**A TERM PAPER**

**ON**

**PLANT HORMONES**

**BY**

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**CHAPTER ONE**

**INTRODUCTION**

It is 60 years since Went and Thimann (1937) published their classic book Phytohormones. At that time, the term phytohormone was synonymous with auxin, although the existente of other phytohormones, such as cell division factors, was anticipated on the basis of physiological experiments. It is impressive that aside from some confusion about the structure of auxin, many of the basic phenomena of auxin physiology were already known at that time. It is equally impressive that much auxin biology, including the CholodnyWent hypothesis (Went and Thimann, 1937) regarding the role of auxin in mediating gravi- and phototropism, the pathway of auxin biosynthesis, and the mechanism by which auxin causes cell wall loosening, remains controversial. Since 1937, gibberellin (GA), ethylene, cytokinin, and abscisic acid (ABA) have joined auxin as phytohormones, and together, they are regarded as the “classical five” (Figure 1). This group is expected to grow as the hormonal functions of other compounds are recognized and as new hormones are discovered (see Creelman and Mullet, 1997, in this issue). As is evident from this short review, recent progress on hormone biosynthesis and on hormonal transduction pathways has been impressive. Also evident is that there are many blanks still to be filled in. With the application of the powerful new techniques of chemical analysis and molecular genetics, the rate at which new discoveries are made will continue to accelerate.

Plant hormones are a group of naturally occurring, organic substances which influence physiological processes at low concentrations. The processes influenced consist mainly of growth, differentiation and development, though other processes, such as stomatal movement, may also be affected. Plant hormones1 have also been referred to as ‘phytohormones’ though this term is infrequently used.

**CHAPTER TWO**

**LITERATURE REVIEW**

Plant hormones play important roles in regulating developmental processes and signaling networks involved in plant responses to a wide range of biotic and abiotic stresses. Significant progress has been made in identifying the key components and understanding the role of salicylic acid (SA), and ethylene (ET) in plant responses to biotic stresses. Recent studies indicate that other hormones such as abscisic acid (ABA), auxin, gibberellic acid (GA), brassinosteroids (BR) and peptide hormones are also implicated in plant defence signaling pathways but their role in plant defence is less well studied. This term paper will ensure to explain plant hormones, their types and everything about them.

**The Development of the Plant Hormone Concept and Early Work.**

The plant hormone concept probably derives from observations of morphogenic and developmental correlations by Sachs between 1880 and 1893. He suggested that "Morphological differences between plant organs are due to differences in their material composition" and postulated the existence of root-forming, flower forming and other substances that move in different directions through the plant (10). At about the same time Darwin (3) was making his original observations on the phototropism of grass coleoptiles that led him to postulate the existence of a signal that was transported from the tip of the coleoptile to the bending regions lower down. After further characterizations by several workers of the way in which the signal was moved, Went in the Netherlands was finally able to isolate the chemical by diffusion from coleoptile tips into agar blocks, which, when replaced on the tips of decapitated coleoptiles, resulted in the stimulation of the growth of the decapitated coleoptiles, and their bending when placed asymmetrically on these tips. This thus demonstrated the existence of a growth promoting chemical that was synthesized in the coleoptile tips, moved basipetally, and when distributed asymmetrically resulted in a bending of the coleoptile away from the side with the higher concentration. This substance was originally named Wuchsstoff by Went, and later this was changed to auxin. After some false identifications the material was finally identified as the simple compound indoleacetic acid, universally known as IAA (11).

**TYPES OF HORMONES**

**Auxin**

**Nature**

Indole-3-acetic acid (IAA) is the main auxin in most plants. Compounds which serve as IAA precursors may also have auxin activity (e.g., indoleacetaldehyde). Some plants contain other compounds that display weak auxin activity (e.g., phenylacetic acid). IAA may also be present as various conjugates such as indoleacetyl aspartate. 4-chloro-IAA has also been reported in several species though it is not clear to what extent the endogenous auxin activity in plants can be accounted for by 4-Cl-IAA. Several synthetic auxins are also used in commercial applications.

**Sites of biosynthesis**

IAA is synthesized from tryptophan or indole primarily in leaf primordia and young leaves, and in developing seeds.

**Transport**

IAA transport is cell to cell, mainly in the vascular cambium and the procambial strands, but probably also in epidermal cells. Transport to the root probably also involves the phloem.

**Effects**

* Cell enlargement - auxin stimulates cell enlargement and stem growth.
* Cell division - auxin stimulates cell division in the cambium and, in combination with cytokinin, in tissue culture.
* Vascular tissue differentiation - auxin stimulates differentiation of phloem and xylem.
* Root initiation - auxin stimulates root initiation on stem cuttings, and also the development of branch roots and the differentiation of roots in tissue culture.
* Tropistic responses - auxin mediates the tropistic (bending) response of shoots and roots to gravity and light.
* Apical dominance - the auxin supply from the apical bud represses the growth of lateral buds.
* Leaf senescence - auxin delays leaf senescence.
* Leaf and fruit abscission - auxin may inhibit or promote (via ethylene) leaf and fruit abscission depending on the timing and position of the source.
* Fruit setting and growth - auxin induces these processes in some fruit.
* Assimilate partitioning - assimilate movement is enhanced towards an auxin source possibly by an effect on phloem transport.
* Fruit ripening - auxin delays ripening.
* Flowering - auxin promotes flowering in Bromeliads.
* Growth of flower parts - stimulated by auxin.
* Promotes femaleness in dioecious flowers (via ethylene).

In several systems (e.g., root growth) auxin, particularly at high concentrations, is inhibitory. Almost invariably this has been shown to be mediated by auxin-produced ethylene. If the ethylene synthesis is prevented by various ethylene synthesis inhibitors, the ethylene removed by hypobaric conditions, or the action of ethylene opposed by silver salts (Ag+), then auxin is no longer inhibitory.

**Ethylene.**

The breakthrough in unraveling the biosynthetic pathway of ethylene was the discovery in 1979 that 1 -aminocyclopropane-1 -carboxylic acid (ACC) is the immediate precursor of ethylene (reviewed in Yang and Hoffman, 1984). The first committed step in ethylene biosynthesis is the conversion of S-adenosyl-L-methionine to 5'-methylthioadenosine and ACC; this is also the key regulatory step in ethylene biosynthesis. The enzyme that catalyzes this reaction, ACC synthase, was partially purified before the corresponding gene was cloned (reviewed in Kende, 1993; Zarembinski and Theologis, 1994). ACC synthase is encoded by a multigene family whose members are differentially expressed in response to developmental, environmental, and hormonal factors. For example, by using gene-specific probes, the differential expression of tomato ACC synthase family members has been investigated. Transcripts of one isoform increased during fruit ripening, those of another increased in response to wounding, and those of a third form increased in response to treatment with auxin (Olson et al., 1991 ; Yip et al., 1992). ACC synthase genes expressed in response to a particular stimulus (e.g., the application of auxin) are more similar to genes controlled by the same stimulus in other species than they are to other ACC genes in the same species (Liang et al., 1992; Trebitsh et al., 1997). The final step in ethylene biosynthesis, the conversion of ACC to ethylene, is catalyzed by ACC oxidase. ACC oxidase was first identified by expressing the tomato cDNA pTOM13 in an antisense orientation, which resulted in greatly reduced ethylene production in tomato (Hamilton et al., 1990). The deduced amino acid sequence of pTOM13 is similar to that of dioxygenases that require Fez+ and ascorbate as cofactors. When these cofactors were added to assays for ACC oxidase, enzyme activity was completely recovered (Ververidis and John, 1991). Later, it was found that COz is also an essential activator of ACC oxidase (FernándezMaculet et al., 1993). Numerous cDNAs for ACC oxidase have been isolated from different species (see Barry et al., 1996). As is the case with ACC synthase, ACC oxidase is encoded by small multigene families. Although the initial evidence indicated that ethylene synthesis is controlled at the level of ACC synthase, there is now considerable evidence that ACC oxidase also plays a significant role in regulating ethylene biosynthesis. By using gene-specific probes for three ACC oxidase genes of tomato, distinct patterns of expression in various organs and at different stages of development have been observed (Barry et al., 1996). Moreover, the positive feedback loop in which treatment of tissue with ethylene often stimulates ethylene production by that tissue appears to take place through enhanced expression of ACC synthase and ACC oxidase (reviewed in Kende, 1993). Besides being converted to ethylene, ACC can also be irreversibly conjugated to form N-malonyl-ACC (Kionka and Amrhein, 1984). Malonylation of ACC regulates the level of ACC and thus the production of ethylene. Ethylene can be metabolized by plant tissues to ethylene oxide and ethylene glycol, but the physiological significance of this metabolism remains to be established. As a gas, ethylene can readily diffuse from plant tissues, so metabolism is not essential for its removal.

**Gibberellin**

Gibberellin (GA) was originally identified as a substance secreted from the fungus Gibberella fujikuroi, which causes ‘bakanae’ (or foolish seedling) disease in rice (Kurosawa 1926). GA promotes plant growth by stimulating degradation of negative regulators of growth called DELLA proteins. The rice GA receptor gibberellin insensitive dwarf1 (GID1) interacts with the rice DELLA protein slender rice1 (SLR1) in a GA-dependent manner. The binding of GID1 to DELLA results in ubiquitination and degradation of DELLA via a ubiquitin E3 ligase SCF complex and the 26S proteasome (UeguchiTanaka et al. 2005; Griffiths et al. 2006). GAs are produced not only by higher plants, but also by fungi and bacteria (MacMillan 2001). It is supposed that GAs in fungi and bacteria are secondary metabolites that act as signaling factors to establish the interaction with host plants. GA has received little attention in the elucidation of signaling components involved in defence responses. However, emerging evidence suggests that GA signaling components play major roles in plant disease resistance and susceptibility.

**Abscisic acid**

ABA is involved in the regulation of many aspects of plant growth and development including seed germination, embryo maturation, leaf senescence, stomatal aperture and adaptation to environmental stresses (Wasilewskaa et al. 2008). Several recent papers have reported that ABA plays important roles in plant defence responses (Mauch-Mani and Mauch 2005; Mohr and Cahill 2007; de Torres-Zabala et al. 2007; Adie et al. 2007). However, the role of ABA in plant defence appears to be more complex, and vary among different types of plant-pathogen interactions. In general, ABA is shown to be involved in the negative regulation of plant defence against various biotrophic and necrotrophic pathogens. For example, the ABA-deficient sitiens mutant of tomato showed more resistance to B. The ABA-deficient aba2-1 mutant of Arabidopsis showed more resistance to Fusarium oxysporum (Anderson et al. 2004) and the aba1-1 mutant showed less susceptibility to Hyaloperonospora arabidopsidis (Mohr and Cahill 2003) compared to wild type plants. The Arabidopsis mutants impaired in ABA biosynthesis or sensitivity show more resistance to Pst DC3000 (de TorresZabala et al. 2007) and B. cinerea (Adie et al. 2007). Likewise, exogenous application of ABA enhances susceptibility of various plant species to bacterial and fungal pathogens. For example, application of ABA enhanced the susceptibility of Arabidopsis plants to Pst (de TorresZabala et al. 2007), soybean plants to Phytophthora sojae (Mohr and Cahill 2001) and rice plants to Magnaporthe grisea (Koga et al. 2004). Recently, Yasuda et al. (2008) reported that ABA treatment suppressed SAR induction indicating that there is an antagonistic interaction between SAR and ABA signaling in Arabidopsis. Taken together, these results suggest that ABA acts as a negative regulator of defence responses in various plant pathosystems. However, the role of ABA as a positive regulator of defence has also been reported (Mauch-Mani and Mauch 2005). ABA activates stomatal closure that acts as a barrier against bacterial infection (Melotto et al. 2006). As a result, ABA deficient mutants show more susceptibility to Pst. In addition, treatment with ABA protects plants against A. brassicicola and P. cucumerina indicating that ABA acts as a positive signal for defence against somenecrotrophs (Ton and Mauch-Mani 2004).

**Salicylic Acid (SA)**

Salicylates have been known for a long time to be present in willow bark, but have only recently been recognized as potential regulatory compounds. Salicylic acid is biosynthesized from the amino acid phenylalanine.

**Effects**

* Salicylic acid (Chapter F2) plays a main role in the resistance to pathogens by inducing the production of ‘pathogenesis-related proteins’. It is involved in the systemic acquired resistance response (SAR) in which a pathogenic attack on older leaves causes the development of resistance in younger leaves, though whether SA is the transmitted signal is debatable.
* SA is the calorigenic substance that causes thermogenesis in Arum flowers.
* It has also been reported to enhance flower longevity, inhibit ethylene biosynthesis and seed germination, block the wound response, and reverse the effects of ABA.

**Brassinosteroids**

Brassinosteroids (BRs) are a unique class of plant hormones that are structurally related to the animal steroid hormones and involved in the regulation of growth, development and various physiological responses in plants (Bajguz 2007). Although, BRs are known to influence various developmental processes including seed germination, cell division, cell elongation, flowering, reproductive development, senescence, and abiotic stress responses in plants, very little is known about their role in plant responses to biotic stresses.

**CHAPTER THREE**

**CONCLUSION**

Although combining the disciplines of biochemistry, molecular genetics, and physiology has led to major advances in our understanding of the role of hormones in plants, much more remains to be learned. The biosynthesis of IAA and cytokinins in higher plants is still poorly understood, and only in the case of ethylene has a receptor been identified. As the entire genome of Arabidopsis is sequenced over the next few years, a plethora of genes, including those involved in hormone metabolism and signal transduction, will become available; the challenge will be to determine their functions. The levels of IAA and cytokinin have been altered in transgenic plants, mostly with constitutively expressed promoters (reviewed in Klee and Romano, 1994). Similar experiments with ABA and GA biosynthetic genes can be anticipated. In the future, these analyses should be refined by using specific promoters so that manipulation of hormone levels in certain cells, organs, and tissues and at specific times can be achieved (e.g., Gan and Amasino, 1995). Transgenic plants with modified hormone levels or altered hormone responses may offer an alternative to the practice of spraying plants with hormones to manipulate their growth and development.

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