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Allelochemicals as growth regulators: A review

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ABSTRACT

Allelopathy has been interweaved with agriculture and the use of allelochemicals as growth regulator is of great interest. Some allelochemicals (agrostemin, triacontanol, brassinosteroids, strigolactones, jasmonic acid, salicylic acid) act as growth regulators when applied at low concentrations. This review summarizes the allelochemicals used as natural growth regulators and also includes the synthetic bioregulators (brassinosteroid/ strigolactone analogues; strigolactone mimics).

Keywords: Allelopathy, allelochemicals, bioregulator, brassinosteroids, growth regulators, strigolactone analogues, strigolactone mimics, synthetic bioregulators.

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1. INTRODUCTION

The term ‘Allelopathy’ was first defined by Molisch in 1937 (42) as the chemical interaction between plants and microorganisms. In 1984, Rice enlarged the definition with all direct positive or negative effects of a plant on another plant or on micro-organisms due to the release of “biochemicals” into the environment (53). Currently, the most recognized concept of allelopathy is as “any process involving secondary metabolites generated by plants, algae, bacteria and fungi that influence the growth and development of agriculture and biological systems” (30). These secondary metabolites are known as “allelochemicals” and have beneficial or detrimental effects on the targeted organisms in the same habitat (11,53). Allelochemicals are divided into 14-chemical classes, viz., water-soluble organic acids; simple unsaturated lactones; long-chain fatty acids and polyacetylenes; naphthoquinones, anthraquinones and complex quinines; simple phenols; benzoic acid and derivatives; cinnamic acid derivatives; coumarins; flavonoids; condensed and hydrolysable tannins; terpenoids and steroids; amino acids and polypeptides; alkaloids and cyanohydrins; sulphides and glycosides; and purines and nucleosides (53).

Allelopathy is a significant ecological mechanism in natural and managed ecosystems. It plays important role in vegetation succession as a phenomenon which allows the dominance of certain plant species on the local biodiversity (44). Allelochemicals are very attractive as growth regulators due to several advantages: increases the crops yields and promote sustainable agriculture development (10,12,52,70).

This paper aims to provide an overview of the allelochemicals (Fig 1) and synthetic bioregulators (Fig 2) as growth regulators.

2. ALLELOCHEMICALS

Allelochemicals are important regulators of plant growth and development and their physiological effects on plants are shown in Table 1.

2.1 Agrostemin

Agrostemin was isolated from the seeds of corn cockle (*Agrostemma githago* L.), a common weed of wheat and other cereals (25). It is a mixture of amino acids of natural origin and other organic compounds (tryptophan, adenine, folic acid, allantoin, etc.) having induced many favourable effects on crop growth and development. For example, it stimulates seed germination, promotes root growth, increases plant absorption capacity and chlorophyll content, enhances photosynthetic efficiency and metabolic capacity, improves quality and increases yield. Its application increases 10-30 % crop yields, lead to better fruit quality and reduces fertilizer cost by 20-30 % (38,65). The yield increase varies among the crops.

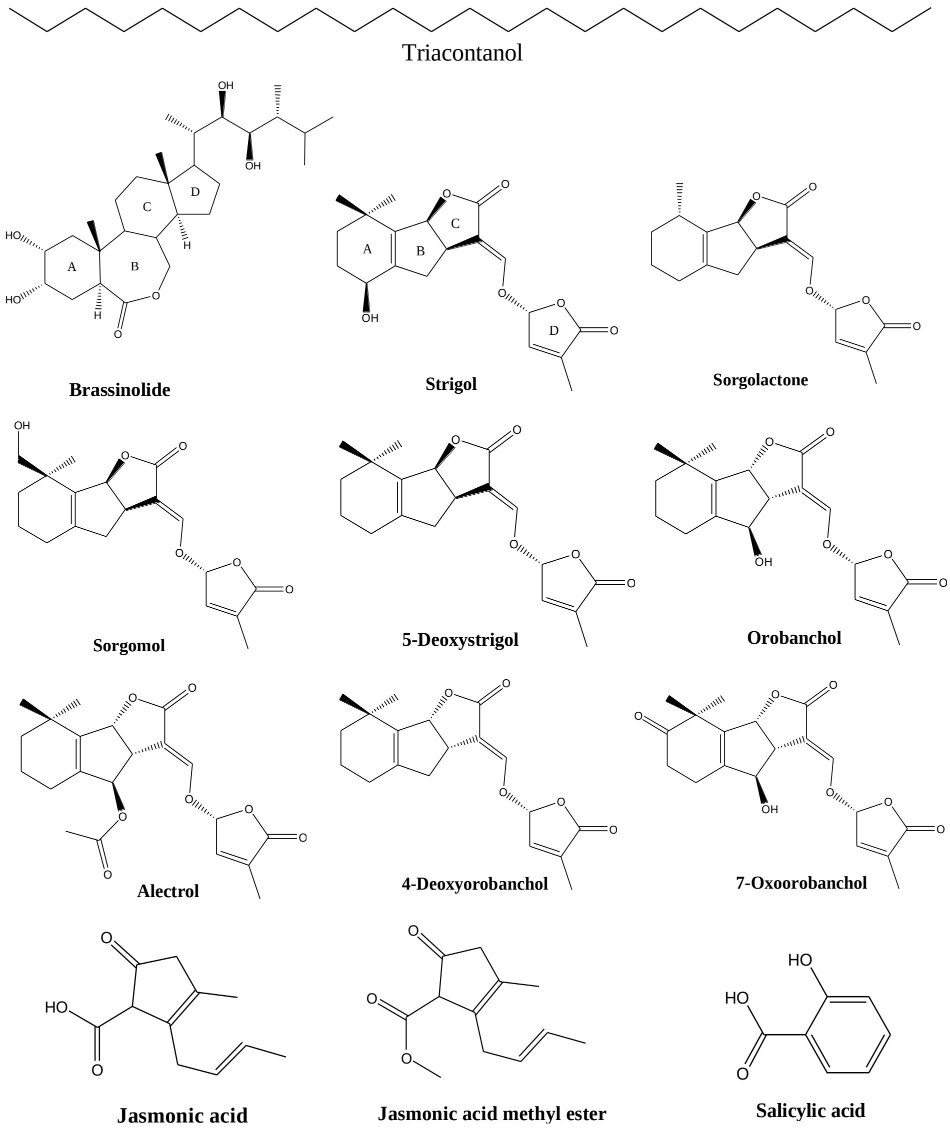


Figure 1. Chemical structures of Allelochemicals used as plant Growth regulators.

2.2 Triacontanol

The plant growth regulatory activity of triacontanol was first reported by Ries *et al.* (55) in alfalfa (*Medicago sativa* L.). He showed that coarsely chopped alfalfa plants increased the growth of other plants. Over the past decades, triacontanol has been used to increase the growth and yield of crops (58). Researchers have also reported the positive

Table 1. Physiological effects of allelochemicals and Growth Regulators on some plants

Test plant	**Biochemical/Physiological Effect (s)**	**References**
Triacontanol		
Cucumber (*Cucumis sativa* L.), Maize (*Zea mays* L.), Tomato (*Lycopersicon esculentum* Mill.)	Increased the concentrations of Ca^{2+}, Mg^{2+} and K^{+}	57
Erythrina variegata L.	Photosynthetic pigments, ribulose-1,5-bisphosphate (RuBPC) and photosynthetic activity	45,46
Rice (*Oryza sativa* L.)	Respiration increased by 20%, NH^{-} and NO_3^{-} uptake promoted hydrolysis, hydration and oxidation in tissues	7
	Led to the identification of 9-*β*-L (+)-adenosine as a second messenger	54
Soybean (*Gycine max* (L.) Merr.)	Increased the activity of nitrate reductase, amylase and peroxidase to reduce soluble protein content	72
Wheat (*Triticum aestivum* L.)	Promote photosynthetic phosphorylation and increase ATP storage	50
Brassinolide		
Arabidopsis thaliana (L.) Heynh.	Improved the osmotic pressure of plants and ability of plants to resist drought	43
	Regulated the number of vascular bundles in buds by promoting the division of the cambium cells	29
Black gram (*Vigna mungo* (L.) Hepper)	Improved the physiological parameters and higher seed yield	31
Eucalyptus robusta Smith	Promoted the seed germination under salinity conditions	76
Foxtail millet (*Setaria italica* (L.) Beauv.	Improved the tolerance of Sigma Broad in foxtail millet by improving the activity of antioxidant enzymes	78
Maize (*Zea mays* L.)	Improved drought resistance of maize by increasing protein synthesis	3
Rice (*Oryza sativa* L.)	Reduced the inhibitory effects of salt stress on seed germination and seedling growth	4
Strigolactone		
Arabidopsis thaliana (L.) Heynh.	Suppresses shoot branching, inhibits the outgrowth of axillary buds	26, 68
	Increases abiotic stress tolerance (salinity and drought stress)	69
	Development of root system architecture (Increase Primary Root Length; Mediated changes in root meristem patterning)	60
Lettuce (*L. sativa* L.)	Promotes plants ability to cope with salt stress	5
Lotus japonicus L.	Increases symbiosis between plants and arbuscular mycorrhizal fungi (AMF)	1
Rice (*O. sativa* L.)	Regulates rice leaf senescence due to phosphate deficiency	73
Tomato	Positively regulates the light-harvesting genes	39
Jasmonic acid		
Cannabis sativa L.	Improves the lignin content in hypocotyls	6
Maize (*Z. mays* L.)	Improves the alkali stress	40
	Induces the chemical defense	20
Narcissus triandrus L.	Promotes the formation and enlargement of bulbs	62
Salicylic acid		
Lemna minor L	Results in high flowering rates	22
Maize (*Z. mays* L.)	Increases the plant height, leaf area and dry matter yield	31
Phaseolus vulgaris L. and tomato	Increases tolerance to heat, cold and drought stress.	64
Tomato and wheat	Improves the chilling resistance	19

role of triacontanol in enhancing growth, yield, photosynthesis, protein synthesis, uptake of water and nutrients nitrogen fixation, enzymes activities, free amino acids, reducing sugars and soluble protein of plants (48). Triacontanol has wonderful yield-increasing effects on food crops (rice, maize, etc) and vegetables (cucumbers, tomato, etc.), the average yield of grain crops increased by 5-15 %, economic crops by 10-15 %, oil crops by 10-20 % and vegetables increased by 10 % to 40 %. It has a significant impact on plant growth under low concentration (48,59,56). In addition, triacontanol promotes rooting of cuttings, improves plant disease resistance, thereby inhibits the cabbage downy mildew, tomato wilt and cucumber damping-off (41).

2.3 Brassinosteroids

Brassinosteroids are a class of steroid hormones with high physiological activity. They play an important role in the growth and development of plants, including root growth, vascular differentiation, fertility and seed germination (67). It fully stimulates the internal potential of plants, increases the stress tolerance of crops and reduces the phytotoxicity of herbicides to crops. It was first isolated from *Brassica* pollen (17) and it has the strongest bioactivity in the Brassinosteroids. It has the structure of a steroidal skeleton of Sa-cholestan, which has a 7-oxalactonic B-ring and two vicinal hydroxyls at the A-ring (C2a and C3cr) and in the side chain (C22R and C23R) (61). In addition, 24-epibrassinolide has been legally registered as a seed treatment agent for various crops in Russia.

2.4 Strigolactones

The strigolactones stimulates the seed germination of parasitic weeds (*Striga* and *Orobanche* spp.) and also induces hyphal branching in arbuscular mycorrhizal fungi (1,63). These are involved in shoot branching, secondary growth, plant stress responses (drought tolerance and disease resistance), root growth and nodulation (21,75). Recent studies have shown that DWARF 14 is a non-canonical hormone receptor for strigolactone (74). The strigolactones are terpenoids with a tetracyclic structure of three fused rings (A,B,C) containing a γ-lactone connected to a butenolide lactone (D-ring) through an enolether linkage. They are mainly synthesized in the roots and transported upward through the xylem to the aerial part (33,34,63). Currently, 36 kinds of natural Strigolactones have been isolated with the same carbon skeleton. These can be divided into the (i). Strigol-type (strigol, sorgolactone, sorgomol, 5-deoxystrigol, etc.) and (ii). Orobanchol-type (orobanchol, alectrol, 4-deoxyorobanchol, 7-oxoorobanchol, 7-hydroxyorobanchol, fabacol, solanacol, etc.) (18,71). Strigol was the first strigolactone isolated from the root exudates of cotton, a non-host plant for *Striga* spp. (14,15). In addition, the sorgolactone and alectrol have the same stimulatory power as strigol (77).

2.5 Jasmonic acid

Jasmonic acid is a naturally occurring growth regulator widely distributed in higher plants. It was detected in several Leguminosae plants and its highest contents were found in young leaves, flowers and fruit, especially the immature pericarp (16). At the early stage of its discovery, jasmonic acid was regarded as inhibitory to phytohormone, but now jasmonic acid had many physiological effects on plants. For instance, from the responses of the process of jasmonic acid system induction, Bt gene introduction and endogenous chemical defence of corns act synergistically (20). Moreover, the application of jasmonic acid on young hemp plantlets promotes the secondary growth and increased the lignin content in hypocotyl of *Cannabis sativa L.* (6).

2.6 Salicylic acid:

Salicylic acid is a water-soluble antioxidant phenolic compound found in plants. It regulates the plant growth and provides resistance to plant stress. Its foliar application at 100 ppm on maize increased the plant height, leaf area, crop growth rate and dry matter yield (31). Previous studies have also revealed that plants soaked in an aqueous solution of salicylic acid showed increased tolerance to heat, cold and drought stress (64). Spraying low concentration (0.01 mM) of a salicylic acid solution significantly improves the chilling resistance of wheat and tomato (19).

3. SYNTHETIC BIOREGULATORS

3.1 Synthetic brassinosteroids or brassinosteroid analogues

These compounds of synthetic origin, were obtained by chemical or biotechnological means. They exhibit any structural similarity with natural brassinosteroids and activity similar to brassinolide. Some examples are shown in Figure 2.

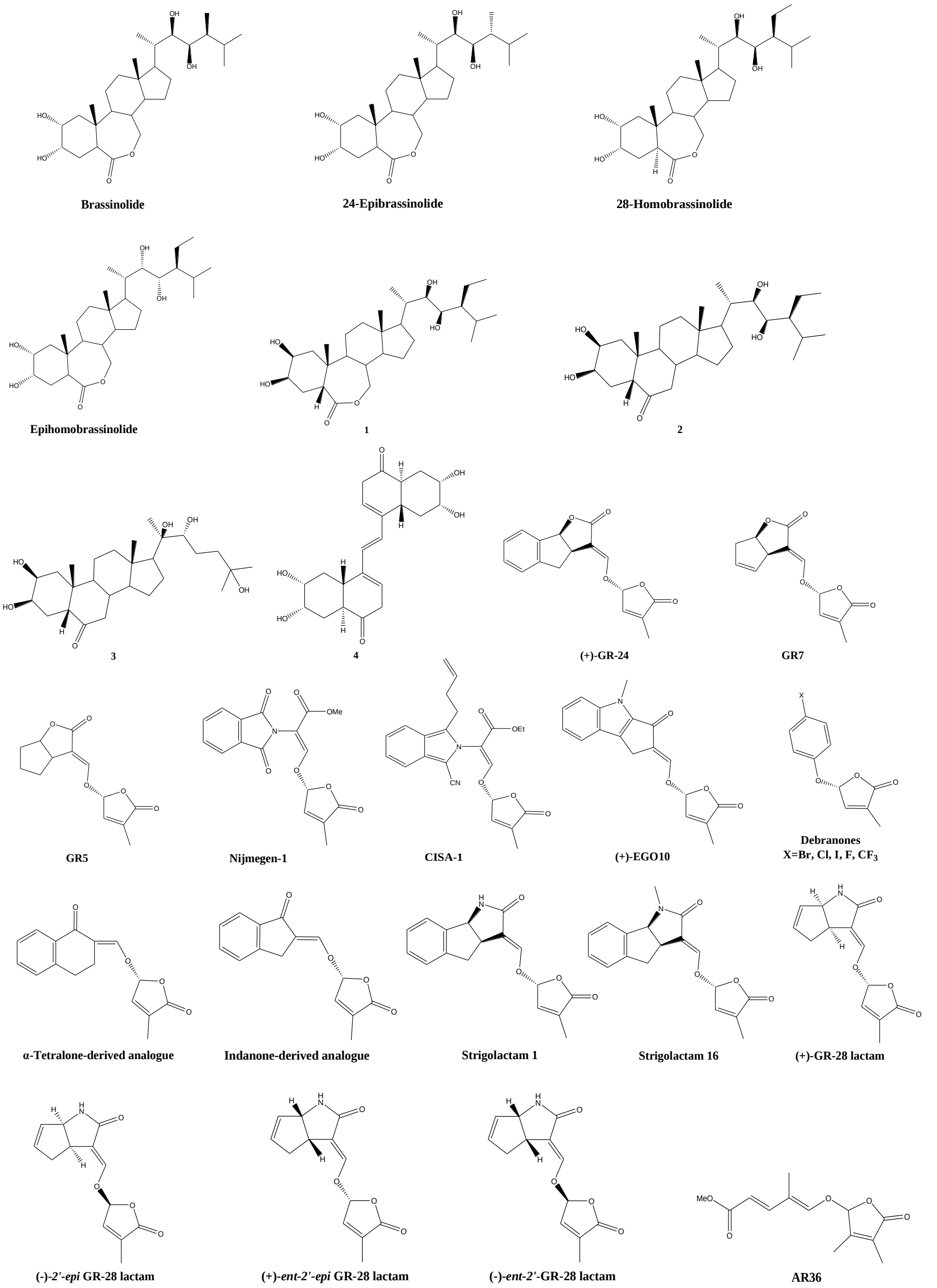
To promote the application of brassinosteroids in agriculture, research on isolation and identification, chemical synthesis, biochemistry and plant physiology of brassinosteroids is expanding. The early synthetic Brassinolides mainly contains only the following: brassinolide, 24-epibrassinolide, 28-homobrassinolide, epihomobrassinolide.

Rice lamina inclination tests of leaf lamina demonstrated that at the same dose, the activity of brassinolide analogues 1 and 2 was 87 % and 51 %, respectively and the activity of compound 1 was similar to that of 28-homobrassinolid (9). The compound 3 has almost the same activity as brassinolide (28). Anderson *et al*. (2) for the first time synthesized Non-steroidal compound 4 to mimic the activity of brassinolide.

3.2 Synthetic strigolactone (SL)

Synthetic SL can be divided into two categories: (i) Analogues, whose structure is very similar to the typical natural SL; (ii) Mimics, which are simpler in structure and biologically similar to strigolactone (Fig. 2).

3.2.1 Synthetic strigolactone Analogues: GR 24 is a well-known representative of the GR derivative family, which has been widely used in agricultural production and scientific research, resulting in the synthesis of GR5 and GR7 due to its simple structure. GR7 is used as a suicide germination agent for the control of *Striga asiatica* (32,79). In addition, the germination activity of Nijmegen-1 is equivalent to GR24 and this substance can be easily synthesized (49,80). EGO10, which can be easily synthesized from the readily available reagent in a three-step reaction, is used as a phytohormone to regulate plant branching (13,51). Goossens, Hannelore *et al*. (27) showed that CISA-1 showed higher activity than GR24 in stimulating *Orobanche* spp. seed germination and inhibiting the parasitic plant. In addition, the activity of CISA-1 and GR24 was comparable for both Arabidopsis and pea in inhibiting the plant branching. At the same time, CISA-1 promotes arbuscular mycorrhizal fungal branching and does not endanger the toxicity of host plant



Brassinolide **24-Epibrassinolide** **28-Homobrassinolide**

Epihomobrassinolide **1** **2**

3 **4** **(+)-GR-24** **GR7**

GR5 **Nijmegen-1** **CISA-1** **(+)-EGO10** **Debranones X=Br, Cl, I, F, CF_3**

α-Tetralone-derived analogue **Indanone-derived analogue** **Strigolactam 1** **Strigolactam 16** **(+)-GR-28 lactam**

(-)-*2'-epi* GR-28 lactam **(+)-*ent-2'-epi* GR-28 lactam** **(-)-*ent-2'*-GR-28 lactam** **AR36**

Figure 2. Chemical structures of synthetic bioregulators

(27). In 2011, Mwakaboko *et al*. (47) reported the synthesis of α-Tetralone-derived analogue and Indanone-derived analogue and the results of activity test. The results showed that the (*R*)-configurations of the two analogues had very high stimulatory activity to *Orobanche crenata* seeds at all concentrations, comparable to GR24 activity, but the (*S*)-configuration did not stimulate germination. Recent studies have shown that strigolactam and strigolactam derivatives with germination activity can be successfully synthesized (35,37).

3.2.2 Synthetic strigolactone Mimics: The activity of such compounds is similar to synthetic strigolactone. Due to its simple structure and high activity, such substance is considered for agricultural application. It was named "debranones" because it inhibits plant branches (23,24,36). These synthetic strigolactone mimics moderately stimulates the seeds germination of *Striga hermonthica*, but significantly stimulates the seed germination of *Orobanche cernua* and *Philipphe ramosa* (23,66). Compound AR36 is very inhibitory to the pea branches, but does not induce the seeds germination of root parasitic weeds (8).

4. CONCLUSIONS

Six types of allelochemicals as plant growth regulators have been reviewed. The agrostemin, brassinolide and triacontanol are widely used as Growth Regulators, but the use of strigolactones, jasmonic acid and salicylic acid is less due to their high cost. Research should focus on discovering more new allelochemicals with growth regulation activity and their use as basic structures or templates for the development of novel, eco-friendly and efficient synthetic growth regulators useful in agriculture.

5. ACKNOWLEDGEMENTS

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