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GIBBERELLIC ACID: PHYSIOLOGICAL ROLES AND PHYTOHORMONAL INTERPLAY

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ABSTRACT

Major developmental processes such as the germination of seeds and ensuing establishment of seedlings are tightly controlled at the transcriptional and translational levels, involving exceedingly complicated changes in physiological conditions. Seeds go from a condition of relative inactivity to intense activity through the action of phytohormones such as gibberellic acid or GA and abscisic acid or ABA. It has been extensively documented and widely accepted that numerous functions within plants are influenced by phytohormones and that the ultimate resulting effect hugely depends on the precise hormonal amalgamation interplay as opposed to the functionality associated with individual plant hormones. This means that the results of plant hormone action depend on a unique hormonal combination as opposed to the actions of each hormone independently. In the last 20 years, many aspects of the channels for transmitting signals of different phytohormones have been elucidated. This has led to the discovery of parts of or full cascading mechanisms. These results offer a foundation of framework, needed to start figuring out how different hormone signal transduction pathways talk to each other. This kind of cross-talk includes a multitude of processes that work at both the hormone sensitivity and at metabolic level, making an intricate system of responses. The research and understanding of gibberellins (GAs) has significant implications in both agriculture and horticulture for plants' ability to adapt to changing environmental stress. In this review, the focus is on how gibberellin works in conjunction with other plant growth promoters and plant growth inhibitors.

KEYWORDS: Abscisic acid; Aleurone; Alpha-amylase; Cordycepin; Cross talk; Cycloheximide; Phytohormones; Polyadenylation; Poly(A)polymerase; RNA Polymerase.

INTRODUCTION

The phytohormone gibberellic acid (tetracyclic diterpenoid carboxylic acids) is an endogenous plant growth promoting hormone. The genes responsible for gibberellin production have been cloned and well characterised in both *Fusarium fujikuroi* and *Arabidopsis thaliana* by Tudzynski, (2005). Despite a stark structural similarity between the fungal and higher plant GA,

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there exist significant differences in both enzymes involved and pathways for biosynthesis, indicating that the two biosynthetic routes have had divergent evolution.

While plant-to-fungus gene transfer is inconceivable, the non-existence of the genes in phylogenetically associated *Fusarium* species is intriguing and prompts researchers to speculate its emergence. Basic research affects biotechnology and can potentially enhance production strains (Tudzynski, 2005). Enhancing production strains may be possible through the adoption of molecular management research, involving genetic engineering and biotechnology techniques such as gene cloning (creating copies), gene amplification (increasing the number of copies), DNA constructs with the mutation of interest (knock-out mutants) and investigations of molecular level regulation (Tudzynski, 2005).

Regulation of changes in physiological conditions are intricately orchestrated in terms of gene expression (transcriptional and translational) throughout the crucial developmental processes of seed germination and subsequent development of embryo into the establishment of seedling. The passage of seeds from an arguably quiescent to an intense activity phase is governed by the phytohormones gibberellin (plant growth promoter) and abscisic acid (plant growth inhibitor).

In grain aleurone tissue, GA turns on alpha-amylases and ABA turns them off. Alpha-amylases are needed to use starch stored in the endosperm (Zentella et al., 2002). Since GA and ABA antagonise one another, cereal aleurone layers provide an excellent framework for investigating the cellular processes' underlying hormonal regulation of the expression of genes (Bethke et al., 1997; Lovegrove and Hooley, 2000).

1. Interaction amongst plant growth regulators

Phytohormones have interconnected and interrelated impacts on various biological functions, and the outcome of plant hormone activity is therefore contingent upon the composition of the combination of hormones as opposed to the actions of an individual hormone all by itself (Castro-Camba, et al., 2022). Numerous constituent elements of the signal transmission channels utilised by different phytohormones have over the past years been unravelled, which has allowed for the partial or complete elucidation of signalling cascades. These discoveries have provided the means to start dissecting the mechanisms causing the interference between various hormone signal transduction pathways. Such interactions involve several processes that work at the level of the steps of enzymatic biosynthesis and responsiveness, resulting in an intricate reaction system.

Dormancy in seeds is a normal occurrence in plants, which is responsible for suppressing germination in unfavourable environmental circumstances and guarantees that seeds reach the grain-filling stage first. ABA is produced by the mother plant and causes the developing seeds to enter a dormant state. The hormonal equilibrium among ABA and GAs functions as a modulator to either remain in a quiescent stage or to begin its growth phase, and a drop in ABA concentration is a prerequisite for germination following seed maturation (Wang et al., 2018).

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When seeds have a weak dormancy, they are more likely to sprout before harvest, which causes a big drop in grain output and quality. Strong dormancy, on the other hand, keeps the seed from germinating. The synergistic activity of ABA and GA-associated regulation largely determines the seed dormancy or germination outcome during development. Hence, abscisic acid and gibberellic acid-related signal pathways work together to mostly control how seeds develop during dormancy or germination (Liu et al., 2010; Zhao et al., 2019). As opposed to GA, which promotes seed germination and drives plant growth, ABA primarily encourages seed dormancy, limits root growth, and makes it easier to tolerate abiotic stress (Muhammad Aslam et al., 2022).

According to Wang and associates (2018), other phytohormones that work in conjunction with ABA or GA, are auxin (IAA), ethylene (C_2H_4), strigolactone (STR), and brassinosteroid (BR), as well as internal signalling pathways like nitric oxide and ROS (reactive oxygen species). Environmental variables like heat and light intensity, also contribute to the processes of seed dormancy or germination. Additionally, Bouquin and associates, (2001); Traw and Bergelson, (2003) and Weiss and Ori, (2007), have shown that GA interacts with brassinosteroids.

The transition from embryogenesis to germination in seeds is regulated in large part by the interplay between phytohormones, specifically gibberellin and abscisic acid. Ritchie and Gilroy, (1998b) and Lovegrove and Hooley, (2000) have illustrated the secretion and translocation of GA from the embryo to the aleurone layer during germination of cereal grains, wherein it stimulates the amplification of many genes that encode enzymes that hydrolyze carbohydrates. ABA on the other hand suppresses the manifestation of these genes. Thereby causing inhibition of germination processes and seed growth, resulting in seed dormancy, according to Bethke and associates, (1997) and also Lovegrove and Hooley, (2000). Furthermore, according to Razem, and associates, (2006), the ratio and antagonistic connection between these two hormones controls the steps involved in the onward journey of plant growth from embryo to seed germination, involving events such embryonic maturation, the development of seeds, and finally culminating in germination.

Conducting comprehensive gene localization investigations in a single species employing techniques like *in situ* RNA hybridization (to observe the mRNA transcripts of interest in cultured cells), target gene promoter-reporter fusion, by immunostaining with specialised antibodies (specific to the protein of interest) to track down all of the genes that make up the complete pathway, it is obvious that molecular genetic analyses techniques are outstanding and will potentially continue to be fruitful, as the impressive complexity of the GA responsiveness channel elements are uncovered by these techniques (Olszewski, et al., 2002). To understand how the genetically identified parts work once they have been cloned, further research into molecular association investigations, biochemical and cell biology laboratory investigations, and gene profiling by microarray analyses (using a gene to which numerous mRNA's bind and can be quantified) will be required. Using diverse plant types has sped up the process of isolating new GA signalling constituents and will potentially be crucial in elucidating distinctions in the significance of these components across species. It will be important to research these components in model organisms, in order to completely grasp the interdependencies amongst them (Olszewski, et al., 2002).

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For several activities in plants, reactive oxygen species, ROS serve as signalling elements. The functions of ROS are still unclear in many ways, though they serve an integral part in the signalling of GA and ABA in aleurone cells of barley, wherein, GA promoted the generation of hydrogen peroxide (H_2O_2), as an ROS, while ABA inhibited its synthesis. The addition of exogenous H_2O_2 also seems to facilitate GA's activation of α-amylases. But the production of α-amylases is inhibited by antioxidants. Therefore, H_2O_2 appears to have a role in GA and ABA signalling and in regulating α-amylase synthesis in aleurone cells (Ishibashi, et al., 2012).

Plants need to be able to successfully protect themselves against biotic and abiotic stressors in the wild. While it is very effective, this protection comes at a high cost and frequently slows growth significantly. The fundamental question of how plants coordinate the ever-changing growth-defence dynamics remains unanswered. Important plant hormones that mediate defence and growth are gibberellic acid (GA) and jasmonate (JA) (Yang et al., 2012).

Plants and microorganisms are perpetually in conflict with each other, consequently both are evolving multiple survival strategies. Strategies are defensive by the host, to protect themselves and offensive by the attacking pathogen. According to Kazan and Lyons, (2014) plants frequently leverage complex signalling channels governed by phytohormones, to protect themselves from pathogens. Pathogens, in response, have devised cutting-edge strategies for subverting phytohormone-controlled resistance. Plant pathogens manipulate hormonal signalling routes and interplay. The pathogenic effectors must necessarily disrupt the molecular mechanisms of host plant phytohormone signalling, in order to parasitise. They essentially engage with phytohormonal receptors, transcriptional activators, and repressor molecules. In this context, jasmonates, salicylates and ethylene are the principal defensive hormones. The phytohormones gibberellin, auxin, cytokinin, abscisic acid, brassinosteroids and strigolactones, in addition to predominantly being attributed with the role of growth, development and resilience to stress, also regulate defence responses in plants, either alone or alongside the principal defensive hormones (Kazan and Lyons, 2014).

α-amylase, which makes up 40-50% of salivary protein, is an essential enzyme for the digestion of starchy foods. Patients with malfunctioning salivary glands necessitate salivary gland restoration accomplished through tissue engineering techniques. The production of gibberellic acid (GA_3), a phytohormone, occurs early in the germination process and stimulates the enzymatic production and the release of the hydrolysing enzyme, α-amylase by the embryo. While researching GA_3 as a prospective technique for influencing stem cells to undergo development into glands that produce saliva, Kasamatsu and co-workers, (2012), isolated adipose-derived stem cells (ASCs), checked them out for toxicity of GA_3 and identified markers that were positive for the mesenchymal stem cell. The pluripotent cells (from human buccal fat pads), are easily accessible to oral and dental surgeons. The toxicity of GA_3 towards adipose-derived stem cells (human ASCs) was also investigated. Morphological and viability characteristics of the cells were not dose-dependently or time-dependently altered by GA_3. An evaluation of the levels of expression (using western blotting and RT-PCR) revealed a GA_3 mediated enhancement of both the mRNA and the protein α-amylase, in the ASC's. On Day 21 following GA_3 (1 mM) therapy, the expression of α-amylase mRNA was seven fold higher than

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it had been on Day 0. Day 0 showed no evidence of α-amylase bands, however after 7 days of GA_3 therapy, the protein was clearly visible, peaking at Day 21. Salivary gland regeneration could be aided by using this induction approach, as the results showed that GA_3 can boost cellular α-amylase expression (Kasamatsu et al., 2012).

2. Gibberellic acid mediated control of enzyme activity

In vivo application of plant hormones activates several preformed enzyme molecules, stored in their dormant; inactive form during dehydration of seeds. *In vitro* addition of the hormone to cell-free extracts can also bring about enzyme activation by generating some mediator chemical signals *in vivo* that modulate enzyme activity. GA-mediated phosphorylation, acetylation, methylation or glycosylation of proteins can also bring about covalent modifications (Doll and Ingram, 2022).

Processing RNA is a crucial post-transcriptional step in regulating gene expression in eukaryotes. One of the important RNA processing steps is the polyadenylation of mRNA at the 3' terminal site. This is achieved through the catalytic activity of poly (A) polymerase. Both hnRNA and mRNA are polyadenylated at the 3' end by incorporation of residues from the substrate ATP in both plant and animal cells. Modulating poly (A) polymerase activity may be a means of regulating mRNA polyadenylation.

Cereal aleurone layers are an ideal system for examining the pathway of the molecular processes implicated in the expression of genes, monitored hormonally, according to Bethke and associates, (1997) and Lovegrove and Hooley, (2000).

Activity of enzyme RNA-polymerase: Researchers have long been interested in the connection between visible growth, apparent development and the activity of the enzyme RNA polymerases. Transcription is potentially a logical option for the control of growth and development processes. The DNA-dependent-RNA-polymerases undergo drastic changes during different phases of development and are concomitant in response to various external or internal factors. The enhancement in the activity of enzyme synthesising RNA (by the activity of the enzyme RNA polymerase) may be either due to the preformed enzymes being activated or due to the *de novo* production of the enzymatic protein.

Activity of the RNA transcription enzyme, RNA polymerase II has been reported to be significantly enhanced in soyabean during germination (Guilfoyle and Malcolm, 1980). During liver regeneration, both RNA polymerases I and II were preferentially reported to have increased (Matsui et al., 1976 Yu, 1975). RNA polymerase levels preferentially increase in resting fibroblasts as they transition into a state of growth, (Mauck, 1977). All the RNA polymerases (I, II and III) have been reported to show enhanced activity during *Xenopus* oogenesis (Order, et al., 1974).

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Temporal regulation: Alteration in the enzymatic activity of RNA-polymerases during various developmental stages has been demonstrated in a number of eukaryotes (Willmann et al., 2011; Tognacca et al., 2020).

Hormonal regulation: Many plant and animal systems have been linked to the regulation of RNA polymerase activity by hormones (Thiel et al., 2008; Yamamuro et al., 2015).

The addition of gibberellic acid during the enzyme isolation steps (such as grinding, layering, or incubation buffers) increased RNA production in the plant system, as discovered by Johri and Varner (1967). However, no increase in RNA synthesis occurred when the nuclei, in isolation, were exposed to GA for as long as two hours before the RNA synthesis. Adding GA early on (during chopping and grinding) resulted in the greatest boost to RNA synthesis; adding GA later on resulted in a diminishing enhancement effect. Adding GA to either the filtrate or the crude extract with nuclei resulted in a similarly significant increase in RNA production response. Furthermore, it has been demonstrated that the average molecular weight of RNA generated by hormone-treated nuclei is greater than that of RNA synthesised by control nuclei. Despite the lack of an *in vitro* reaction, chromatin preparations from plants treated with 2,4-dichlorophenoxyacetic acid (a herbicide) exhibit more polymerase activity than those from untreated plants (O'Brein et al., 1968).

Chromatin isolated from 2-day etiolated cucumber embryonic axes treated with the plant hormones indoleacetic acid (IAA), gibberellin A7 (GA_7), or kinetin demonstrated enhanced capacity to carry out RNA synthesis in both the presence as well as in the absence of bacterial RNA polymerase (Johnson and Purves, 1970). The preparations from washed beetroot tissue have been shown by Duda and Cherry (1971) to alter chromatin and nuclei-directed RNA production, additionally the supply of subsequently isolated chromatin templates is improved by washing the tissue with a combination of gibberellic acid and auxin. Studies on sugar-beet nuclei in isolation show that these hormones have an impact on gene transcription, which in turn affects RNA production. Further research on this topic by Hou and Pillay (1975) revealed that chromatin RNA polymerase activity is increased when gibberellic acid is applied on to soybean hypocotyls, but it is decreased when chromatin is isolated from hypocotyls that have been pre-treated with AMO-1618 (inhibits gibberellin biosynthesis and slows down germination). The increased ability to synthesise RNA in response to gibberellic acid therapy may be caused by increased RNA polymerase synthesis.

Auxin has been shown to enhance RNA synthesis activity (i.e., rRNA) in etiolated soyabean tissue by increasing RNA polymerase I activity (to a tune of 5-8-fold) directly and not by altering the chromatin template (Guilfoyle et al., 1975). Further study by Gulfoyle, (1980) has shown that auxin-treated etiolated soybean seedlings showed a 10–20-fold rise in RNA polymerases I and a 6-fold rise in levels of RNA polymerases II. This rise in the concentration of RNA polymerases is the result of the enzymes' *de novo* production, as demonstrated by the incorporation of ^{35}[S] to the sulphur containing amino acid, methionine, into the subunits of the enzyme RNA polymerase. The control of transcription in auxin-induced soybean hypocotyl does not appear to be caused by structural changes to the subunits of RNA polymerase (Guilfoyle, 1980).

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Enhancement in activity of the transcriptional enzyme (RNA polymerases I) has been demonstrated in pea buds following GA_3 treatments (Tomi et al., 1983a). RNA polymerase activities from tissue treated with GA_3 and control tissue were assessed after partial purification and GA_3 was found to enhance RNA polymerase II activity but produced no noticeable alteration in the properties of RNA polymerase II. Boosting RNA polymerase activity and enhancing the chromatin template are both signs of elevated RNA synthesis after GA_3 interventions (Tomi et al., 1983a, 1983b).

Activity of enzyme Poly (A) polymerase: According to a study on barley aleurone layers (Jacobsen and Zwar, 1974), GA_3 increased poly $(A)^+$ RNA. Wheat embryo-less half-seeds treated with GA_3 showed poly (A) polymerase activity that was two- to three-fold higher than control seeds, which may explain why cereals have higher rates of polyadenylation of mRNA (Berry and Sachar, 1981). The strong suppression of GA_3-mediated promotion of poly (A) polymerase by cycloheximide (CHI, a fungicide obtained from the bacterium *Streptomyces griseus*) and amino-acid substitutes demonstrates that hormonal control of enzyme activity relies on *de novo* protein synthesis.

Using cordycepin (a potent inhibitor of transcription), Berry and Sachar (1982) demonstrated that GA_3-triggered poly (A) polymerase activity was unaffected, lending support to the idea that the aleurone layers of wheat are equipped with a conserved message for poly (A) polymerase that can facilitate enzyme protein synthesis. A GA_3-induced upregulation of a conserved poly (A) polymerase gene was suppressed by ABA.

In germinating wheat excised embryos, cycloheximide and amino acid analogues significantly suppress GA_3-mediated augmentation of poly (A) polymerase activity, whereas cordycepin has no effect, as reported by Lakhani and associates, (1983). These outcomes imply that the stored mRNA in the latent wheat embryos is accountable for the transcription of the poly (A) polymerase that is essential for wheat seed development. Treatment of an excised embryo with cordycepin substantially boosted the activity of poly (A) polymerase compared to untreated-standards, suggesting that cordycepin has an adverse effect on a blocker of the activity of poly (A) polymerase.

Berry and Sachar (1984) revealed that the activity of enzyme poly (A) polymerase is highly correlated with the maturation of wheat kernels. Young kernels showed increased activity, while mature kernels showed decreased activity. It has been shown that there is only one molecular variant of poly (A) polymerase present in the kernel at any given time. Lakhani and Sachar (1985) demonstrated a threefold elevated levels of poly(A)polymerase activity and a concomitant increase in the polyadenylated (poly $(A)^+$RNA in excised-wheat embryos, after 72 hours of germination. GA_3 treatment of wheat embryos resulted in a 1.8-2.0 fold increase in the activity of the poly(A)polymerising enzyme and an increase in the amount of tagged polyadenylated-RNA by a factor of two compared to controls. Cycloheximide (CHI) counteracted the stimulatory impact of GA_3 by decreasing the levels of both (poly(A)polymerase activity and poly$(A)^+$RNA). The authors hypothesised that ABA and GA_3 work at the post-transcriptional level to control the activity of the enzyme (poly(A)polymerase) in the wheat embryos. The degree at which the activity of the enzyme (poly(A)polymerase) dipped in control and GA_3-incubated embryos of

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wheat after translational inhibition with CHI was compared. The GA_3-treated embryos showed a faster fall. Thus, GA_3 stabilises the enzyme, allowing for an increase in its activity; it also regulates the enzyme's activity post-transcriptionally, leading to a higher concentration of poly $(A)^+$ RNA. Labelling the enzyme gave conclusive proof that poly (A) polymerase is synthesised *de novo*, in wheat embryos (Lakhani et al., 1989) and in mungbean (Mathur et al., 1989) in the presence of $^{35}[SO_4]^{2-}$ and subsequently recovering the ^{35}[S] -labelled cysteine from the purified preparation.

Activity of enzyme acid phosphatase: Half-seeds of wheat (without embryos) treated with GA_3 and P^{14} showed selective *de novo* enzyme production of an acid-phosphatase isozyme that was labelled with P^{14}. Presence of stored mRNA for acid phosphatase was indicated by the fact that cycloheximide and not cordycepin could inhibit the hormone stimulated enzyme activity (Akiyama et al., 1981a; Akiyama et al., 1981b). In barley endosperm, GA_3-treatment was reported to activate preformed enzyme molecules of acid phosphatase (Bailey et al., 1976).

Activity of enzymes o-diphenolase, RNAse, peroxidase, protease: MicroRNAs or miRNAs are a type of highly preserved tiny pieces of non-coding RNA that are very important in controlling how genes are expressed. Stored miRNAs have been identified in wheat embryos for proteins like o-diphenolase, RNAse, and peroxidase and in cotton embryos for protease (Taneja and Sachar, 1976). Additionally, lectins have been reported to be translated from their saved mRNAs, as reported by Peumans and coworkers, (1980) in pea, (*Pisum sativum*), and in wheat, and by Peumans and associates, (1982) in rye, (*Secale cereale*).

Activity of enzyme S-adenosyl methionine synthetase: Stimulation of S-adenosyl methionine synthetase in germinated wheat embryos was considerably inhibited by cycloheximide and analogues of amino acids. However, the inhibitory influence of amino acid equivalents was reduced, when they were added together with their corresponding amino acids. Labelling the enzyme with $^{35}[SO_4]^{2-}$ *in vivo* gave conclusive proof of its *de novo* synthesis. Cordycepin, which is an effective transcription inhibitor, did not prevent AdoMet synthetase from being synthesised *de novo* thereby suggesting that wheat embryos store mRNA for this enzyme (Mathur et al., 1991b). Thus, stored mRNAs serve as a template for *de novo* translation of specific enzymes. How the regulatory control mechanism triggers active translation of stored mRNAs in germinating embryos is not known (Sano, et al., 2020).

Activity of enzyme zymogen β-amylase: In barley aleurone, GA_3 is responsible for activation of zymogen β-amylase by proteolysis and cleavage of disulphide bonds (Jacobsen et al., 1970; Shinke and Mugibayashi, 1972). GA_3-stimulated activity of PCG transferase (phosphorylcholine-cytidyl and phosphorylcholine-glyceride transferases) in barley aleurones was not inhibited by amino acid analogues, thereby, supporting the activation hypothesis as the basis of enzyme regulation, according to Johnson and Kende, (1971) and Ben-Tal and Varner, (1974). However, since one of the substrates (diglyceride) of this enzyme was inseparable from the membrane bound enzyme, its concentration was not under control during *in vitro* assay of enzyme activity. Therefore, GA_3 could be responsible only for increasing levels of diglyceride and not of PCG transferase (Bewley and Black, 1978).

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Activity of enzyme monophenolase: The two-fold increase of monophenolase in embryo-less wheat half-seeds that had been treated with GA_3 was not substantially hindered by RNA and protein synthesis inhibitors. (Taneja and Sachar, 1974), indicating that new (*de novo)* synthesis of proteins was not mandatory for the phytohormone-triggered activity of the enzyme. Evidence in support of activation of monophenolase by GA_3 has been provided (Berry and Sachar, 1982) by showing that activated monophenolase exhibited altered molecular properties. The GA_3-treatment brought about a shift in pH optimum from pH 7.0, (the optimum for control enzyme) to pH 9.0. In GA_3-treated tissue, a relatively high thermostability was conferred on monophenolase (55°C) and also the electrophoretic mobility of its multiple forms was altered. Subsequently. Saluja and Sachar, (1982) observed two activity peaks of monophenolase (M.W. 45,000 and 1,80,000) in half-seeds treated with GA_3 (48 hr) as against a single molecular form (M.W. 45,000) of monophenolase in the untreated controls. The two kinds of monophenolase, isolated from the half-seeds treated with GA_3 exhibited an ideal enzyme activity at pH 9.0, compared to the pH optimum of the untreated control molecular type at pH 7.0. When half-seeds were allowed to imbibe phosphate buffer for 48 hrs, the impact of GA_3 on monophenolase enzymatic functionality was perfectly mirrored (Saluja et al., 1987) and the activation brought about by GA_3 and Pi was effectively stopped by ABA.

The hormonal regulation of monophenolase by GA_3 as early as 2-12 hours, is an early response (Saluja et al., 1989a). Tissue treated with GA_3 showed a shift in its optimal pH value, from 7.0 to 9.0. The GAs treatment of half-seeds for 12 hours, however, could not bring about oligomerization of monophenolase into a high molecular weight form (M.W. 1,80,000) because only one molecular form of monophenolase (45,000 Daltons) was observed.

3. Gibberellin binding proteins

It is currently thought that most of the physiological and biochemical responses elicited by plant hormones, analogous with steroid hormones in animal systems, are initiated by interaction of hormones with their respective receptors. Thus, the primary signal generated by hormones is a conformational change in the receptor molecule (by binding at specific sites on the receptor), which in turn modulates other enzyme proteins. These binding sites have been shown to have high affinity and high specificity for different phytohormones and are present within the cell membrane and cytosol of the cell. However, it remains to be seen whether such a recognition mechanism truly represents hormone-receptor complexes that can elicit a biochemical response (Ueguchi-Tanaka, et al., 2007; Ito, et al., 2018; Bao et al., 2020).

Hormone-receptor interactions

Kende and Gardner, in 1976 and Stodart and Venis, in 1980, outline the following conditions as necessary for plant hormone receptor binding:

1. There must be a finite number of receptor molecules, so that GA uptake can be saturated.

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2. Since the hormone-receptor binding is potentially non-covalent, it can be shown that a non-radioactive ligand can be substituted for a radioactive one, and vice versa.

3. The intensity of the biochemical response should be proportional to the concentration of the hormone-receptor complex if binding sites accurately represent the receptor molecules. There should be a correlation between Kd (dissociation constant of the complex between the hormone and the receptor, refers to that concentration of hormone at which 50% of the total binding-sites of the receptor are occupied by the bound hormone) and the quantity of hormone required to induce fifty percent of the maximal biochemical response. At any given time, fewer hormone molecules should be needed to occupy half of the accessible binding sites for a highly effective hormone than for a less active ligand. If the Kd is lower, the more specific the binding is for the ligand.

4. The binding must be biologically meaningful. Hormones bind not only to their receptors, but also to their metabolising enzymes, transport proteins or to the enzymes involved in their degradation. Hence, it is necessary to characterise the plant hormone after dissociating it from the binding site. Conclusive evidence that one is working with receptor protein can be obtained by demonstrating the known hormone-mediated activity in a mutated receptor by delivering a hormone-receptor complex.

In vivo [^{3}H] GA-binding

Presuming that GA must react with a macromolecule in the cell in order to effect a physiological response, [^{3}H]GA_3 or [^{3}H]GA_5 have been administered to dwarf peas (Kende, 1967; Musgrave, et al., 1969; Musgrave and Kende, 1970) but no stable macromolecule - GA complex was found. These workers have also shown that there was no saturation of GA uptake in dwarf pea. Also, in barley aleurones, no saturation of GA uptake with time or with increasing concentration was observed (Srivastava, 1987).

In 1974, Stodart and coworkers established that [^{3}H]GA_1 supplied to dwarf pea epicotyls (*in vivo* by incubation for 12 hr) was bound non-covalently to a high mol.wt. (HMV) and an intermediate mol.wt. (IMV) element from a 20,000 g extract and that only the bio-active form, [^{3}H] Keto GA_1 could compete for binding to these elements whereas the inactive form [^{3}H] pseudo-GA, and [^{3}H] GA_3 could not.

These observations have been confirmed and extended by Keith and Srivastava, (1980) by adopting a slightly modified procedure. Binding sites of GA_1 were detected when slices of dwarf pea were subjected to pre-incubation in [^{3}H] GA_1 (at 0°C, for three days) on at least 2 soluble proteins with an estimated molecular weight of $6x10^5$ Daltons and 4 to $7x10^4$ Daltons. With a Kd value of $6x10^8$ and $1.4x10^6$ M, respectively. It was demonstrated that binding for physiologically active GA_5 was saturable and selective under *in vivo* circumstances. Applying low temperatures prevented [^{3}H] GA_1 metabolism or its accumulation into the inner compartments from complicating a study of binding characteristics under equilibrium conditions.

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In vitro [^{3}H] GA - binding

[^{3}H] GA's binding to a soluble macromolecule (100,000 g) in cucumber cytosol was shown by sephadex chromatography (Keith et al., 1981). That hormone binding to a protein was experimentally shown by heat treatment and protease treatment which destroyed specificity of the binding which was not disrupted by DNase, RNase or Lipase. Keith et al. (1981) demonstrated that [^{3}H] GA_4 binding was pH-sensitive, saturable, and reversible and was considerably influenced by bioactive GA_5 but the inactive gibberellin is not. This can be accomplished by performing equilibrium-dialysis utilising protein enriched fraction (made by ammonium sulphate precipitation).

Sephadex filtration is based on noncovalent binding of [^{3}H] GA_4 to a protein wherein the filter paper assay, relies on the binding capacity of the protein onto the DEAE-cellulose-filter-discs and that the binding is saturated and easily reversed with GA. The biologically active GA_5 competed for binding of the soluble protein (Keith *et al.*, 1982).

At 4^0 C, Sephadex chromatography was used to demonstrate the binding of [^{3}H] GA_1 to a soluble macromolecular component that was found in the cytoplasm (100,000 g) of maize leaf sheaths. It appears that the high-molecular-weight binding constituent (of more than 500 kD), was a protein that specifically bonded to [^{3}H]GA_1 and not to a metabolite. The binding was pH-dependent and blocked by both functional and nonfunctional GAs (Keith and Rappaport, 1987).

A subcellular fraction from wheat endosperm that was rich in aleurone grains and exhibited specific binding for [^{3}H] GA_1 has been identified (Jelsema et al., 1975, 1977). The unique GA-binding sites were 0.45 pmol. mg^{-1} of protein, and the Kd was 1.5 x 106 M. Additionally, ABA, which blocks the activity of GA *in vivo*, was demonstrated to block GA binding *in vitro* (Jelsema et al., 1977).

As reported by Konjevic and coworkers, (1976), [^{14}C] labelled GA_3 bound to pea stem protein molecules was successfully isolated and examined. Using ion-exchange chromatography on a DEAE-Sephadex A-50 column, it was demonstrated that these soluble GA-protein complexes segregate into four radioactive zones, each of which elutes with a different KCl concentration. The non-covalent interaction between the ligand hormone and the protein fraction was indicated by its disruption upon ethanol treatment.

4. Possible mechanism of gibberellin receptor action

Gibberellic acid (GA_3) exerts a pleiotropic effect on diverse physiological and biochemical functions in plant cells. Possibilities of gibberellin-receptor action as given by Srivastava, (1987) are:

1. Different receptor sites in the same plant tissue may have different affinities for binding to the same chromatin region at different times in the plant's life cycle.

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2. Hormone-receptor complexes are formed when signal molecules local to a tissue or organ engage with the receptor molecule and change the conformation of the chromatin binding region.

3. Different plant tissues have receptor molecules with varying chromatin-binding region architectures and GA-binding region architectures.

CONCLUSIONS

There is a growing interest amongst researchers due to the profound pleiotropic effects that gibberellins have on plants' development, their defence mechanisms, and their general performance. Interactions with other plant growth regulators (PGRs) are rather complex. The gibberellic acid (GA) mechanism is in tandem with growth-inducing phytohormones (auxins, brassinosteroids) and in contradiction to stress-related PGRs (ethylene, jasmonates, abscisic acid). The characteristics and outcomes of these correlations in nature depend on the interplay of all the hormones as internal factors and the variable external factors. The modulation of certain plant responses is made possible by identifying the genes and proteins at the epicenter of these complex associations. Additionally, the associations of GAs with novel potential PGRs and other substances offer a way to precisely articulate plant performance patterns, especially in pertinent crops.

It is noteworthy to highlight that the relationship involving GAs signalling and the capacity of plants to respond to various stresses makes it easier for them to acquire higher levels of endurance, which may be essential for their ability to adjust to the circumstances brought on by an environmental event involving climate change.

Since the phytohormone directly or indirectly impacts numerous aspects of plants,

Gibberellins are credited with sparking the "Green Revolution" that dramatically improved crop productivity during the 20th century. The complex challenges facing agriculture are currently how to sustain or strengthen this output in the midst of a constantly expanding global population and climatic variability, which will render crops vulnerable from rising biological and environmental challenges.

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