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Gibberellic Acid Production by Fungi- A Review

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Abstract

The gibberellins (GAs) are one of the major groups of growth promoting hormones, which play an essential role in regulation of growth and development of angiospermic plants. Gibberellins are diterpenoid acids biologically derived from tetracyclic diterpenoid hydrocarbons and produced in good quantity by microorganism. A number of micro-organisms have been reported to produce GA3 and GA like substances. Among these, the fungal cultures are able to produce GA like activities in higher yields. These GA producing fungal species could be exploited well to meet with the growing demands of exogenous GA for the agricultural crops to increase yield.

Keywords: gibberellins growth promoting hormones, diterpenoid acids, microorganism, fungal cultures, agricultural crops etc.

Introduction: Research on the gibberellins stems from the work of E. Kurosawa (reviewed in Moore, 1979). He is credited for having discovered GA in 1926, producing the "bakanae" effect (pathological longitudinal growth) in rice, and maize seedlings treated with spent-culture medium from the fungus *Gibberella fujikuroi* in the sexual form *(Fusarium moniliforme).* A decade later, Yabuta and Sumiki, in 1938, isolated and crystallized two biologically active substances, which they named “gibberellins A and B”. Soon afterwards, the first plant gibberellin was identified by Macmillan and Suter (1958) from *Phaseolus coccineus* seeds. Thereafter, by 1956, GAs were shown to be natural components of plants tissues both by West and Phinney in USA and by Radley in England (reviewed in Moore, 1979). A number of micro-organisms have been reported to produce GA3 and GA like substances. To date, 136 GAs from higher plants (128 species), 28 GAs from fungi (7 species), and only 4 GAs (GA1, GA3, GA4, and GA20) from bacteria (7 species) have been identified (MacMillan, 2002). The GAs are divided into two groups the C20-GAs and the C19-GAs. The C20-GAs gather molecules with 20 carbon atoms, and the C19-GAs have lost the C-20 and carry a γ–lactone ring. In addition to free GAs, plants contain several GA conjugates, including GA-O-β-glucosides and β–glucosyl ethers (reviewed Crozier et al., 2001).

Gibberellin Biosynthesis: Plants Vs Fungi

Higher plants and fungi have evolved their complex gibberellic acid biosynthetic pathways convergently as it was indicated by the amino acid sequence homology analysis of the proteins in their biosythetic pathways (Hedden et al., 2001). All terpenes are formed by condensation of two or more isoprene units and are classified on the basis of the number of isoprene units they contain. Isopentenyl diphosphate (IPP) is the five-carbon activated building block of terpenes, which isomerizes to dimethylallyl diphosphate (DMAPP). DMAPP and IPP are also the starting points for a series of head-to- tail condensations and cyclization to yield geranyl diphosphate (GPP), farnesyl diphosphate (FPP), and geranylgeranyl diphosphate (GGPP) (Domenech et al., 1996 and Linnemannstons et al., 2002). GGPP undergoes cyclization in two closely linked steps to give rise to the first fully cyclized compound, ent-kaurene Two enzymes sequentially catalyze this reaction—copalyl diphosphate synthase (CPS) and ent-kaurene synthase (KS)—and commit GGPP on the pathway to GA biosynthesis. These enzymes occur in plastids. a series of oxidations at C-19 lead to the formation of ent-kaurenoic acid, which is hydroxylated at C-7 to yield ent-7α-hydroxykaurenoic acid. This latter compound yields GA12-aldehyde by contraction of the B ring and a further oxidation at C-6. Enzymes involved in these oxidations, ent-kaurene oxidase, ent-kaurenoic acid hydroxylase, and GA12-aldehyde synthase, are membrane-bound cytochrome P450 monooxygenases, enzymes are believed to be located on the endoplasmic reticulum. (Bomke and Tudzynski 2009 and Tudzynski, 2005).

These first steps of the pathway are identical in the higher plants and in the fungus. After GA12-aldehyde, the pathways in higher plants and *Gibberella fujikuroi* differ. In G. fujikuroi, GA12-aldehyde is first 3β- hydroxylated to GA14-aldehyde, which is then oxidized at C-7 to form GA14 (Hedden et al. 1974 and Urrutia et al. 2001). Desaturation of GA4 at C-1,2 results in the formation of GA7, which is converted to the main product in *G. fujikuroi*, GA3, by 13-hydroxylation. GA1 isformed as a minor product by 13-hydroxylation of GA4 and is not converted to GA3 (MacMillan, 1997).

In plants, GA12-aldehyde is converted to GA12, which is either oxidised at C-20 to form the 19-carbon gibberellin, GA9, or is first 13-hydroxylated to GA53, which is then oxidized at C-20 to yield GA20. GA9 and GA20 are formed in parallel pathways, both involving oxidation of C-20 to alcohol and aldehyde, and the final formation of biological active 19-carbon GAs by loss of C-20. In plants, the oxidation and removal of C-20 is catalysed by a multifunctional GA 20-oxidase (Lange et al., 1994 and Phillips et al., 1995). At the end of the pathway, both GA9 and GA20 are converted to GA4 and GA1, respectively, by introduction of a 3β-hydroxyl group.

Thus, a major difference between the GA pathways in *G. fujikuroi* and plants is the stage at which the hydroxyl groups are introduced. In the fungus, GA12-aldehyde is 3β- hydroxylated to GA14-aldehyde, whereas in plants GA12-aldehyde is converted to GA12, which is then 13- hydroxylated to GA53. In fungi, 13- hydroxylation takes place only in the final step to form GA3 from GA7, whereas in plants the final step is the 3β-hydroxylation of GA9 and GA20 to GA4 and GA1, respectively.

Gibberellin biosynthesis in G. fujikuroi differs from that in higher plants in several respects: a single enzyme (CPS/KS) catalyzes both steps in the formation of ent-kaurene from GGPP, 3β-hydroxylation occurs early in the pathway as one of the reactions catalyzed by GA14 synthase, a highly multifunctional cytochrome P450 monoxygenase that converts ent-kaurenoic acid to GA14 (3β-hydroxy GA12), and 13-hydroxylation is the final step in the pathway to GA3. Furthermore, removal of C20 is accomplished by a cytochrome P450 rather than a dioxygenase. The genes for the GA-biosynthetic enzymes are clustered in G. fujikuroi, whereas they are dispersed throughout the genome of the higher plant *Arabidopsis thaliana.*

Gibberellin as plant hormone: Gibberellins are tetracyclic diterpenoid acids that are involved in a number of developmental and physiological processes in plants (Crozier et al. 2000; Davies 1995). These processes include seed germination, seedling emergence, stem and leaf growth, floral induction and flower and fruit growth (King and Evans 2003; Pharis and King 1985; Sponsel 2003). Gibberellins are also implicated in promotion of root growth, root hair abundance, inhibition of floral bud differentiation in woody angiosperms, regulation of vegetative and reproductive bud dormancy and delay of senescence in many organs of a range of plant species (Bottini and Luna 1993; Fulchieri et al.

1993; Reinoso et al. 2002; Tanimoto 1987). In most (if not all) of these processes gibberellins act in combination with other phytohormones and additional regulatory factors, so that the signaling pathways are highly integrated (Trewavas 2000).

Role of gibberellin in fungal biology: In fungi, there is no known role for gibberellins; rather they seem to be secondary metabolites that may play a role as signaling factors towards the host plant. In the past microbial synthesis of gibberellins by using various strains of the fungus *F. moniliforme, G. fujikuroi, Sphaceloma manihoticola, Phaeosphaeria, Nerospora crassa and Aspergil- lus niger* have been studied. Among these, F. *moniliforme* was found most effective fungus for the production of gibberellin. This fungus produces many types of GAs in culture media as well as in the inoculated plants amongst which GA3 has received the greatest attention. GA3 is also produced by *F. graminearum, F. solani, F. semitectum, F. oxysporum, and F. arenaceum.* Fungal secondary metabolites are mimicking of plant effector molecules like auxins, gibberellins and abscisic acid. Fungal secondary metabolites that modulate plant growth or even can subvert the plant defense responses such as programmed cell death to gain nutrients for fungal growth and colonization. Nevertheless, gibberellic acids produced as SMs in the rice-infecting F. fujikuroi were good examples of phytohormone mimics (Bömke and Tudzynski, 2009). Fungal gibberellins were involved in plant infection, e.g., as growth modulators like IAA, cytokinins, and ABA. Interestingly, other *Fusarium* species seem to have lost the ability to synthesize gibberellic acid, suggesting that this is an advantage for *F. fujikuroi* over other pathogens (Wiemann et al., 2013). *Aspergillus fumigatus* also produced gibberellins, and the role of this fungal species was also rectified by its regulatory effect on the phytohormones (ABA, SA, and JA) under stress condition. (Pusztahelyi et al. 2015, Frontiers in Plant Science, vol. 6 article 573)

Latest reports on GA production in fungi:

- Hasan (2002) reported that a number of fungal species viz., *Aspergillus flavus, A. niger, Fusarium oxysporum, Penicillium corylophilum, P. cyclopium, P. funiculosum* and *Rhizopus stolonifer* which have been found to inhabit the rhizosphere and rhizoplane of fababean *(Vicia faba),* melochia (*Corchorus olitorius*), sesame (*Sesamum indicum*) and soyabean (*Glycine max*) produced gibberellin (GA) but *F. oxysporum* was found to produce both GA and indole-acetic acid (IAA). The optimum period for GA and IAA production by *F. oxysporum* was 10 days in the mycelium and 15 days in the filtrate at 28°C.
- Bilkey et al. (2010) found that the optimum conditions for gibberellic acid production in *Aspergillus niger* were 12 days of incubation at 30 °C and pH 5.0. Agitation increased both indole-3-acetic acid and gibberellic acid production.
- Srivastava et al. (2003) screened nineteen *Fusarium* strains for the production of gibberellin in the culture media to evaluate their roles in hybrid rice production. Quantitative estimation of gibberellin from different strains of *Fusarium* showed presence of gibberellin in variable amounts. Range of gibberellin production varied between 0.66 to 600 mg g-1 dry weights of the mycelium. However, most of the strains produced 50-180 mg gibberellin on mycelium dry weight basis. Thin layer chromatography and high performance liquid chromatographic separation confirmed the presence of GA3, GA4 and GA7 in the sample. Effect of culture filtrate of showed significant increase in the second leaf length of rice (Pusa 5A CMS Line) and it could be used to produce droopy leaves in male sterile lines for more hybrid rice production.

- Bhalla et al. (2009) categorized 28 strains of *Fusarium* as low, moderate, and high gibberellin producers on the basis of quantitative analysis of produced gibberellins by HPLC. For the first time, *Fusarium solani* was also reported as high GA 3 producing strain.
- Rachev et al. (1997) showed that the mutant strain of *Fusarium moniliforme* 3211 was characterized by a high GA7 concentration and the optimum time for production of GAs was 240th hour after the start of cultivation. Interestingly, when hydrophobic macroreticular resin Amberlite XAD-2 added at the 144th hour, the concentration of total GAs increased compared to normal cultivation.
- Uthandi et al. (2010) experimentally proved that *Fusarium fujikuroi* isolate SG2 produced gibberellins (1175 µg/ml) in modified medium having low concentration of nitrogen and carbon
- Zainuddin et al. (2008) isolated a total of A total of 25 strains of *Fusarium* species belonging to *F. fujikuroi* (a pathogen of bakanae disease), *F. proliferatum*, *F. sacchari*, *F. subglutinans* and *F. verticillioides* from rice plants showing typical bakanae symptoms in Malaysia and Indonesia and screened for their secondary metabolites. The objectives of their studies were to determine the physiological variability based on production of moniliformin (MON), fumonisin (FB1), gibberellic acid (GA3) and fusaric acid (FA).
- Lee et al. (2012) isolated and examined two endophytic fungi viz., *Phoma glomerata* LWL2 and *Penicillium sp.* LWL3 for their potential to secrete phytohormones viz. gibberellins (GAs) and indoleacetic acid (IAA) and mitigate abiotic stresses like salinity and drought. The endophytic fungi significantly promoted the shoot and allied growth attributes of GAs-deficient dwarf mutant Waito-C and Dongjin-beyo rice. Analysis of the pure cultures of these endophytic fungi showed biologically active GAs (GA1, GA3, GA4 and GA7) in various quantities.
- Lee et al. (2005) isolated Fifty-four fungi were isolated from the roots of 4 kinds of *Sesamum indicum* and examined the production of GAs was spectrophotometrically. *Penicillium commune* KNU5379 produced more GA3, GA4, and GA7 than *Gibberella fujikuroi*, *Fusarium proliferatum*, and *Neurospora crassa* which are known as GAs-producing fungi
- Deshmukh P.D. and Shinde S.Y (2016) screened 28 species belonging to 10 genera isolated from rhizosphere, rhizoplane, phyllosphere, phylloplane and endophytic mycoflora of *Cajanus cajan*, for gibberellic acid production and showed that 14 species viz., *Aspergillus flavus*, *Aspergillus terreus*, *Aspergillus wentii*, *Alternaria tenuis*, *Alternaria longipes*, *Aureobasidium pullulans*, *Cladosporium lignicola*, *Drechslera australiensis*, *Fusarium moniliforme*, *Fusarium solani*, *Penicillium citrinum*, *Rhizoctonia solani*, *Trichoderma polysporum* and *Trichoderma flavofuscum* had ability to produce Gibberellic acid.
- More et al. (2015) isolated Fusarium species from Belgaum agriculture soil and screened for GA3 production under submerged fermentation. The most promising strain showing maximum GA3 yield (strain M104) was chosen by them to study the effect of various parameters on GA3 production, like incubation time (1-12 days), initial pH (5.0-8.0), incubation temperature (20-50°C), pH (5.0 - 8.0), and carbon and nitrogen sources.

Concluding remarks: At present, the research and developmental efforts on the production of GAs are on a low key. A critical analysis of all production aspects to understand various parameters and the evaluation of the possible uses of these in the production of GA3 at higher yield and lower cost has not been dealt systematically. Gibberellic acid (GA3) is the main product of gibberellins in fungi (Bruckner and Blecschmidt, 1991). GA3 is a high value industrially important biochemical selling at $ 27-36/g in the international market, depending upon its purity and potency. Therefore, its use at present is limited to high premium crops. In the recent past gibberellin has been used to increase the rice panicle length and to produce droopy leaves for producing more hybrid seeds (Hanqiao et al. 1997). As the demand of gibberellin is increasing, the research and developmental efforts on the production of GAs has been intensified.

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