Chapter 8
Plant Growth Hormones and Other Phytochemicals

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8.1 Introduction

Plants need light, carbon dioxide, water, and minerals, including nitrogen in soil, for its growth. With these conditions, the plant has the ability to transform some simple materials into complex organic substances that compose all living organisms. In this way, plant hormones and phytohormones have a very important function or activity in the growth regulation. Hormones are organic substances that are produced in a tissue and transported to another, where they provoke a physiological response. They are active in very low concentrations. The term hormone comes from the Greek and means "impetus."

It is known that in many instances, plant development can be dramatically influenced by a set of five structurally simple phytohormones, auxins, ethylene, cytokinin, abscisic acid (ABA), and gibberellins, each of which can elicit different responses. Experimental and theoretical approaches to this problem have prompted a long-standing debate concerning the relative importance of variations in phytohormone concentration versus differential sensitivity of different plant cells to particular phytohormones (Palme et al. 1991).

This chapter intends to show the most important information, such as definition, structure, action, and lastly the advances, about the main groups of plant hormones auxins, ethylene, cytokinin, ABA, and gibberellins.

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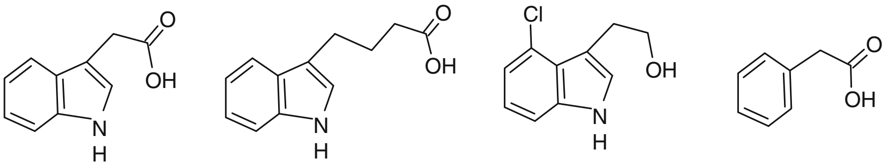
8.2 Auxins

The term auxin (from Greek "auxein," meaning "to increase" or "to grow") includes a spectrum of compounds that differ structurally and bring about a variety of auxin-type responses, albeit to varying degrees.

Since the original discovery of auxin as an indole compound that gave the grass coleoptile curvature (or growth) is tested, the definition of auxins has been broadened to include not only indole-3-acetic acid (IAA) but several other indole as well as non-indole compounds. Simon and Petrasek (2011) presented that many heterogeneous synthetic substances have auxin activity, complicating studies of structure–activity and the search for a common mode of action (Ferro et al. 2010). Even the most frequently used synthetic auxins, 2,4-dichlorophenoxyacetic acid (2,4-D) and naphthalene-1-acetic acid (NAA), do not completely share their mechanism of action with native IAA. Only indole-3-butyric acid (IBA), phenylacetic acid (PAA), and 4-chloroindole-3-acetic acid (4-Cl-IAA) (Fig. 8.1) are synthesized by plants and therefore qualify as "endogenous auxins," but their roles and mechanisms of action have not been satisfactorily described (Simon and Petrasek 2011).

8.2.1 Indole-3-Acetic Acid

IAA is the most widely distributed, naturally occurring auxin in vascular plants, dicots, monocots, gymnosperms, and ferns. There are also reports of IAA being present in mosses and liverworts, as well as in some green algae (e.g., *Caulerpa*). IAA is a weak acid with a pH of 4.85. It occurs in dissociated state at neutral pH solutions. IAA is involved in nearly every aspect of plant growth and development, from embryo to adult reproductive plant. The processes regulated include pattern formation in embryo development, induction of cell division, stem and coleoptile elongation, apical dominance, induction of rooting, vascular tissue differentiation, fruit development, and tropic movements such as bending of shoots toward light or of roots toward gravity.



Indole-3-acetic acid (IAA)

Indole-3-butyric acid (IBA)

4-chloroindole-3-acetic acid (4-Cl-IAA)

Phenylacetic acid (PAA)

Fig. 8.1 Chemical structure of four endogenous auxins. Indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), 4-chloroindole-3-acetic acid (4-Cl-IAA), and phenylacetic acid (PAA)

It is difficult to unambiguously define typical “auxin activity.” Auxin displays morphogenic properties that are modulated by the environment and defined by dynamic changes in its perception and signal transduction. This machinery has been intensively studied during the past decade and includes effects that are either dependent or independent of gene expression (Bhalerao and Bennett 2003). Thus, “auxin action” may be understood as the sum of all these processes (Simon and Petrasek 2011). Later research convincingly demonstrated that auxin is required together with other plant hormones for both cell division and oriented cell expansion (Perrot-Rechenmann 2010), influencing all aspects of plant development (Vanneste and Friml 2009).

The isolation of plant mutants related to auxin showed that the modification of the regulation of auxin biosynthesis, transport, or signaling generates severe alterations in many aspects of plant development. For example, the auxin overproducer mutant *Yucca* leads to defects in vascular tissue formation (Cheng et al. 2007). Disruption in auxin transport, in the mutant *pin1*, leads to defects in floral development (Okada et al. 1991). Finally, mutation in auxin signaling can trigger a global dwarfism as for the auxin-resistant *axr112* mutant (Lincoln et al. 1990), the absence of root formation as for the monopteros (*mp*) mutant (Hamann et al. 2002), or even embryo lethality as for the *abp1* null mutant (Chen et al. 2001). This demonstrates that in plants, the phytohormone auxin plays a central role in plant growth and development.

Auxin is considered as a morphogen since it regulates the development in a dose-dependent manner (Bhalerao and Bennett 2003). It highlights the importance of auxin gradients and the necessity of a subtle regulation of auxin concentration at the scale of organ, tissues, or even cells. To achieve such regulation, plants have developed various mechanisms aimed at controlling auxin homeostasis and the dynamics of auxin redistribution. In addition, various tissues exhibit distinct sensitivity to auxin, thus reflecting that the responsiveness (perception and signaling) is also tightly modulated (Tromas and Perrot-Rechenmann 2010).

8.2.2 Auxin-Binding Soluble Proteins

Shishova and Lindberg (2010) reported that for more than 100 years, the most intriguing question in plant physiology has been how IAA might trigger such enormous variety in physiological responses. According to recent knowledge, a broad spectral activity is observed, which might correlate with changes in the number and properties of auxin receptors. These proteins are responsible for recognition of the hormone and the initiation of further signal transduction chains, resulting in a specific physiological response. Thus, one of the main properties of the auxin receptor is its capability to bind auxin. An investigation of auxin-binding sites in plant cells started almost 30 years ago (Hertel et al. 1972). It has showed a heterogeneity of these sites both in affinity and localization. So, the pool of plant cell auxin-binding proteins (ABPs) consists of two groups: soluble and membrane-bound proteins.

Early biochemical investigations identified a number of auxin-binding soluble proteins such as 1,3-glucanase (MacDonald et al. 1991), β-glucosidase (Campos et al. 1992), glutathione S-transferase (Bilang et al. 1993), and superoxide dismutase (Feldwisch et al. 1994). Two soluble ABPs with a relatively low affinity for IAA were purified and reported to stimulate RNA synthesis in isolated nuclei (Kikuchi et al. 1989). Later, it was shown that one of these protein-bound RNA polymerase II had DNA-binding activity (Sakai 1992). Another polypeptide, a 65-kDa protein, was also found to have a nuclear localization (Prasad and Jones 1991). A soluble ABP 44-kDa protein showed a close link to auxin effects on elongation growth and high affinity labeling of chlorinated auxins (Reinard and Jacobsen 1995; Reinard et al. 1998).

8.3 Gibberellins

The first reports about gibberellins (GAs) came from a group of Japanese scientists who focused some of their studies on a disease called bakanae, which particularly affected rice produced by local farmers (Hori 1903). Bakanae disease is caused by one or more *Fusarium* species. This disease produces a myriad of symptoms, including seedling blight, root and crown rot, stunting, and the classic symptoms of etiolation and abnormal elongation induced by the fungal production of gibberellins (Sun and Snyder 1981; Webster and Gunnell 1992; Nicholson et al. 1998).

Although bakanae disease was described and identified more than 100 years ago in Japan, it is still not clear which *Fusarium* species are associated with the various symptoms of the disease (Ou 1985). Earlier studies in Japan contributed to the identification of a pathogen known as "*Fusarium moniliforme*" in a broad sense (Ou 1985). However, this taxon comprises a number of distinct species, now collectively named the *Gibberella fujikuroi* species complex. The formation of *Gibberella's* sexual stage can distinguish mating populations, or biological species, within this group (Hsieh et al. 1977; Kuhlman 1982; Leslie 1995).

In the 1950s, the British firm Imperial Chemical Industry (ICI) began a program to select for strains of *F. moniliforme* that had a greater capacity to produce gibberellins, and attempts were made to optimize liquid and surface fermentation studies. After some purification steps, a gibberellin was isolated and called "gibberellic acid." These gibberellins had the molecular formula $C_{19}H_{22}O_6$ and had various physiological properties of the gibberellin A that was previously discovered in Japan. This fact stimulated Japanese researchers to produce gibberellins and separate them into three products: gibberellins A_1, A_2, and A_3. Gibberellin A_3 was identified as the gibberellic acid produced by ICI (Takahashi 1986).

In the 1960s, a series of studies were carried out on the application of GAs on various plants, poultry, animals, and microorganisms (Mees and Elson 1978). Since then, several production techniques have been developed in order to make the process more reproducible and economically viable.

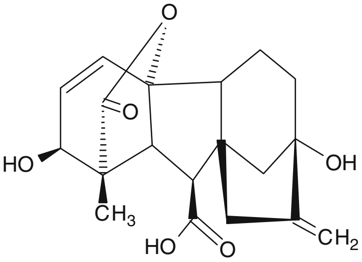


Fig. 8.2 Basic structure of the GAs

Currently, there are 136 gibberellins (GAs) isolated from plants, produced by microorganisms such as fungi and bacteria or obtained synthetically (Blake et al. 2000; Bömke and Tudzynsk 2009). Gibberellins are designated by GAn where "n" corresponds, approximately, to the order of its discovery.

All gibberellins have an *ent*-gibberellane (Fig. 8.2) ring system and are divided in two main types based on the number of carbon atoms, the C_{20}GAs which have a full complement of 20 carbon atoms and C_{19}GAs in which the twentieth carbon atom has been lost by metabolism. Besides the carbon number, the gibberellins differ in the number and position of hydroxyl groups, on the oxidation state of C_{20}, and the presence or absence of lactone bridge between C_{10} and C_{19}.

The effects of GAs on plant growth and development are mediated through gene expression modulation, as RNA and protein synthesis inhibitors interfere with these processes. To further understand the molecular mechanism by which GA regulates the growth and development of plants, it is necessary to identify and analyze more genes that are controlled by GA. Microarrays provide high-throughput, simultaneous analysis of mRNA for hundreds and thousands of genes (Aharoni and Vorst 2002); however, there are only a few reports on the microarray analysis of GA-regulated gene expression in *Arabidopsis* and rice (Ogawa et al. 2003; Yamauchi et al. 2004; Yang et al. 2004; Yazaki et al. 2004). A throughput analysis of transcript profiles in GA-regulated gene expression using different plant tissues and organs remains pertinent, and further characterization of the individual genes will help in understanding how GA regulates the growth and development of plants.

8.3.1 Gibberellic Acid

Gibberellic acid (GA_3) is an important member of the gibberellin family and acts as a natural plant growth hormone, controlling many developmental processes, and is gaining great attention all over the world due to its effective use in agriculture, nurseries, tissue culture, tea gardens, etc. (Davies 2004; Shukla et al. 2005). GA_3 is used in ppm levels, and its use results in various physiologic effects. Some of its applications are presented in Table 8.1.

Table 8.1 Applications of GA_3

Application	Action/benefit	Reference
Application on flowering of *Helleborus niger* and *Helleborus* x *ericsmithii*	Progressive decrease of the time to flower	Christiaens et al. (2012)
Effects of GA_3 and calcium chloride in restoring the metabolic alterations resulting from salt stress in linseed	Increased plant height, number of branches, number of leaves, leaf area, fresh and dry weights	Khan et al. (2010)
Influenced all the vegetative parameters of "Chandler" strawberry	Crown height, crown spread, petiole length, leaf number, and leaf area	Sharma and Singh (2009)
Pea seeds	Stimulate shoot growing	Baumgartner et al. (2008)
Potato cultivation	Promote cell multiplication and elongation, breaking of dormancy	Alexopoulos et al. (2007)
Fruitful tree "Yu Her Pau" litchi	Raise fruit weight	Chang and Lin (2006)
Passiflora nitida Khunt	Effect on germination—breaking of dormancy	Passos et al. (2004)
Grapes of cultivars Vênus	Raise berries mass and number, decrease seeds number	Botelho et al. (2003)

The cost of GA_3 has precluded its use in promoting plant growth, except for certain high-value plants. A reduction of its production costs could lead to wider applications for a variety of crops (Linnemannstons et al. 2002).

Recently, studies have been carried out to decrease GA_3 production costs using several approaches, such as screening fungi, optimizing the nutrients and culture conditions, using agro-industrial residues as a substrate, developing new processes (immobilized cells, fed-batch culture, airlift bioreactor) and minimizing the extraction procedure costs (Rodrigues et al. 2012).

8.4 Cytokinins

Cytokinins (CKs) are a class of phytohormones that play an important role at all phases of plant development from seed germination to senescence. At the organism level, CKs take part in the control of many biological processes throughout the life of plants. They act on induction expression of some genes, promotion of mitosis, and chloroplast development and by releasing buds from apical dominance or by inhibiting root growth (Riefler et al. 2006; Kakimoto 2003; Sakakibara 2006; Werner et al. 2001). Moreover, CKs were found to negatively regulate stress signaling (Nishiyama et al. 2011) and iron accumulation in the leaf (Werner et al. 2010). In tomatoes, salt and drought stresses were linked to reduced CK content (Albacete et al. 2008; Ghanem et al. 2008; Kudoyarova et al. 2007).

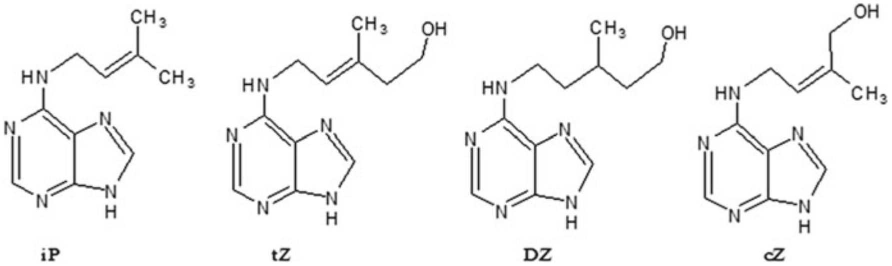


Fig. 8.3 Chemical structures of isoprenoids CKs: N^6-(Δ^2-isopentenyl) adenine (iP), *trans*-zeatin (tZ), *cis*-zeatin (cZ) and dihydrozeatin (DZ)

The CKs was discovered during the 1950s because of the powerful ability of these purine derivatives to trigger plant cell division in vitro. Rapidly thereafter, a variety of additional activities of the hormone were described, including the capability to induce the formation of shoots from unorganized callus tissue, to retard leaf senescence, to stimulate pigment accumulation, and to support plastid development (Heyl et al. 2012).

Currently, there are numerous studies about the possible uses and functions of CKs, such as delay of senescence (Gan and Amasino 1995; Kim et al. 2006), root proliferation (Werner et al. 2001, 2003), apical dominance (Shimizu-Sato et al. 2009; Tanaka et al. 2006), nutritional signaling (Samuelson and Larsson 1993; Takei et al. 2001), and shoot meristem function (Higuchi et al. 2004; Kurakawa et al. 2007; Nishimura et al. 2004; Miyawaki et al. 2006). The CKs also mediates the responses to variable extrinsic factors, such as light conditions in the shoot and availability of nutrients and water in the root, and has a role in the response to biotic and abiotic stress. Together, these activities contribute to the fine-tuning of quantitative growth regulation in plants.

The CKs has been targeted in many plant species to improve their tolerance to different environmental stresses (Barna et al. 1996; Huynh et al. 2005; Havlova et al. 2008; Zhang and Ervin 2008). Exogenous application of CK has been shown to have potential in alleviating heat injury in various higher plants (Skogqvist 1974; Liu et al. 2002; Schrader 2005). For example, retarded leaf senescence and reduced cell membrane lipid peroxidation in creeping bentgrass were observed via exogenous zeatin riboside application and enhanced antioxidant response. This fact was suggested as a possible mechanism for the observed reductions in heat injury (Liu et al. 2002; Zhang and Ervin 2008), also indicating that CK is thought to protect plants under stress via its antioxidant properties (Wang et al. 2012).

Naturally occurring CKs are adenine derivatives that carry either an isoprene-derived side chain or an aromatic side chain at the N^6 terminus, called isoprenoid CKs or aromatic CKs, respectively (Mok and Mok 2001; Sakakibara 2006). The isoprenoid CKs are classified into one of the four basic molecules: N^6-(Δ^2-isopentenyl) adenine (iP), *trans*-zeatin (tZ), *cis*-zeatin (cZ), and dihydrozeatin (DZ) (Fig. 8.3). Each CK molecule is distinguished by characteristics of the side chain, namely, the presence or the absence of a hydroxyl group at the end of the prenyl chain and the stereoisomeric position.

Among isoprenoid CKs, *trans*-zeatin is considered central due to its general occurrence and high activity in the most bioassays. Its stereoisomer, *cis*-zeatin, is characterized by weak activity in bioassays. Dihydrozeatin and N^6-(Δ^2-isopentenyl)-adenine are also commonly present in lower and vascular plants (Emery et al. 1998; Sakakibara 2006; Stirk et al. 2008).

N^6-Benzyladenine and its derivatives, representing aromatic CKs, have been detected in a number of plant species as minor components of the total CKs. Hydroxylated derivatives of N^6-benzyladenine in meta or ortho position of benzyl group are commonly named as meta- and ortho-topolin, respectively (Strnad et al. 1997). Kinetin, the most known CK, has furfuryl ring at the N^6-position of adenine and was identified in both animal cellular DNA and plant tissue extracts (Barciszewski et al. 2000).

All forms of CKs may be reversible or irreversible conjugated with sugars and amino acids. In most bioassays, CK bases are the most active, and therefore, CK conjugation contributes to the regulation of their activity. CK conjugates seem to serve as storage, transport, and deactivate forms because they are resistant to degradation by cytokinin oxidase/dehydrogenase (Auer 2002; Blagoeva et al. 2004).

8.5 Abscisic Acid

Absicisic acid (ABA) belongs to a class of metabolites known as isoprenoids, also called terpenoids. ABA, which contains 15 carbon atoms, belongs to a class of metabolites known as isoprenoids also called terpenoids (Fig. 8.4). ABA was discovered in the early 1960s. Originally it was believed to be involved in the abscission of fruit and dormancy of woody plants. However, in later studies, it became evident that ABA is necessary for seed development, adaptation to several abiotic stress, and sugar sensing (Zeevaart and Creelman 1988; Nambara and Marion-Poll 2005; Schwartz and Zeevaart 2010).

ABA is not only synthesized by higher plants, it is also produced by certain algae (Zeevaart and Creelman 1988), by several phytopathogenic fungi (Zeevaart and Creelman 1988; Tudzynski and Sharon 2002) and by bacteria (Karadeniz et al. 2006).

The metabolism pathway of ABA has been studied in plants and fungi. Since 1987, there were many in vivo and in vitro biochemical studies of ABA metabolism, including studies of ABA-deficiency mutants, that have established an outline of the probable biosynthesis route. It was thought that all isoprenoids were synthesized

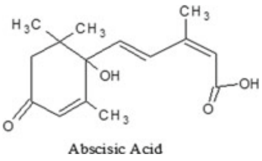


Fig. 8.4 Abscisic acid

Table 8.2 Application of ABA in plants

Application	Action/benefit	Reference
Blueberries (*Vaccinium darrowii*)	Increase the firmness	Buran et al. (2012)
Arachis hypogaea L.	Inhibits lateral root primordial initiation	Guo et al. (2012)
Wheat	Effect of cold acclimation and ABA on amino acid content and composition	Kovacs et al. (2011)
Plant defense against pathogens	Processes of plant defense against pathogens such as virus, fungi, and bacteria	Song et al. (2011); Iriti and Faoro (2008); Vysotskaya et al. (2008); De Torres-Zabala et al. (2007)
Arabidopsis roots	Have a negative effect to gravitropic response as regard to root growth in Arabidopsis roots	Han et al. (2009)
Tobacco plants	Increase the hydraulic conductance of whole tobacco roots and stimulated aquaporin expression	Mahdieh and Mostajeran (2009)
Maize seedlings	Induction of cytosolic Ca^{2+} concentration of mesophyll cells	Guo et al. (2008)
Rice	Involvement of H_2O_2 (hydrogen peroxide) in ABA-induced anthocyanin accumulation in rice leaves	Hung et al. (2008)
Canarian laurel trees	Response of gas exchange and osmotic adjustment capacity in drought-treated trees	Sánchez-Díaz et al. (2008)
Carrot (*Daucus carota*)	Somatic embryo development	Shiota et al. (2008)

from mevalonic acid (MVA), but recently, it was shown that carotenoids and ABA are formed by the "non-mevalonate" triose-pyruvate pathway (from pyruvate to isopentenyl diphosphate) in chloroplasts (Milborrow and Lee 1998; Tudzynski and Sharon 2002; Nambara and Marion-Poll 2005).

8.5.1 ABA Effects in Plants

ABA seems to act as a general inhibitor of growth and metabolism, but, like other plant hormones, ABA has multiple roles during the life cycle of a plant (Zeevaart and Creelman 1988; Srivastava 2002). It plays an important role in modifying transpiration of drought-treated plants. It also acts in stomatal conductance affecting the water supply of the plant (Larcher 2003; Guo et al. 2008; Aasamaaa and Sõberb 2011). Other applications of ABA in plants are presented in Table 8.2.

Table 8.3 ABA production by bacteria

Microorganism	Culture medium	ABA production	Reference
Azospirillum brasilense strain Sp 245	NFb medium with NH_4Cl and NaCl	235 ± 17 ng/ml	Cohen et al. (2008)
Azospirillum brasilense strain Sp 245	NFb medium with NH_4Cl	73 ± 8 ng/ml	Cohen et al. (2008)
Isolated endophytic bacteria from sunflower	LB supplemented with polyethylene glycol	20–45 pmol/ml	Forchetti et al. (2007)
P. mirabilis	Brain heart broth	4.20 ± 1.75 μg/100 ml	Karadeniz et al. (2006)
P. vulgaris	Brain heart broth	0.44 ± 0.02 μg/100 ml	Karadeniz et al. (2006)
B. megaterium	Brain heart broth	0.07 ± 0.00 μg/100 ml	Karadeniz et al. (2006)
B. cereus	Brain heart broth	0.03 ± 0.01 μg/100 ml	Karadeniz et al. (2006)
K. pneumoniae	Brain heart broth	0.91 ± 0.10 μg/100 ml	Karadeniz et al. (2006)
E. coli	Brain heart broth	1.45 ± 1.00 μg/100 ml	Karadeniz et al. (2006)

8.5.2 ABA Production by Microorganisms

The presence of ABA was demonstrated in several fungi, such as *Cercospora rosicola*, *C. cruenta*, *Botrytis cinerea,* and other phytopathogenic fungi, as a secondary metabolism product (Zeevaart and Creelman 1988; Tudzynski and Sharon 2002). Budková et al. (2000) demonstrated that micromycetes from soil, *Aspergillus niger* and *Cladosporium cladosporioides*, produced ABA into the culture medium Czapek-Dox and a liquid medium.

Yurekli et al. (1999) utilized white-rot fungi *Funalia trogii* ATCC 200800 and *Trametes versicolor* ATCC 200801 to produce ABA, and as substrate, they utilized olive oil mill wastewater (OOMW) and vinasse, with a dilution ratio of 20:80, v/v (wastewater/distilled water). The higher ABA concentration was obtained utilizing *F. trogii* and vinasse (170.41 μg/ml) and utilizing OOMW as a substrate concentration of 16.28 μg/ml was obtained. *T. versicolor* fungus produced 34.95 μg/ml using vinasse and 5.32 μg/ml utilizing OOMW.

Plant growth-promoting bacteria (PGPB) such as *Azospirillum* produce phytohormones including ABA (Forchetti et al. 2007; Cohen et al. 2008). Bacteria commonly found in the human body which also live in the soil and in water (*Proteus mirabilis*, *P. vulgaris*, *Bacillus megaterium*, *B. cereus*, *Klebsiella pneumoniae*, *Escherichia coli*) also produce ABA (Karadeniz et al. 2006). Some studies that report the production of ABA by bacteria can be seen in Table 8.3.

8.5.3 ABA Analyses

Several methods have been established for measurement of ABA, such as thin layer chromatography (TLC). It has been used with ultraviolet (UV) lamp and the mobile phase of benzene, ethyl acetate, and acetic acid (Budková et al. 2000) and isopropanol, ammonia, and distilled water (Karadeniz et al. 2006). High-performance liquid chromatography (HPLC) coupled to UV detector also has been utilized (Budková et al. 2000; Karadeniz et al. 2006).

Gas chromatography coupled to mass spectrometry (GC–MS) was reported for analysis of ABA (Forchetti et al. 2007; Cohen et al. 2008).

Recently, liquid chromatography–electrospray ionization tandem mass spectrometry (LC–ESI-MS/MS) has been applied to the determination of phytohormones including ABA (Hou et al. 2008; López-Carbonell et al. 2009).

8.6 Ethylene

Ethylene is an unsaturated hydrocarbon which plays various important functions in plant growth and development, such as seed germination, flower and fruit development, dormancy, abscission, senescence, certain plant defense mechanisms, and a number of interactions with other plant hormones (Abeles et al. 1992; Arteca 1996; Binder 2008).

Ethylene is produced by higher plants and also by bacteria and fungi (Kanellis et al. 1999; Al-Masri et al. 2006). In higher plants, ethylene is biosynthesized from methionine by a well-defined pathway in which methionine is first converted to *S*-adenosyl methionine (SAM) which is then used for the production of 1-aminocyclopropanecarboxylic acid (ACC) by the enzyme ACC synthase. ACC oxidase converts ACC to ethylene (Yang and Hoffman 1984).

Ethylene is a gaseous hormone, and because of this, gas chromatography has been utilized for ethylene analysis. Orberá Ratón et al. (2012) and Thuler et al. (2003) utilized GC equipped with a PORAPAK-N 80/100—INOX column that operated isothermally at 70 °C with nitrogen as gas carrier and flame ionization detector. Visible/short-wave near-infrared (Vis/SW NIR) spectroscopy technique was proposed for the determination of ethylene content in tomatoes by Xie et al. (2009).

8.6.1 Effects of Ethylene in Plants

One of the most studied ethylene effects were reported in fruit ripening. Fruit ripening can also be diverse; however, it involves many closely related changes such as color change, softening of walls, and conversion of starch to sugar (Barry and Giovannoni 2007). Fruits known as climacteric, such as banana, apple, avocado, and tomato, produce ethylene which influences the fruit ripening process. Other fruits that are known as nonclimacteric, such as grape, citrus, and strawberry, show no climacteric and no significant production of ethylene. Even though, they show ripening-related changes (Srivastava 2002; Barry and Giovannoni 2007).

Applications of ethylene in plants are shown in Table 8.4.

Table 8.4 Applications of ethylene in plants

Application	Action/benefit	Reference
Arabidopsis thaliana	Ethylene in the response of root hair cells	Galland et al. (2012)
Gentiana scabra flowers	Ethylene production of unpollinated flowers was very low, but pollination increases ethylene production	Shimizu-Yumoto and Ichimura (2012)
Mexican "Ataulfo" mango	Improving the uniformity in ripening	Tovar et al. (2011)
Spinach (*Spinacia oleracea* L. cv Bison)	Effect of ethylene on ascorbic acid (antioxidant) metabolism during dark-induced leaf senescence	Gergoff et al. (2010)
Tomato and pepper fruits	Existence of extensive common regulons suggests the conservation of ripening mechanisms in climacteric and nonclimacteric fruits	Lee et al. (2010)
Carrot	Exposure to methyl jasmonate and ethylene treatments enhanced the accumulation of bioactive phenolic compounds and phenylalanine ammonia lyase enzyme activity in carrot tissue	Heredia and Cisneros-Zevallos (2009)
Sand verbenas (*Abronia* spp.)	Effects on the germination	Drennan (2008)
Guzmania lingulata Mez. "Anita"	Endogenous ethylene production contributes substantially to floral induction. Ethylene treatment on a single young leaf induced flowering as well	Dukovski et al. (2006)
Hydroponically grown strawberry plants	Ethylene levels from leaves are useful as an early indicator of stress conditions within the system	Hogan et al. (2006)
Potato tuber (*Solanum tuberosum* L.)	Determination of hormonal requirements for wound-induced suberization	Lulai and Suttle (2004)
Carnation cultivars (*Dianthus caryophyllus* L.)	Continuous and short exposures of ethylene reduce the vase life of flowers	Wu et al. (1991)

8.6.2 Ethylene Production by Microorganisms

Beside plants, ethylene can be produced by microorganisms and can be obtained by cracking the petroleum, a process that requires crude oil and has severe effects on the environment (Tudzynski and Sharon 2002).

Ethylene production by fungus *Sclerotinia sclerotiorum* was observed by Al-Masri et al. (2006). Zhu et al. (2012) analyzed ethylene production by six strains of *B. cinerea* (a mass-destructive, necrotrophic plant pathogen that causes grey mold) and all were confirmed to produce ethylene. On grape juice agar (GJA) medium, *B. cinerea* produced ethylene without methionine (Met) addition. When Met was added, the fungus produced more ethylene than that on Czapek and potato dextrose agar (PDA) media.

Orberá Ratón et al. (2012) isolated bacteria and fungi from sugarcane rhizosphere and the isolated microorganisms. Four isolates produced ethylene, which correspond to *Bacillus* sp. B63 (134.12 ng/mL), *Brevibacillus* sp. (B65 279.44 ng/mL), *Bacillus* sp. B90 (870.8 ng/mL), and *Paenibacillus* sp. B100 (166.88 ng/mL).

A comparison of plant growth-promoting potential of rhizospheric bacteria from endophytic bacteria, both isolated from sugar cane, was studied by De Santi Ferrara et al. (2012). In the study, the ability of these bacteria to produce amino acids IAA and ethylene was assessed. The putative endophytes released significantly higher amounts of amino acids than the rhizospheric bacteria, while the latter produced higher quantities of ethylene and were more actively antagonistic to fungi. Both types of bacteria released similar amounts of IAA.

8.7 Phytochemicals

Phytochemicals are non-nutritive plant chemicals that have protective or disease-preventive properties. They are nonessential nutrients, meaning that they are not required by the human body for sustaining life (Karthishwaran et al. 2010; Srivastava et al. 2010; Badugu 2012; Neerati et al. 2012). Plant produces these chemicals as a natural defense against disease and infection, and they have been used throughout human history for various purposes. It has been recognized that natural compounds play an important role in modern pharmaceutical care. Numerous studies of folk medical practices have been undertaken to verify the real properties of some plants used in ancestral treatments (Kamanzi Atindehou et al. 2002; Neerati et al. 2012; Brusotti et al. 2013).

There are many phytochemicals known and each works differently. These phytochemicals have various health benefits such as antioxidant, antimicrobial, anti-inflammatory, cancer-preventive, antidiabetic, and anti-hypertensive effects (Kumar et al. 2009; Nisha Raj and Radhamany 2010; Srivastava et al. 2010). Antioxidant properties of plants have been studied to reduce oxidative stress which may cause various degenerative diseases (Bektas et al. 2005; Pereira et al. 2009). Antioxidant activity can be attributed to phenolic compounds (Girones-Vilaplana et al. 2012; Lv et al. 2012; Silva et al. 2012; Sousa et al. 2013; Jaberian et al. 2013), flavonoids (Girones-Vilaplana et al. 2012; Sousa et al. 2013), and vitamins (Girones-Vilaplana et al. 2012; Jaberian et al. 2013).

Extracts of plants were tested against fungi and bacteria and demonstrated antimicrobial activity. Brusotti et al. (2013) showed that tannin resulted more active against bacteria, while the saponin showed a pronounced activity against fungus *Pyricularia grisea*. Others studies have demonstrated a correlation between antibacterial activity and phytochemicals (alkaloid, saponin, phenol) (Akgul and Gulshen 2005; Doughari and Manzara 2008; Jaberian et al. 2013).

Phytochemicals have been utilized in other studies such as antiproliferative activities (Lv et al. 2012; Kontogianni et al. 2013), antipyretic activity (saponin, tannins, and flavonoids) (Sasmal et al. 2012), and anti-inflammatory activity (phenolic compounds and betacyanins) (Silva et al. 2012).

8.8 Conclusions

Auxins, gibberellins, ABA, cytokinins, and ethylene are the main groups of plant hormones. There are numerous reports that present the main applications and the way of action of these hormones, each of them having their specificities and potentialities. The transport and mode of action of each hormone are being elucidated. However, there are some technological barriers to surpass concerning the economical production and purification of these important biomolecules. In this way, many researchers are seriously involved to find best conditions for these bioprocesses.

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