, methyl JA)	Injury and insect defense, flower development, root growth inhibition, maturation.	1987
Strigolactone (SL)	Carotenoid derivative (tersenoid)	Root cortex and vascular tissue	Apoplasmic (root exudate)	Pruning inhibition, AMF symbiosis, root architecture, stimulation for parasitic plants.	2008
Karrikin (KAR)	Butenolide (furanone)	Exogenous (fire smoke); endogenous KL (KAI2 Ligand) is unknown	Soil solution/diffusion	Seed germination, seedling development, photomorphogenesis, stress tolerance.	2004/2010
Peptide Hormones	Small peptide (4–80 amino acids)	Meristem, vascular tissue, wound area	Apiplastic/phloem	Meristematic homeostasis, organ shedding, root development, defense, stomatal development.	1991–2000s

2 The Classical Five: The First Historically Recognized Phytohormones

2.1 Auxin

(a) Discovery and Historical Development: The basis of auxin research lies in experiments conducted by Charles Darwin and his son Francis in 1880 on phototropism in oat coleoptiles. Darwin and his son demonstrated that the tip of the coleoptile detected light and transmitted a signal downwards; however, they were unable to determine the chemical nature of this signal. In 1913, Peter Boysen-Jensen confirmed that a chemical substance was transported downwards by sealing the coleoptile tip with gelatin. Arpad Paal experimentally proved in 1919 that this substance initiated growth.

In 1926, the Dutch botanist Frits Went, in his experiments with *Avena coleoptiles*, transferred the active growth compound onto agar blocks and named it 'Auxin' (from the Greek auxein, meaning 'to grow'). In 1931, Kögl and Haagen-Smit isolated indole-3-acetic acid (IAA) from human urine, and it was later confirmed that this compound was the plant's naturally occurring auxin. Auxin was the first phytohormone identified in history and represents a turning point in the development of plant science. Synthetic auxin analogs (2,4-D, NAA), developed in the 1940s and 1950s, have found widespread use in agriculture as herbicides and growth regulators [1–3].

(b) Chemical Structure and Types: Auxins are aromatic organic acids that essentially have an indole ring and a carboxylate group. IAA (Indole-3-acetic acid) is the naturally occurring plant auxin and is synthesized from the amino acid tryptophan. Structural analogs and synthetic derivatives also exhibit auxin-like effects (Table 2).

Table 2: Major auxin types and their general characteristics.

Class	Main Compound	Building Type	Source
Natural indole derivatives	IAA (Indole-3-acetic acid)	Indole + acetic acid chain	All higher plants; dominant endogenous auxin.
Natural indole derivatives	IBA (Indole-3-butyric acid)	Indole + butyric acid chain	It strongly stimulates root formation; in some species, it is endogenous.
Natural indole derivatives	PAA (Phenylacetic acid)	Phenyl + acetic acid	In some plants; weak activity.
Synthetic naphthalene derivatives	NAA (Naphthalene acetic acid)	Naphthalene + acetic acid	Root growth stimulant; for commercial use.
Synthetic phenoxy derivatives	2,4-D, MCPA	Phenyl-oxy + acetic acid	Herbicides are toxic in high doses.
Synthetic derivatives	Picloram, dicamba	Pyridine/benzoic acid derivatives	Broadleaf weed killer.

(c) Role in Plant Physiology: Auxin is the 'master regulator' of plant physiology and plays a decisive role in many fundamental processes.

- **Cell Elongation and Growth:** Auxin promotes an increase in cell volume by relaxing cell walls through acidification (acid growth theory). This effect is particularly pronounced in the shoot stem and the apical region of the coleoptile. As auxin concentration increases, cell elongation accelerates; however, exceeding the optimum dose reverses growth. Roots and shoots respond differently to the same auxin concentration: one concentration may inhibit the root while stimulating the shoot [4].
- **Phototropism and Gravitropism:** The plant's orientation towards light (phototropism) and growth in the direction of gravity (gravitropism) occur due to the asymmetry of auxin distribution. In a shoot brought to a horizontal position, auxin concentrates on the lower surface due to the effect of gravity, causing that side to elongate faster and the shoot to rise upwards (positive gravitropism). In the root, however, the same auxin accumulation suppresses growth, resulting in downward growth (positive gravitropism).
- **Apical Dominance:** Auxin, released from the apical meristem at the tip of the plant's main shoot, is transported downwards, suppressing the development of lateral buds. This phenomenon is known

as 'apical dominance' and sets the stage for the plant to form a single main stem. When the apical meristem is removed, the lateral buds are activated, initiating more branched growth.

- **Adventitious and Lateral Root Formation:** Auxin, particularly the IBA form, strongly stimulates adventitious root formation. This property is widely used in plant propagation via cuttings. A certain auxin accumulation is also necessary for initiating lateral roots; however, very high concentrations can suppress lateral root development.
- **Vascular Differentiation:** Auxin influx directs the differentiation of conducting tissues such as xylem and phloem. Auxin gradients trigger the transformation of procambium cells into conducting tubules, ensuring the continuous renewal of the vascular system.
- **Fruit Development:** After fertilization, the seed embryo synthesizes high amounts of auxin; this auxin promotes the growth and maturation of fruit tissue. Parthenocarpic (seedless) fruit formation can also be triggered by exogenous auxin application; this principle is used in agricultural applications in grapes, tomatoes, and other cultivated plants.
- **Leaf Drop and Organ Abscision:** As long as auxin is maintained at sufficient concentrations along the leaf petiole, it inhibits the development of the abscess zone. As auxin levels decrease, ethylene synthesis increases, and the abscisal layer forms, leading to leaf drop.
- **Pollen Tube Growth and Flowering:** Auxin plays a role in flowering processes, particularly in the growth of floral organs and stamen development. It has also been observed to delay the onset of flowering in some species.

(d) Hormones it works with and substances that reduce its effect: The balance between auxin and cytokinin determines whether plant tissues will form roots or shoots; root formation is observed when auxin is dominant, and shoot formation when cytokinin is dominant. The relationship with strigolactones is complex and exhibits a mixture of synergy and antagonism: Auxin stimulates strigolactone biosynthesis, while auxin and strigolactone together regulate apical dominance. Gibberellins and auxin exert a synergistic effect on cell elongation, both stimulating stem growth in a coordinated manner. Ethylene is synthesized as a byproduct triggered by high auxin concentrations and regulates or inhibits growth in some tissues. Abscisic acid, on the other hand, generally antagonizes the effect of auxin; ABA increases under stress conditions while auxin sensitivity decreases. Jasmonic acid, particularly in the wound area, interacts with auxin balance, establishing a equilibrium between regrowth and defense.

2.2 Cytokinin

(a) Discovery and Historical Development: Research into cytokines began in the 1940s during studies on plant tissue culture. Researchers noticed that certain extract substances added to the medium stimulated cell division. Folke Skoog and Carlos Miller solidified the concept of cytokinins in 1955 by isolating kinet (6-furfuryladenine) from autoclaved DNA. This discovery led to the introduction of the term 'cytokinin', meaning a substance that stimulates cell division, into the scientific literature.

In 1963, D.S. Letham isolated zeatin from maize, making it the first naturally occurring cytokinin obtained from a plant. Skoog and Miller's most striking finding was that the auxin/cytokinin ratio determined morphological fate: a high auxin/low cytokinin ratio promoted root formation, while a low auxin/high cytokinin ratio promoted shoot formation. This principle forms the basis of current tissue culture protocols [2,5–7].

(b) Chemical Structure and Types: Cytokinins are adenine (aminopurine) derivatives that carry various side chains at the N6 position. They are divided into two main structural categories: isoprenoid and aromatic (Table 3).

Table 3: Classes of cytokines and representative compounds.

Class	Main Compound	Building Type	Sources/Notes
Isoprenoid cytokines (natural)	trans-Zeatin (tZ)	Adenine + isoprenyl side chain	Most common in plants; high activity.
Isoprenoid cytokines (natural)	Dihydrozeatin (DHZ)	Reduced form of zeatin	Dominant in seeds and young tissues.
Isoprenoid cytokines (natural)	Isopentenyladenine (iP)	Adenine + dimethylallyl	Found in chloroplast ribosome RNA.
Aromatic cytokines (natural)	Kinetin (K)	Adenine + furfuryl group	The first cytokine isolated from autoclaved DNA.
Aromatic cytokines (natural)	6-Benzyladenine (BA/BAP)	Adenine + benzyl group	Very common in plant tissue culture; long-lasting active.
Synthetic phenylurea derivatives	TDZ (Thidiazuron)	Thidiazole + phenylurea	High activity; used in shoot proliferation.
Synthetic phenylurea derivatives	CPPU (Forchlorfenuron)	Chlorophenylurea	Fruit size enhancer; agricultural application.

(c) Role in Plant Physiology:

- **Cell Division and Tissue Differentiation:** Cytokinin is found in high concentrations in all tissues where active cell division occurs, including root meristem, shoot meristem, young leaves, and developing seeds, and directly stimulates mitotic division. In tissue culture media, a high cytokinin/auxin ratio promotes shoot differentiation, while a low ratio supports callus formation.
- **Delaying Senescence:** One of the most important discovered properties of cytokinins is their capacity to delay leaf senescence. Cytokinins prevent chlorophyll breakdown and protein degradation; this allows leaves to remain photosynthetically active for a longer period. Cytokinin application causes a phenomenon called the green island effect, which is evident when the succulent parts remain alive while the surrounding tissues turn yellow. This property is used to increase the durability of cut flowers.
- **Nutrient Mobilization:** Cytokinins are powerful ‘sink’ regulators. Tissues with high cytokinin content attract nutrients (especially nitrogen compounds and carbohydrates) from their surroundings. Seeds increase cytokinin synthesis during fruit development and grain filling, thereby attracting photosynthetes.
- **Chlorophyll and Photosynthesis Protection:** Cytokinins protect chloroplast integrity and support photosynthetic activity. Decreased cytokinin levels during drought or nutrient deficiency stress accelerate leaf yellowing (chlorosis); exogenous cytokinin application can slow this process.
- **Lateral Shoot Development:** Cytokinin plays a critical role in breaking apical dominance. When cytokinin is applied to auxin-suppressed lateral buds, these buds are activated. This property is used in agricultural applications, particularly in ornamental plants, for compact growth and increased branching.
- **Seed Germination and Breaking Dormancy:** Cytokinins reduce the light dependence of seeds in some species and help break dormancy. Especially under conditions of limited light, cytokinin application can increase germination rates.
- **Stress Response:** Under drought conditions, root-derived cytokinin production decreases; this decrease accelerates the senescence process in leaves and ultimately reduces the photosynthetic area. However, some studies have shown that artificially maintaining high cytokinin levels alleviates drought stress. In the presence of nitrogen, cytokinin biosynthesis increases, and this increase acts as a bridge between nitrogen assimilation and growth.

(d) Hormones It Works with and Substances that Reduce Its Effect: The dynamic ratio balance between cytokinin and auxin is the most fundamental hormone interaction determining the morphological fate of plant tissues. Gibberellin and cytokinin work synergistically to coordinate cell division and differentiation. Abscisic acid functions in opposition to cytokinin: ABA accelerates leaf senescence while cytokinin delays it; under drought conditions, shifts in the balance of the two hormones determine the senescence process. Strigolactones modulate branch development, partly by utilizing cytokinin mechanisms. There is also an antagonistic relationship between ethylene and cytokinin; ethylene promotes fruit ripening while cytokinin may slow this process.

2.3 Gibberellins

(a) Discovery and Historical Development: The discovery of gibberellins began with research into 'bakanae' (stupid seedling) disease, which devastated rice fields in Japan. In 1926, Japanese botanist Eiichi Kurosawa attributed the abnormal elongation in diseased seedlings to a chemical substance produced by the fungus *Gibberella fujikuroi*. Yusuke Sumiki isolated this active compound between 1926 and 1938 and named it gibberellin. Gibberellic acid (GA_3) was re-isolated and its structure elucidated by Cross, Galt, and Hanson in England in 1954, and introduced to the Western scientific world. When it was understood that gibberellins are produced not only by pathogenic fungi but also by normal plant tissues, this group truly gained the status of phytohormones. Since then, over 136 different gibberellin structures (GA_1–GA_{136}) have been identified; however, only a small fraction of these are biologically active. The most important active forms are GA_1, GA_3, GA_4, and GA_7. GA_3 is the gibberellin with the widest commercial use [8,9].

(b) Chemical Structure and Types: Gibberellins are diterpenoid compounds derived from the isoprenoid (terpenoid) biosynthesis pathway. These molecules, built on a tetracyclic (four-ring) backbone, are classified into two main groups: C_{19} and C_{20}. C_{19}-GAs (with an ent-gibberellin backbone) generally exhibit higher biological activity (Table 4).

Table 4: The main biologically important gibberellins.

Gibberellin	Construction Group	Activity	Main Plant/Context
GA_1	C_{19}-GA; dihydroxy	High	Rice, peas; the main form controlling stem elongation.
GA_3 (Gibberellic Acid)	C_{19}-GA; trihydroxy	High	The standard in commercial production is obtained from a fungal source.
GA_4	C_{19}-GA; dihydroxy	High	Arabidopsis; flower development, apple fruit quality.
GA_7	C_{19}-GA; trihydroxy	High	An alternative to GA_3 in some species.
GA_{20}	C_{19}-GA; precursor	Medium	Precursor of GA_1; 20-oxidase substrate.
GA_{12}, GA_{53}	C_{20}-GA; precursor	Low (precursor)	The common precursor of active GAs in all plants.

(c) Role in Plant Physiology:

- **Stem Elongation and Height Growth:** The most striking effect of gibberellins is their ability to increase stem height. When GA is applied to dwarf mutants, the plant returns to its normal height; these experiments have definitively proven the essential role of GA in stem elongation. The mechanism of action occurs through both the stimulation of cell division and the enhancement of cell elongation. In the development of high-yielding 'green revolution' varieties in the 1960s, the fact that this plant was programmed to remain dwarf (gibberellin-insensitive or deficient) played a key role.

- **Seed Germination:** Gibberellins are critically important in bringing the seed out of dormancy and initiating germination. In cereals such as barley, GA_3 stimulates the aleurone layer, initiating the release of hydrolytic enzymes such as alpha-amylase and protease, which play a role in starch digestion. This process makes the nutrients stored in the endosperm available for use by the embryo.
- **Flowering Timing:** In long-day plants and biennial species, vernalization (cold exposure) and long photoperiod conditions stimulate gibberellin biosynthesis, triggering flowering. In biennial plants such as cabbage, carrots, and beets, exogenous GA application leads to direct flowering, bypassing the rosette stage of the first year.
- **Breaking Dormancy:** Gibberellins are effective not only in breaking seed dormancy but also bud dormancy. Applying GA to buds that have entered dormancy due to climatic conditions can restart shoot growth. This property has economic value, especially in the fruit growing sector.
- **Parthenocarpy and Fruit Development:** GA stimulates parthenocarpy (fruit development without fertilization). In grapes (especially the Sultani variety), GA application increases fruit size and improves quality by thinning the cluster structure. Positive effects of GA applications on fruit size have also been observed in tomatoes, apples, and pears.
- **Sex Determination:** In monoecious plants (bearing both male and female flowers), GA application increases male flower formation; this effect counteracts the effect of ethylene application, which promotes female flower formation. This effect is of agricultural importance in cucurbit species such as cucumber and squash.
- **Hair and Epidermal Development:** GA affects the density and distribution of hairs (trichomes) in some plants; it also plays a role in the differentiation of some epidermal cell types.

(d) Hormones It Works with and Substances That Reduce Its Effect: Abscisic acid is the strongest physiological antagonist of gibberellins; particularly during seed dormancy and germination, the two hormones balance each other as opposing forces. There is generally an antagonistic relationship between ethylene and gibberellin: ethylene inhibits stem elongation while GA stimulates it; however, ethylene becomes dominant during fruit ripening. Auxin and gibberellin work synergistically in cell elongation and vascular tissue development. Cytokinin and gibberellin also coordinate cell growth and division. Brassinosteroids share biosynthetic pathway components with gibberellins, jointly regulating plant height and structural development. Strigolactone, however, can limit branch growth and stem development by suppressing gibberellin biosynthesis under conditions of high nutrient deficiency.

2.4 Abscisic Acid (ABA)

(a) Discovery and Historical Development: There is an interesting historical coincidence in the discovery of abscisic acid: in the 1960s, three independent research groups, while studying different biological events such as leaf fall, shoot domination, and cotton boll maturation, isolated the same inhibitory compound. It was determined in 1967 that these substances, which Addy and Wightman named 'abscisicin I', the Wareing group 'dormin', and Ohkuma and Addicott 'abscisicin II', were chemically identical, and the common name 'abscisic acid' (ABA) was adopted. ABA is a sesquiterpene (C15) compound, and it is now definitively known that it is formed via carotenoid degradation [10].

Initially considered only as an 'inhibition hormone', ABA's central role in responses to drought, salinity, cold, and other abiotic stresses has been rapidly elucidated since the 1980s. Today, ABA is among the most studied hormones in plants.

(b) Chemical Structure and Types: ABA is an organic sesquiterpenoid acid derived from the isoprenoid pathway and having a terpenoid structure. Chemically, it is named 2-cis,4-trans-abscisic acid

($C_{15}H_{20}O_4$). The molecule has a carboxylic acid group at one end and a cyclic ring at the other. Although ABA has a single basic chemical structure, conjugated (bound) and storage forms such as ABA-glucose ester (ABA-GE) also exist in plants. These storage forms enable an immediate response by rapidly converting to free ABA under stress (Table 5).

Table 5: ABA and related compounds.

Compound/Form	Building Type	Physiological Context
(+)-ABA (biologically active form)	Sesquiterpenoid; cyclopentanone ring + conjugated carboxylic acid	The main endogenous active form is the stress response.
ABA-glucose ester (ABA-GE)	ABA + glucose conjugate	Storage/inactive form; found in the vacuole and apoplast.
Phaseic acid	ABA catabolite	ABA degradation product; weak activity.
Dihydrophasic acid	Reduced phasic acid	The final ANA metabolite; inactive.
PA (8′-hydroxy-ABA)	ABA catabolite precursor	The first step in ABA inactivation.

(c) Role in Plant Physiology:

- **Water Stress and Stomatal Regulation:** The most critical and best-documented function of ABA is to close the stomata. When the plant's roots or leaves sense water deficiency, ABA levels rise rapidly. This increase triggers guard cells: the release of K^+ ions and osmotic substances lowers turgor pressure, and the stomata close. This mechanism is the fastest and most effective defense line against water loss through evaporation under drought conditions.
- **Seed Dormancy:** ABA reaches high concentrations during seed maturation, initiating the dormancy mechanism; this causes the seed to wait instead of germinating immediately under unfavorable conditions. Sufficient ABA levels in the seed are essential for true dormancy. Mutants lacking ABA exhibit a viviparous phenotype, meaning the seeds can germinate while still on the parent plant.
- **Accumulation of Storage Proteins and Lipids:** During seed maturation, ABA stimulates the accumulation of storage proteins such as legumin and vicilin, and storage lipids such as triacylglycerol. These proteins and fats are used as a nutrient source by the embryo during germination.
- **Winter Dormancy and Bud Closure:** The decreasing day length and falling temperatures in the autumn months trigger ABA accumulation in the buds. This accumulation causes the buds to become dormant, encased in scales. In spring, as GA dominance increases, the effect of ABA recedes, and the budding.
- **Root Growth and Soil Exploration:** Moderate levels of ABA stimulate root growth, leading the plant to root deeper during drought periods. This effect is a seemingly contradictory aspect of abscisic acid: it simultaneously reduces water loss in the leaves while promoting root growth and directing the plant towards water seeking.
- **Stress Memory (Epigenetics):** It is known that plants develop 'stress memory' during recurring drought periods. ABA contributes to the formation of this memory by influencing epigenetic mechanisms (DNA methylation, histone modifications); thus, the response to the next stress event occurs more quickly and effectively [11,12].
- **Biotic Stress Response:** ABA is known to play a role not only in abiotic but also in biotic stress (fungal, bacterial) responses. ABA levels generally increase upon exposure to a pathogen; this increase may strengthen the defense in some cases and weaken it in others. This complex interaction with SA and JA is still a subject of research.

(d) Hormones It Works with and Substances That Reduce Its Effect: Gibberellin is the strongest antagonist of ABA; the two hormones balance each other as opposing forces in germination, growth, and storage organ development. Ethylene works in coordination with ABA under stress conditions; for example, water stress increases both ABA and ethylene synthesis, and together they accelerate leaf senescence. Jasmonic acid also enhances some stress responses in parallel with ABA; combined application of JA and ABA can increase stress tolerance.

Cytokinin is the main antagonist of ABA; the balance between cytokinin and ABA is critical for maintaining leaf viability. The relationship between salicylic acid and ABA varies depending on the context; a synergistic effect is observed under some conditions, and an antagonistic effect under others.

2.5 Ethylene

(a) Discovery and Historical Development: The effect of ethylene on plant growth was discovered entirely by accident. In 1858, trees in a region of Great Britain were observed growing in strange shapes, and it was understood that this was due to gas mixtures leaking from streetlights. In 1901, the Russian botanist Dimitry Neljubow systematically demonstrated that ethylene produced an effect called the 'triple response' in pea seedlings, causing horizontal growth, shortening, and apical hook formation [13].

The relationship between ethylene and fruit ripening was established in the 1910s, and R. Gane chemically confirmed in 1934 that ethylene is released from ripening fruits. Ethylene is the first and only example of a plant hormone functioning in the gas phase; this unique characteristic differentiates both research processes and agricultural applications. The biosynthesis pathway (Methionine → SAM → ACC → Ethylene) was fully elucidated by Shang Fa Yang and Norman Hoffman in 1977 [14,15].

(b) Chemical Structure and Types: Ethylene (C_2H_4) is the simplest alkene compound containing a double bond between two carbon atoms. It is a colorless gaseous molecule with a very slight fruity-sweet odor. Only one active form exists for biosynthesis. Instead of directly applying ethylene for agricultural use, carrier compounds (ethephon = 2-chloroethylphosphonic acid) that are soluble in water and subsequently converted to ethylene are used (Table 6).

Table 6: Ethylene and related compounds.

Compound	Building Type	Usage/Notes
Ethylene (C_2H_4)	The simplest alkene; a gas	Endogenous hormones; maturation, senescence, stress.
ACC (1-Aminocyclopropan-1-carboxylic acid)	Cyclopropane derivative amino acid	A direct precursor to ethylene biosynthesis.
Ethephon (CEPA)	2-Chloroethylphosphonic acid; liquid	Agricultural ethylene source; converted to ethylene in practice.
1-MCP (1-Methylcyclopropane)	Cyclopropane derivative; gas	Ethylene suppressant; used in post-harvest preservation.
AVG (Aminoethoxyvinylglycine)	Ethylene biosynthesis inhibitor	It inhibits the ACC synthase enzyme; it delays fruit ripening.

(c) Role in Plant Physiology:

- **Fruit Ripening:** Ethylene is the primary hormone that triggers ripening in climacteric fruits (apples, bananas, tomatoes, pears, peaches, melons). As the fruit ripens, ethylene production increases, creating a self-stimulating cycle (autocatalytic ethylene). With ripening, fruit starch is converted to sugar, flavor and aroma compounds are synthesized, the fruit flesh softens, and the color changes. Unripe fruit exposed to ethylene gas ripens faster than normal; in commercial cold storage, ethylene is suppressed with 1-MCP to extend shelf life.

- **Leaf, Flower, and Fruit Abscission:** Each organ detaching from the plant—leaves that have completed their developmental stage, yellowed flowers, and mature fruits—increases ethylene production. Ethylene activates enzymes in the abscission zone, breaking down intercellular bonds and causing the organ to fall off. This mechanism is critical for facilitating harvesting, regulating the natural cycle, and ensuring nutrient recovery.
- **Senescence and Aging:** Ethylene is also described as a general 'aging hormone'. It accelerates chlorophyll breakdown, protein degradation, and tissue aging. Ethylene plays a central regulatory role in the process of flower wilting and leaf shedding.
- **Adventitious Root Formation:** Increased ethylene production under stressful conditions such as waterlogging (anaerobiosis) triggers adventitious root formation in the parts of the stem near the water surface. This adaptation allows the plant to obtain oxygen even underwater.
- **Sex Determination in Monoecious Plants:** In plants such as cucumbers, melons, and squash, ethylene application increases the proportion of female flowers, while gibberellin application increases the number of male flowers. This effect is used as a control tool in commercial vegetable cultivation, especially in hybrid seed production.
- **Germination and Dormancy:** In some species, ethylene application breaks seed dormancy and initiates germination. This effect is particularly noticeable in seeds that require light or cold treatment.
- **Epinasty:** Ethylene causes the leaf petioles to bend downwards (epinasty); this response is particularly noticeable in plants exposed to flooding.
- **Triple Response in Roots:** Seedlets exposed to ethylene exhibit the classic 'triple response': the hypocotyl and root shorten and thicken, growth slows, and an apical hook forms. This response is the plant's defense mechanism against mechanical obstructions while growing underground.

(d) Hormones It Works with and Substances That Reduce Its Effect: Ethylene and ABA work in parallel and coordinated fashion in fruit ripening, leaf fall, and stress responses. High auxin levels stimulate ethylene biosynthesis; therefore, both auxin and ethylene increase in ripening fruits and areas of intensive growth. JA and ethylene exhibit a synergistic effect, particularly in defense responses and wound signaling [16]. Cytokinin, on the other hand, delays the senescence process accelerated by ethylene; there is an antagonistic balance between the two hormones regarding leaf senescence. Salicylic acid can slow ripening in apples by inhibiting the ethylene biosynthesis enzyme (ACC synthase); this effect is used to increase the durability of cut flowers. Gibberellin and ethylene function as opposing forces, particularly in determining fruit size and sex.

3 Newly Discovered and Expanding Groups of Hormones

3.1 Brassinosteroids (BR)

(a) Discovery and Historical Development: The discovery of brassinosteroids is based on extensive plant growth factor screening conducted by USDA (U.S. Department of Agriculture) researchers in the early 1970s. In 1970, Mitchell et al. observed that an extract of rapeseed (Brassica napus) pollen caused unexpected growth in bean seedlings; the active component of this extract was purified by Grove et al. in 1979 and named 'brassinolide' [17,18]. The name 'brassinosteroid' was given in reference to the fact that the compound is obtained from the Brassica genus of the Crucifereae (cruciferous family).

Initially considered solely as growth-promoting factors, brassinosteroids gained true phytohormone status in the 1990s through the analysis of Arabidopsis dwarf mutants (det2, dwf1, bri1). These mutants exhibited pleiotropic phenotypic changes such as dwarfism, chlorophyll accumulation, impaired photomorphogenesis, and sterility; revealing that BR regulates not only growth but a broad physiological network. Brassinosteroids are structurally similar to steroid hormones in animals, being the only group of phytohormones with a steroid skeleton; however, functional differences are significant [19,20].

(b) Chemical Structure and Types: Brassinosteroids are polycyclic compounds with a steroid backbone. The basic structure is built upon a cholesterol-like framework consisting of four rings (A, B, C, D). To date, more than 70 naturally occurring brassinosteroids have been identified (Table 7).

Table 7: Major brassinosteroids and their activity levels.

Compound	Structural Feature	Activity	Main Source/Note
Brassinolide (BL)	Lactone containing 7α-oxazone and 6-oxo group	Highest	*Brassica napus* pollen; reference BR.
Castorol (CS)	6-Oxo group; BL precursor	High	Present in most plants; commercial source.
24-Epibrassinolide (24-EBL)	C24 epimer; synthetic analog	High (agricultural)	Widely used in agricultural applications; drought tolerant.
Homobrassinolide (HBL)	BL analog; an extramethyl group	High	Common in commercial formulations.
Teasterol	Early biosynthesis intermediate	Low	Precursor in the BL pathway.
Dolicolid	Steroid structure; modified B ring	Medium	Identified in legumes.

(c) Role in Plant Physiology:

- **Cell Elongation and Stem Growth:** The most significant effect of brassinosteroids is the stimulation of cell elongation and division, particularly in the shoot. Arabidopsis mutants deficient in BR exhibit extreme dwarfism and dark green leaf color; this phenotype is completely corrected with BR application. BR is also suitable for quantitative evaluation via a test system (Lamina Inclination Assay) that dramatically increases the length of the second node in bean seedlings.
- **Photomorphogenesis and Light Response:** The effect of BR on photomorphogenesis is quite striking. BR-deficient mutants appear de-ethiolate, even when grown in the dark, like plants growing in the light: short and thick stems, open cotyledons, and chlorophyll accumulation. This observation reveals that BR is essential for dark growth. Light signaling and BR signaling integrate to coordinate seedling development and photomorphogenesis.
- **Stress Tolerance:** Extensive evidence exists that brassinosteroids enhance tolerance to both abiotic and biotic stress. Exogenous BR application under conditions of salt, drought, cold, heat, heavy metal, and UV-B stress increases antioxidant enzyme activity, strengthens osmotic regulation capacity, and maintains membrane integrity. The agricultural use of 24-epibrassinolide and homobrassinolide is based on this potential.
- **Vascular Tissue Development:** BR directly affects the differentiation of xylem and phloem. In BR deficiency, vascular tissue integrity is disrupted; the formation of a proper conduction system is impaired. BR also stimulates secondary cell wall synthesis, supporting the formation of lignocellulose.
- **Pollen Development and Flowering:** BR synthesis and signaling are essential in male gametophytes; BR deficiency mutants are often sterile. Pollen germination and tube growth are also dependent on BR. This feature is important for hybrid seed production.

- **Fruit Development:** BR affects fruit size and shape. In plants such as tomatoes and cucumbers, BR application increases fruit size. BR activity is also high during seed filling.

(d) Hormones It Works with and Substances That Reduce Its Effect: Brassinosteroids and auxin exhibit a strong synergistic effect on cell elongation; when applied together, the combined effect is greater than the sum of the two. Gibberellin and BR also regulate cell elongation in a coordinated manner; longer cell differentiation can be observed when GA is dominant, and more intense and shorter differentiation when BR is dominant. Jasmonic acid shows synergistic effects with BR in some tissues and contexts, and antagonistic effects in others. There is a complex context-specific balance between salicylic acid and BR: the balance between plant growth and defense depends on the ratio of these two hormones. Karrikin-BR interaction has also begun to be elucidated in recent years; it has been reported that KAR signaling can suppress BR biosynthesis.

3.2 Salicylic Acid (SA)

(a) Discovery and Historical Development: The history of salicylic acid dates back to one of the oldest medical practices in human history: the use of willow bark as a fever reducer and analgesic. Ancient Egyptian, Sumerian, and Greek sources mention the healing effects of willow bark. In 1828, the German pharmacist Johann Buchner isolated the active compound salicin from willow bark; in 1838, the Italian chemist Raffaele Piria obtained salicylic acid from salicin. In 1897, Bayer Laboratories commercialized this compound under the name “aspirin”, thus giving birth to the first significant drug in the history of modern pharmacology.

The role of salicylic acid in plant defense was understood much later. In the 1970s, Joe Kuc and his colleagues observed the development of systemic resistance to viral infection in tobacco plants; in the 1990s, Métraux and his colleagues confirmed that SA was associated with this systemic resistance [21]. It became clear in the mid-1990s that SA is a central harbinger of the defense mechanism called “systemic acquired resistance” (SAR) [22,23].

(b) Chemical Structure and Types: Salicylic acid (2-hydroxybenzocarboxylic acid) is a simple phenolic acid with a hydroxyl and a carboxyl group attached to a benzene ring. This molecule, which is extremely simple in structure, has more than one active form (Table 8).

Table 8: Salicylic acid and related compounds.

Compound	Building Type	Physiological Role
Salicylic Acid (SA)	Phenolic acid; hydroxybenzoic acid	The primary active form is SAR, stress response.
Methyl Salicylic Acid (MeSA)	SA methyl ester; volatile	Distant carrier of systemic signal (phloem + gas).
Salicylic Acid Glucoside	SA + glucose conjugate	Warehouse form; inactive; can be converted to free SA.
Salicylate (salicylic acid anion)	Ionized form of SA	The dominant form in the cell at physiological pH.

(c) Role in Plant Physiology:

- **Systemic Acquired Resistance (SAR):** The main physiological context in the discovery of SAR is the plant’s activation of its entire body after a pathogen settles in a tissue. SAR, which increases at the site of local infection, is transported to distant tissues via the phloem and in the air in the form of methyl-SA gas. In this way, uninfected leaves increase their defense capabilities before being attacked;

this state of readiness is called SAR. Pathogenesis-related proteins (PR-1, PR-2, PR-5) synthesized within the scope of SAR exhibit antifungal and antiviral activity.

- **Biotic Stress Defense:** SA strengthens the defense not only against viruses but also against bacteria and fungi. In a process called immune priming, plants previously treated with SA respond much more strongly and quickly to the same pathogen during a second encounter. Physically preventing the spread of the pathogen by creating a necrotic zone (hypersensitive response) is also one of the processes coordinated by SA.
- **Abiotic Stress Tolerance:** Extensive evidence exists that SA enhances tolerance not only to biotic stress but also to abiotic stress conditions such as salinity, drought, heavy metals, UV-B, and temperature stress. Exogenous SA application has been shown to improve growth under stress in tomatoes, wheat, maize, and numerous horticultural crops. SA limits reactive oxygen species (ROS) damage by increasing the activity of antioxidant enzymes (SOD, CAT, APX, POX) [24].
- **Flowering and Thermogenesis:** In some plants, such as the voodoo lily (*Sauromatum guttatum*), SA contributes to heat production (thermogenesis) released before flowering. This heat facilitates the diffusion of scent compounds that encourage insects to carry the pollen. SA also promotes flowering in some plants; its interaction with florigen signaling is still being investigated.
- **Photosynthesis and Chlorophyll Preservation:** Moderate SA applications can increase photosynthetic efficiency, preserve chlorophyll content, and support enzyme activities. Exogenous SA has proven its protective effect on the photosynthetic apparatus, especially in stressed plants.
- **Vascular System and Water Transport:** SA contributes to some mechanisms affecting xylem water transport. The practice of soaking cut flowers in aspirin water before disposing of them is based on the xylem-clogging effect of SA.

(d) Hormones It Works with and Substances That Reduce Its Effect: The antagonistic relationship between SA and JA constitutes one of the most striking hormone interactions in plant physiology: pathogen defense is regulated by SA, while insect/wound defense is regulated by JA, and the two pathways often suppress each other. This balance allows the plant to 'decide' which enemy to prioritize with its limited energy resources. SA and ethylene also often work antagonistically; SA can slow fruit ripening and senescence by suppressing the ethylene biosynthesis enzyme (ACC synthase). The relationship between ABA and SA varies depending on the context: under some stress conditions it is synergistic, while in pathogen defense ABA can weaken SA activation. There is a growth-defense balance between BR and SA; high BR activity stimulates growth while weakening the SA signaling pathway.

3.3 Jasmonic Acid (JA) and Jasmonates

(a) Discovery and Historical Development: The discovery of jasmonates began with the jasmine plant (Jasminum grandiflorum), which holds a significant place in the perfume industry. In 1962, Françon and Gallard isolated methyl jasmonate from jasmine essential oil. Jasmonic acid itself was obtained by Doering in 1971 from a fungal culture filter. At that time, these molecules were of interest only from a perfumery perspective.

The critical role of jasmonic acid in plant defense was revealed in 1990 by Farmer and Ryan's studies of the systemic response to insect damage and mechanical injury in tomato plants [25]. These studies clarified that JA is the carrier molecule of the 'alarm' that prepares the plant for enemy attack. It was only in 2009 that the active biological form, (+)-7-iso-JA-ile-L-isoleucine conjugate (JA-Ile), was discovered; this discovery opened a new era in JA research [26,27].

(b) Chemical Structure and Types: Jasmonates are a class of oxylipin (oxygenated lipid) compounds derived from linolenic acid (C18). Their biosynthesis begins in the chloroplast and is completed in the peroxisome. JA and its derivatives form a large family (Table 9).

Table 9: Major jasmonate compounds and their functions.

Compound	Building Type	Physiological Role
Jasmonic Acid (JA)	Cyclopentanone ring + pentanoic acid chain	Key signaling molecule; defense, growth inhibition.
JA-Isoleucine (JA-Ile)	JA + isoleucine amino acid conjugate	The primary active biological form activates the defense and growth pathways.
Methyl Jasmonate (MeJA)	JA methyl ester; volatile	Airborne systemic signal; plant-to-plant communication.
cis-OPDA	12-oxo-phytodienoic acid; JA predecessor	It has its own signaling activity; it may follow a separate pathway.
12-OH-JA	Hydroxylated JA catabolite	JA inactivation; balance regulator.

(c) Role in Plant Physiology:

- **Injury and Herbivore Defense:** Jasmonates are the primary coordinators of the defenses that plants develop against insect attacks and mechanical wound damage. JA-Ile, rapidly synthesized in the damaged tissue, is transmitted throughout the plant as a systemic signal via phloem and gas (MeJA). In response to this signal, defensive compounds such as proteinase inhibitors (which suppress insect digestive enzymes), nicotinoid alkaloids, phytoalexins, and tannins are synthesized.
- **Release of Volatile Terpenes:** JA activation triggers the release of characteristic volatile compounds (terpenoids, green leaf volatiles: GLV) from the injured leaves of plants. Three different meanings have been attributed to these volatiles: (i) warning neighboring plants of approaching danger, (ii) attracting the insect's natural enemies (parasitoid wasps, predators) (indirect defense), (iii) inhibiting the growth of pathogens. This aspect of plant communication has become one of the most exciting topics in 'ecophysiology' research.
- **Inhibition of Root Growth:** High JA application suppresses root elongation, lateral root development, and root hair formation. This effect is a clear indication that the plant prioritizes defense over growth.
- **Pollen Development and Male Sterility:** JA is essential for anther and pollen development. JA biosynthesis mutants are male sterile, and pollen tube growth and pollination are dependent on this hormone. Therefore, the JA signaling pathway is considered an important target in obtaining male sterile lines.
- **Flowering and Stamen Development:** JA deficiency leads to failure of flowering; this phenotype is clearly observed in mutants with impaired JA biosynthesis or sensing. Stamen filament elongation and anther dehiscence (bursting and pollen release) are JA-dependent processes.
- **Fruit Ripening:** In some fruit species (tomatoes, strawberries), JA and ethylene coordinate fruit ripening. In tomato fruit, JA can accelerate ripening by stimulating ethylene biosynthesis.
- **Stomatal Behavior:** JA has the capacity to close stomata in coordination with ABA. Under multiple stress conditions, such as water stress and simultaneous insect attack, this effect helps the plant survive by conserving its resources.

(d) Hormones It Works with and Substances That Reduce Its Effect: The antagonism between JA and SA in insect defense and anti-pathogen defense is one of the most fundamental hormone trade-offs in plant physiology. JA and ethylene often function synergistically in defense responses; when administered together, defense genes can be activated much more strongly. There is a complex balance between auxin and JA depending on the context: in some tissues, auxin supports JA, while JA can suppress the auxin response at high concentrations. Gibberellin antagonizes the growth-suppressive effect of JA; under low nutrient conditions, JA increases while GA decreases, shifting the growth-defense balance towards defense. The interaction between brassinosteroids and JA varies depending on the context; in immunity, BR can sometimes suppress the JA pathway. ABA and JA generally function synergistically in stress responses.

3.4 Strigolactones (SL)

(a) Discovery and Historical Development: The discovery story of strigolactones begins with research into parasitic weeds. In 1966, Cook and colleagues observed that the root secretions of cotton plants stimulated the seeds of *Striga hermonthica* (witch hazel); they isolated the active compound and named it 'strigol' [28]. Given that witch hazel causes billions of dollars in damage to grain fields, this discovery is of great agricultural significance. For the next forty years, strigolactones were considered only as soil chemical signals to parasitic plants.

In 2005, Kohki Akiyama and friends revealed another critical function of strigolactones: strigolactones, when administered as root secretion, stimulate hyphaetic branching in arbitrary mycorrhizal fungi (AMF), facilitating their symbiotic colonization of the plant root [29]. This discovery proved the role of strigolactones in soil communication. However, the biggest surprise came in 2008: Gomez-Roldan, Umehara, and colleagues simultaneously and independently demonstrated that strigolactones are endogenous plant hormones that inhibit branch development; these publications, released in Nature, opened a new era in hormone science [30,31]. Since then, more than 30 naturally occurring SL structures have been identified [32,33].

(b) Chemical Structure and Types: Strigolactones are terpenoid compounds that are carotenoid breakdown products. Canonical strigolactones consist of a three-ring lactone (A-B-C) with a butenolide (D) ring attached by an etheric bond (Table 10). The D ring is absolutely essential for biological activity. Non-canonical strigolactones deviate from this conventional structure.

Table 10: Strigolactone classes and representative compounds.

Building Type	Representative SL	Plant	Main Physiological Effect
Canonical/strigol type (A-B-C-D)	Strigol, orobankal, solanasol	Cotton, tomatoes, poplar	Strong striga stimulation, AMF symbiosis, branch pruning.
Canonical/orobankol type	5-Deoxy-strigol (5DS), orobankol	Rice, tomatoes, peas	Common canonical form; interaction with D14.
Non-canonical	Carlactone acid (CLA)	Arabidopsis, corn	D-ring-less hormone activity; endogenous stress response.
Non-canonical	Avenool	Oats (*Avena sativa*)	No eno-ether bridge; unique parasite stimulation.
Non-canonical	Zealactol	Corn (*Zea mays*)	Non-canonical; original Egyptian SL.
Synthetic analog	GR24 (rac)	Research standard	SL mimetics are used in most studies.

(c) Role in Plant Physiology:

- **Apical Dominance and Branch Pruning:** Strigolactones are key hormones that determine the branch structure of the plant stem. SL is synthesized in the root in coordination with auxin signaling and transported upwards (acropetally), preventing the awakening of lateral buds. Under nutrient deficiency conditions, SL synthesis increases, the number of branches decreases, and the plant concentrates its resources on fewer but stronger shoots. Conversely, in well-nourished plants, SL levels decrease and more lateral branches develop.

- **Arbitrtrophic Mycorrhiza (AM) Symbiosis:** Substrates (SLs) released into the root zone (rhizosphere) act as germination and hyphaetic branching signals for AMF spores in the soil. The fungus detects the SLs, locates the plant's roots, and establishes a mutualistic relationship. Through this relationship, the plant increases its phosphorus and water uptake while providing the fungus with carbohydrates. This function of SLs is being investigated to improve the effectiveness of AMF inoculation in agricultural applications.
- **Dangerous Warning for Parasitic Plants:** SLs (Subtle Signals) are also used as 'hidden messages' by obligate parasitic plants such as *Striga* (witch hazel), *Orobanche*, and *Phelipanche*. These parasites detect the SLs emitted from the host plant, germinate their seeds, and are attracted to the plant. Germination without contact results in death. Therefore, cultivating host plants that produce low SLs or disrupt the parasite's SL detection system is becoming one of the biological control strategies.
- **Root Growth and Architecture:** While SL weakly suppresses primary root elongation, its effect on lateral root formation is complex: moderate doses of SL positively influence lateral root development; high doses may suppress it. It has also been observed to stimulate root hair elongation. These effects play a role in the plant's restructuring of the root system to optimize nutrient uptake.
- **Leaf Shape and Senescence:** SLs affect leaf shape and size; they have also been reported to accelerate leaf senescence in coordination with ethylene. Under nutrient deficiency conditions, SLs are thought to contribute to preserving plant youth by rapidly shedding older leaves.
- **Anthocyanin Accumulation:** SL application has been shown to stimulate anthocyanin synthesis in some plants (apple, *Arabidopsis*). Anthocyanins function as antioxidants against oxidative stress and also attract pollinators as attractive color pigments.
- **Stress Response:** SL biosynthesis increases under drought and high salinity conditions. SL has been reported to stimulate stomatal closure and increase water use efficiency. It has also been observed to contribute to the strengthening of antioxidant capacity under various abiotic stress conditions.

(d) Hormones It Works with and Substances That Reduce Its Effect: A bidirectional relationship exists between auxin and SL: Auxin stimulates SL biosynthesis; SL, in turn, adds an additional inhibitory effect to auxin signaling within the context of apical dominance. Together, they coordinately regulate branch pruning. Cytokinin acts antagonistically to SL: cytokinin activates lateral buds while SL suppresses them; whether a bud awakens or not depends on the local balance of these two hormones. The relationship between gibberellin and SL varies depending on nutritional status; in nutrient deficiency, SL is dominant while GA levels decrease. ABA and SL show a synergistic effect in drought response, responding together to water stress. Ethylene works in coordination with SL during the leaf senescence process. Karrikin and SL share closely related signaling pathways (the MAX2/D3 F-box protein is common); however, their physiological outputs differ slightly.

3.5 Karrikines (KAR) and KAI2 Ligand (KL)

(a) Discovery and Historical Development: The discovery of karrikins is based on the scientific investigation of the rapid regeneration of vegetation after fires. Botanists have observed for centuries that some seeds germinate in unusually large numbers in fire-affected areas; however, the mechanism of this phenomenon remained unclear for a long time. In 2002, Judy Ecker and Kimberley Dixon's group proved through laboratory experiments that smoke water contains the active compound that triggers this germination.

In 2004, Gavin Flematti (University of Western Australia) and colleagues isolated the active compound from the aqueous extract of smoke from burned plant material and identified it as 3-methyl-2H-furo [2,3-c] pyran-2-one. This discovery was published in Science; subsequently, a second butenolide compound with a similar structure was also identified. In 2004, Flematti et al. named this family of compounds "karrikines" (KAR) [34].

A critical next step was taken with the understanding that karrikins are not merely exogenous fire-inducing chemicals. Researchers found that the KAI2 (KARRIKIN INSENSITIVE 2) receptor, which responds to KARs, also responds to the plant's own produced endogenous ligand, KAI2 Ligand (KL), whose structure is not yet fully elucidated. KL is thought to be of apocarotenoid origin and, when discovered, presents findings that have the potential to create a new category of phytohormones [35–37].

(b) Chemical Structure and Types: Karrikines are butenolide compounds formed from burnt plant material. Their structure is similar to the D ring of strigolactones; however, they lack A-B-C rings (Table 11).

Table 11: Major karrikin compounds and their properties.

Compound	Building Type	Activity/Notes
KAR_1 (Karrikinolide)	Furanone + pyran ring; butenolide	The highest biological activity; the reference point in all studies.
KAR_2	Methyl-butenolide analog	Activity near KAR_1 may be dominant in different species.
KAR_3	Dimethyl-butenolide analogue	Moderate activity.
KAR_4	Methoxybutenolide analogue	Weak activity; studied on Striga.
KL (KAI2 Ligand)	Probably an apocarotenoid; not isolated	Endogenous; presumed to be present in all plants.

(c) Role in Plant Physiology:

- **Seed Germination:** The best-documented effect of karrikins is their stimulation of seed germination. In plants adapted to Australia's fire ecology (Banksia, Stylidium, Conostylis, etc.), seeds remain dormant in the soil for years; KAR_1 released from fire smoke triggers germination. However, this effect is not limited to fire ecology: seeds of tomatoes, lettuce, cabbage, and numerous field crops have also been shown to respond to karrikins. KAR_1 increases germination success, especially under conditions such as low light and suboptimal temperature [36,38].
- **Seedling Development and Photomorphogenesis:** Following seed germination, karrikins play a role in the regulation of hypocotyl elongation, cotyledon opening, and light-oriented growth in the early stages of seedling development. KARs can weaken the shade avoidance response, allowing seedlings to grow more stably in dim conditions. This effect has adaptive value for seedlings grown in open areas after fires.
- **Root System Architecture:** Karrikins moderately suppress primary root elongation while strongly stimulating root hair growth. Increased root hairs improve water and nutrient absorption from the soil; this effect is particularly advantageous under nutrient deficiency stress. They have also been reported to regulate the number and distribution of lateral roots.
- **Abiotic Stress Tolerance:** In recent years, extensive evidence has accumulated regarding the role of karrikins in stress tolerance. KAR_1 and KAR_2 applications have improved the survival and growth performance of plants under drought, salinity, heat (temperature), and heavy metal (cadmium) stresses. This effect is largely achieved through the strengthening of antioxidant defenses, increased osmotic regulatory capacity, and protection of the photosynthetic apparatus [39,40].
- **Arbitrtrophic Mycorrhiza (AMF) Symbiosis:** The structural similarity of karrikins to strigolactones suggests that they may also function in AMF symbiosis. Studies have shown that the KAI2 signaling

pathway contributes to mechanisms regulating AMF infection; this function is partly shared with SL and partly carried out independently.

- **Volatile Signaling:** A study published in Science in 2024 showed that KAI2 is a critical component in plant-to-plant signaling via volatile compounds [41]. This finding unexpectedly expanded the known physiological functions of the karrikin signaling pathway.
- **Hormonal Homeostasis:** Comparative transcriptomic studies have shown that KAR/KAI2 signaling plays a crucial role in regulating ABA and cytokine homeostasis (balance). This effect points to a different hormonal homeostasis mechanism than SL signaling (D14 pathway) [37,42].

(d) Hormones It Works with and Substances That Reduce Its Effect: Karrikines and strigolactones form two distinct signaling branches that share the MAX2 (D3) F-box protein; SL utilizes the D14 receptor, while KAR utilizes the KAI2 receptor. The outcomes are partially divergent: KAR is predominantly involved in germination and photomorphogenesis, while SL is involved in branch pruning. KAR/KAI2 signaling regulates ABA and cytokinin homeostasis; this interaction is particularly critical during seed germination. Evidence exists that in the interaction between gibberellin and KAR, KAR can enhance GA biosynthesis, consistent with KAR's germination-stimulating effect. A complex interaction exists between auxin and KAR signaling: in seedling growth, KAR adapts to light response by suppressing the IAA signaling pathway. The interaction between JA and KAR is context-dependent; in some stress responses, these two pathways operate in parallel.

3.6 Peptide Hormones

(a) Discovery and Historical Development: The discovery of plant peptide hormones began in 1991 when Clarence Ryan and Gregory Pearce isolated a polypeptide called the system, consisting of 18 amino acids, from tomatoes [43]. The system is the first plant peptide hormone that triggers the synthesis of proteins produced after leaf damage, protecting the plant. This discovery revealed that plants also use molecules similar to hormonal peptides in animal nervous systems, causing great astonishment.

Then, in 1996, CLV3 (CLAVATA3) was published; this peptide was identified as the source of a critical signal regulating meristem size. With the successive discovery of peptide families such as phytosulfokin (PSK), RALF, IDA, CEP, RGF/GLV, and others in the 2000s and 2010s, this field became the fastest-growing frontier of phytohormone science. Today (by 2026), over 300 small peptide signals have been identified, and the field of 'peptide hormones' has solidified its place as an independent research discipline [44].

(b) Chemical Structure and Types: The peptide group is presented according to its structural characteristics and discovery date (Table 12).

Table 12: Major plant peptide hormone families.

Peptide Family	Length	Structural Feature	Year of Discovery
Sistemin	18 aa	Linear; specifically in Solanaceae	1991
CLV3/CLE	12–13 aa (mature)	Sulfate-containing hydroxyproline + arabinosyl modification	1996/2000
TDIF (CLE41/44)	12 aa	CLE domain; glycosylated	2008
PSK (Phytosulfokine)	5 aa	Two tyrosine sulfate groups	1996
RALF (Rapid Alkalization Factor)	~50 aa	Cysteine-rich; disulfide-bridged; base pH stimulant	2001
RGF/GLV/CLEL	13 aa	Sulfate-containing tyrosine; root meristem regulator	2010
IDA (Inflorescence Deficient in Abscission)	~12 aa (mature)	Hydroxyproline-containing; small secreted peptide	2003
CEP (C-terminally Encoded Peptide)	15 aa	Hydroxyproline-rich; root-derived soil signaling	2013
PEP (Plant Elicitor Peptides)	8–36 aa	Extended family; precursor propeptides	2006

(c) Role in Plant Physiology:

- **Apical Meristem Homeostasis (CLV3-WUS Cycle):** The meristem is the central hub of stem cells that continues to produce new organs throughout the plant. The CLV3 peptide is secreted by stem cells in the meristem center, maintaining meristem size through a feedback loop. CLV3 interacts with the stem cell stimulant WUSCHEL (WUS) in a negative feedback loop: as WUS increases, CLV3 increases; as CLV3 increases, WUS is suppressed. When this balance is disrupted, the meristem either overexpands or rapidly depletes; both situations are disastrous for plant development.
- **Vascular Cambium Regulation (TDIF):** TDIF (Xylem Differentiation Inhibitory Factor; CLE41/CLE44), secreted from phloem cells, maintains proliferation of the procambium (vascular meristem) and suppresses xylem differentiation. This keeps the cambium active and ensures that secondary stem growth (bark ring formation) continues in an orderly fashion. This peptide signaling is critical for secondary growth in woody plants.
- **Organ Deposition (IDA):** The IDA (Abscission-Failed Inflorescence) peptide is one of the key messengers that triggers the abscission process in organs. During the period when the flower is about to detach, IDA is released at the abscission site, leading to the release of cell wall-degrading enzymes. IDA has been shown to play a role in flower, leaf, and fruit abscission; this peptide controls the timing of abscission in coordination with ethylene.
- **Root Growth and Root Hair Development (RGF, RALF, CLE):** RGF/GLV peptides determine the size of the root meristem and the identity of cortex cells. RALF peptides control cell growth by raising (basicating) the pH in the root elongation zone; they also regulate poll channels and osmotic conditions. CEP peptides, under nitrogen deficiency conditions in the soil, pass from the root to the phloem, transmit signals to distant tissues, and initiate the systemic nitrogen response.
- **Defense and Immunity (PEP, Sistemin):** Members of the PEP (Plant Stimulating Peptides) family are released as 'danger signals' in situations such as cellular damage, pathogens, or insect attacks. These peptides are also defined as DAMP (Damage-Associated Molecular Pattern) signals and activate both local and systemic immune responses. Sistemin, on the other hand, is the insect attack-specific response coordinator in tomato plants; damage in a single area initiates proteinase inhibitor synthesis throughout the entire plant.
- **Stomatal Development:** Peptides STOMAGEN/EPFL9, EPF1, and EPF2 from the EPF (Epidermal Pattern Factor) family regulate stomatal number and stomatal opening. These peptides function as "space occupation signals", enabling stomata to avoid neighboring cells. This peptide system, which targets stomatal density, stands out as a biotechnological target for drought tolerance.

(d) Hormones It Works with and Substances That Reduce Its Effect: Peptide hormones exhibit extensive cross-interaction with classical phytohormones. In the CLV3-WUS system, cytokinin promotes WUS activation, indirectly increasing CLV3 levels; thus, cytokinin indirectly affects meristem size via the peptide. TDIF coordinates root and vascular growth by affecting auxin homeostasis and PIN protein expression. IDA and ethylene work in coordination during organ abscission; auxin, however, can antagonize the effect of IDA at the abscission site. CEP peptides interact with ABA and cytokinin in the systemic nitrogen response. The system stimulates jasmonic acid biosynthesis; application of the system is ineffective in jasmonic acid deficiency mutants.

4 Interaction and Crosstalk of Hormones

Phytohormones do not function in isolation; rather, they influence each other within a complex network of coordination and balance. These interactions are essential for growth-defense balance, abiotic stress tolerance, reproduction, and life cycle coordination. Table 13 summarizes the main bidirectional hormone interactions.

Table 13: Key interactions between phytohormones, their contexts, and examples.

Hormone Pair	Type of Interaction	Physiological Context	Example Effect
Auxin–Cytokinin	Antagonist (ratio-dependent)	Organ morphogenesis, apical dominance	High Auxin → root; high CK → shoot.
Auxin–SL	Synergy + sequential arrangement	Apical dominance, branch pruning	Auxin stimulates SL synthesis; together they repress branch lines.
Auxin–Ethylene	It depends on the context	Fruit, root, and organ shedding	High auxin levels trigger ethylene synthesis.
GA–ABA	Antagonist (the strongest opposite)	Seed dormancy and germination	GA initiates germination; ABA stops it.
GA–DELLA–Others	Integrator hub	Growth, light, stress	DELLA connects directly to JA/light/auxin pathway components.
SA–JA	Antagonist (classic)	Biotic stress: pathogens, insects, etc.	High SA → JA is suppressed; high JA → SA is suppressed.
JA–Ethylene	Synergist (defense)	Injury and necrotrophic pathogens	Together they activate defense genes.
ABA–SA	It depends on the context	Pathogen response and water stress	Synergistic in water stress; SA may be suppressed in pathogen response.
SL–Cytokinin	Antagonist (bud)	Branch bud activation	SL suppresses bud formation; CK activates it.
SL–ABA	Synergist (water stress)	Drought tolerance, stomata	Together they close the stoma; saving water.
BR–Auxin	Synergistic (growth)	Cell elongation, shoot	Together, they stimulate elongation more than their sum.
BR–JA	It depends on the context	Growth-immunity balance	BR dominant → growth; JA dominant→immune.
SA–Ethylene	Antagonist (maturation)	Fruit and flower life	SA reduces ethylene biosynthesis; shelf life is extended.
KAR–SL	Partially overlapping, partially separate	Germination and branch pruning	MAX2 is shared; KAR → germination, SL → branch suppression.
KAR–ABA/GA	Antagonist/synergist	Seed germination	KAR suppresses ABA and increases GA, initiating germination.
CLV3/CLE–Cytokinin	Synergist (meristem)	Meristematic homeostasis	CK increases WUS activation; indirectly stimulates CLV3.
IDA–Ethylene	Synergist (abscision)	Leaf, flower, and fruit shedding	Together, they activate the abscess zone.
Sistemin–JA	JA biosynthesis stimulant	Insect defense	Without the system, JA production will be insufficient.

As this table clearly shows, a large proportion of hormonal interactions are 'context-dependent'. The same two hormones can exhibit synergy or antagonism in different tissues, different developmental stages, or different stress conditions. This flexibility is an evolutionary solution that allows plants to manage an infinite number of environmental conditions with a very limited number of chemical signals.

5 Agricultural Applications and Environmental Impacts of Growth Regulators

Plant growth regulators (PGRs) are indispensable components of modern agriculture. From the use of auxins (IBA, NAA) in vegetative propagation for rooting cuttings, to the application of gibberellins to increase fruit size in grapes; from the inclusion of TDZ in tissue culture protocols for shoot propagation, to ethylene-based ripening technologies (Ethephon), PGRs are present in every stage of modern plant production.

In recent years, strigolactone analogs (GR24) and karrikin preparations have become the focus of research, particularly in terms of drought and salinity stress management and sustainable agricultural practices. These compounds, effective at nanomolar concentrations, can offer alternatives to traditional BBDs with their low environmental risk and high yield potential.

From an environmental perspective, the indiscriminate and excessive use of BODs carries several risks, primarily including contamination of groundwater, impacts on soil microbiome balance, and accumulation through the food chain. Synthetic auxins (2,4-D, 4-CPA), in particular, are restricted or banned in many countries due to their acute toxic and carcinogenic effects. In ethylene applications, a waiting period of 7–21 days before the products are ready for consumption is recommended. Gibberellins and cytokinins are considered safer BODs with a relatively low toxicity profile (Category III); however, research on their long-term ecological effects is ongoing [45–47].

6 Conclusion and Future Perspectives

Phytohormones are a rapidly expanding field of research in recent years, playing a central role in the regulation of plant growth and development. This family of hormones, not limited to the classic five (auxin, cytokinin, gibberellin, abscisic acid, and ethylene), now includes newer members such as brassinosteroids, salicylic acid, jasmonic acid, strigolactones, karrikins, and peptide hormones, coordinating almost all processes of plant physiology.

This review has been prepared to meet the needs of agricultural engineers and applied researchers. It aims to provide a practical perspective without getting bogged down in complex molecular details, by systematically addressing each hormone class in terms of its discovery history, chemical structure, physiological roles, and interactions with other hormones. Particular emphasis is placed on stress tolerance, growth-defense balance, and crosstalk between hormones.

Today, knowledge of phytohormones is critical not only from a fundamental scientific perspective but also in the production of resilient plants to the drought, salinity, heat stress, and biotic threats posed by climate change. The intelligent and sustainable use of plant growth regulators in agriculture has become a vital tool for increased yields, resource efficiency, and environmental protection.

Future Perspectives

The following issues are expected to come to the forefront in the coming period:

1. Development of structural diversity of strigolactones and adaptable analogs for agricultural applications;
2. Discovery of endogenous ligand (KL) of karrikins and their agricultural uses outside of fire ecology;
3. Precise regulation of stomatal density, meristem control and organ shedding by targeting peptide hormones with CRISPR technology;
4. Holistic modeling of hormone crosstalk and its use in breeding climate change resistant varieties.

In conclusion, a better understanding of the phytohormone networks that have been shaped by millions of years of evolutionary processes will be one of the cornerstones of sustainable agriculture in the face of increasing global population and changing climate conditions. Our greatest hope is that this review will contribute to agricultural production by building a bridge of knowledge between researchers and practitioners.

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