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Review
OLIGOGALACTURONIDES IN THE GROWTH AND DEVELOPMENT OF PLANTS

Revisión bibliográfica
Los oligogalacturónidos en el crecimiento y desarrollo de las plantas

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ABSTRACT. Oligogalacturonides consist of a linear chain of galacturonic acid molecules linked by α-1-4. bonds. These macromolecules are located in the pectic portion that constitutes the cell wall of plants and under natural conditions are released from pectin through the action of pectic enzymes from the plant itself or from microorganisms that invade plant tissues.They can regulate the synthesis and action of some hormones, and different processes of organogenesis and growth in plants. From a mixture of these molecules a product commercially called Pectimorf® has been obtained that favors the growth and formation of roots, the differentiation of the cells of the pericycle and it has exerts an inducing effect on the processes of differentiation of somatic embryos, also that it increases the yield of several crops. Oligogalacturonides are proved to reduce heavy metal toxicity and counteract some of the negative effects of water stress. Due to their biological functions, these macromolecules can be considered suitable to create new biostimulants for the benefit of agriculture.

Key words: galacturonic acid, biostimulants, stress, organogenesis, hormones

RESUMEN. Los oligogalacturónidos consisten en una cadena lineal de moléculas de ácido galacturónico unida por enlaces α-1-4. Estas macromoléculas se localizan en la porción péctica que constituye la pared celular de las plantas y en condiciones naturales se liberan de la pectina mediante la acción de enzimas pécticas de la propia planta o proveniente de los microorganismos que invaden los tejidos vegetales. Ellos pueden regular la síntesis y acción de algunas hormonas, y distintos procesos de organogénesis y crecimiento en las plantas. A partir de una mezcla de estas moléculas se obtuvo un producto denominado comercialmente Pectimorf® que favorece el crecimiento y la formación de raíces, la diferenciación de las células del periciclo, ejerce un efecto inductor sobre los procesos de diferenciación de embriones somáticos e incrementa el rendimiento de varios cultivos. También se ha demostrado que los oligogalacturónidos pueden reducir los efectos provocados por metales pesados y contrarrestar algunos de los efectos negativos del estrés hídrico. Por sus funciones biológicas estas macromoléculas pueden considerarse idóneas para crear nuevos bioestimulantes en beneficio de la agricultura.

Palabras clave: ácido galacturónico, bioestimulantes, estrés, hormonas, organogénesis

INTRODUCTION

Agriculture plays a fundamental role in the development of the economy and in the diet of society.

In recent years, this activity has been affected by the environmental conditions triggered by climate changes. It is expected that if this problem is not addressed in an appropriate manner it could lead to unfavorable economic and social consequences.

These variations in the climate can lead to accelerate the decomposition of soil organic matter, affect the fertility of soils, and promote its salinization by rising sea levels and the proliferation of diseases in plants. In semi-arid areas, a higher frequency and severity of drought and excessive heat are expected conditions that can significantly limit the growth and yield of crops (1).

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This situation has caused concern among scientists and has led to many of their research aimed at mitigating its effects by discovering new products to improve plant development and enhance agriculture. Within these products are the oligosaccharins.

These molecules are generated by enzymatic hydrolysis of the cell wall of plants and fungi that at low concentrations have biological activity; and are involved in various plant development processes (2).

They are considered biostimulants because they are bioactive molecules whose function is to improve the physical-chemical properties of plants, yields and the quality of crops. Since they are not toxic to man or the environment, they are proposed as an alternative to the use of agrochemicals (3).

The oligosaccharins are classified as endogenous or exogenous, according to whether they are obtained or released from the cell walls of the plant or the pathogen. Among the endogenous ones, the best known are oligogalacturonides and xyloglucans. Oligoglucans, oligochitins, poly and oligochitosanas and lipo-oligosaccharides of chitin (4,5) are among the exogenous.

Oligogalacturonides (OGAs) are one of the most studied oligosaccharins. These oligosaccharides are released from the pectic polysaccharides that make up the cell wall during the degradation of these structures by the pectic enzymes of the plant itself or from the microorganisms that invade plant tissues (5).

In the present work the chemical characteristics of the oligogalacturonides are exposed, that make them functional from the biological point of view, their role in the growth and development of the plants, and their potentialities to attenuate the stress.

These properties allow them to be considered suitable candidates to be part of new agricultural biostimulants.

Structural characteristics of oligogalacturonides

OGAs are linear oligosaccharides of D-galacturonic acid units linked by α (1-4) type bonds (6,7). The pyranoside ring of D-galacturonic acid appears in the chair conformation $^4C1$ corresponding to its more stable form (6,8,9). The glycosidic bonds in the C-1 and C-4 are also in the axial-axial position and the number of D-galacturonate residues that the oligosaccharide contains defines its degree of polymerization (10).

These molecules can be present in plant tissues in unsaturated form with a double bond between the C-4 and C-5 of the terminal residue or in the form of oxidized C-1 OGAs, in which the residue of the reducing end is a galactaric acid. It is frequent that galacturonic acid residues are methylated determining a greater or lesser degree of esterification in the pectin. The most important characteristics to be considered in the macromolecule are the esterification and polymerization degree, molecular mass, content and binding site of neutral sugars and the distribution of non-uronic substituents (6,9).

The polymerization degree of these molecules is the structural factor of greatest significance in the definition of their biological function (2,6).

Pectic fragments with a degree of polymerization greater than 16 present biological activity, but have little mobility in the apoplast, this confers less importance as signaling molecules because it is possible that the same cell wall acts as a barrier to the interaction of these macro-fragments with the cytoplasmic membrane (11). It is further known that the activity of the OGAs decreases when the carboxyl groups (-COOH) are esterified or reduced and when the reducing end of the oligosaccharide is reduced to alditol (9).

OGAs can be obtained by acid or enzymatic hydrolysis of the plant cell wall or polygalacturonic acid. Polygalacturonic acid is obtained by basic or enzymatic demethoxylation of pectin (12,13). The most abundant raw materials for the production of pectins are the residues from the production of apple juice and the extraction of citrus juices (14).

Auxiliary/antiauxin activity of OGAs

The OGAs are currently considered as endogenous bioregulators in the development of plants, since they can regulate the synthesis and action of hormones and different processes of organogenesis and growth; directly regulate many of the physiological processes involved in the formation of organs in plants (15,16). They are involved in the growth and formation of lateral roots, the formation of adventitious roots and the differentiation of the cells of the pericycle (17), in addition to exerting an inductive effect on the differentiation processes of somatic embryos (18). However, several authors state that they behave as antagonists of auxinic activity (15,19,20). The first evidence of this antagonism between auxin and OGAs was shown in segments of pea stems in which the growth induced by auxin was competitively inhibited by elicitors of OGAs (21).

In studies carried out on tobacco plants (*Nicotiana tabacum*) and Arabidopsis (*Arabidopsis thaliana*) OGAs inhibited the induction of root formation by auxin and the formation of flowers from explants that normally do not form organs. In addition, they prevented the auxin stimulation of mitotic activity that leads to the formation of stomata (15). The results in tobacco indicated that OGAs inhibit the induction of auxin-sensitive genes (Nt114, rolB and rolD) and interfere in the activation of auxin-regulated promoters (17). In Arabidopsis they inhibit the auxin induction of the transcription of several genes (IAA-5, SAUR-16) (15,21) and the activation of the synthetic auxin response promoter (15).

It is proposed that the antagonism between these molecules does not involve the silencing of the genes that code for the auxin receptors (TIR1/AFB, T1R1, AFBs), neither requires the activity of a microRNA, nor the post-transcriptional silencing of genes (15), but it occurs when the auxin-regulating genes are induced by the translation of the inhibitor Cycloheximide, suggesting that the OGAs could act in sites after the repressors Aux/IAA, possibly at the level of promoter regions of genes that respond to auxin (19). Furthermore, it is known that the inhibition of auxin responses by OGAs does not require ethylene, jasmonic acid, or salicylic acid and it is independent of the production of reactive oxygen species (15).

Contrarily, there are several studies that show that the mixture of oligogalacturonides commercially known as Pectimorf® developed by the group of bioactive products of the National Institute of Agricultural Sciences has an auxinic effect in plants (22-26). This product is constituted by a mixture of OGAs with different degrees of polymerization of galacturonic acid molecules, which is produced by the enzymatic degradation of the pectin present in the cell wall of the citrus bark. It is a stimulant of rooting, growth and cell differentiation of different plant species; it can activate defense mechanisms and reduce or attenuate environmental stress in plants (2,5,9,27-29). This product is very effective in all stages of cultivation from seedling to production and in different vegetable models (30) as we will see below.

OGAs *IN VITRO* CULTURE

In *in vitro* culture, Pectimorf® has been widely studied, demonstrating its capacity as a substitute for traditional hormones, auxins and cytokinins (26,31), in different stages and in various crops such as sugarcane (*Saccharum officinarum*) (18).), coffee (*Coffea*) (32), citrus fruits (*Citrus*) (16), potatoes (*Solanum tuberosum*) (33), tomatoes (*Solanum lycopersicum*) (34), tobacco (35), bananas (*Musa paradisiaca*) (9), yucca (*Manihot esculenta*) (36), among others (Table 1).

It is argued that *in vitro* cultivation, OGAs can exert an auxinic or cytokininic effect depending on the hormonal balance in the culture medium, in addition to stimulating the synthesis of proteins in cells and acting in cell disaggregation during the obtaining of cell suspensions increasing the efficiency of the process (30.37).

In the cultivation of apices of *in vitro* plants of cassava (*Manihot esculenta* Crantz), clones \`CMC-40' and\` Señorita' in which they used different concentrations of Pectimorf® as a substitute and complement of the growth regulators ANA (naphthaleneacetic acid) and 6-BAP (6- benzylaminopurine). The clone \`CMC-40' with 5 mg L^{-1} of Pectimorf® in substitution of ANA, showed the highest height value (2.88 cm), without significant differences with the control (ANA and BAP), and the treatments where they added the Pectimorf® to 5 and 10 mg L^{-1} respectively, in the presence of ANA and in replacement of the BAP. The results indicated that the bioproduct managed to compensate the effect of auxin (ANA) in the absence of this in the medium; however, there was no marked antagonistic effect when it was present (36).

This auxinic-cytokinin effect was also proven in the *in vitro* culture of the yam (*Dioscorea rotundata* Poir) clone 'Blanco de Guinea' where they evaluated different concentrations of Pectimorf®. From morphoagronomic evaluations (stem length, length of the largest root, and number of leaves, number of de novo knots and number of roots) determined that the concentrations of 6, 9 and 12 mg L^{-1} cause a significant increase on the vegetative development of the plants demonstrating the auxinic effect of the product. However, at lower concentrations and higher than these the product had a cytokinin effect (26).

In the *in vitro* development of the somatic embryogenesis of *Citrus macrophylla* Wester where the medium was supplemented with Pectimorf® the first embryos were formed at five weeks, whereas in the media that did not contain the mixture of OGAs these structures were observed between the six and seven weeks of cultivation. It is known that in order to favor the formation of somatic embryos, the exogenous application of auxins to the culture medium is required; however, the percentages obtained in this investigation were above 50 % in the formation of embryos, without adding auxin (16).

Table 1. Effect of the Oligogalacturonides in the development and growth of different crops

Crop	Concentration	Effect	Reference
In vitro			
Citrics *Citrus*	10 mg L^{-1} OGAs	Accelerates and increases the process of somatic embryogenesis	(16)
Tomato *Solanum lycopersicum*	10 mg L^{-1} OGAs	Stimulates the formation of calluses and the regeneration of multiple outbreaks	(34)
Banana *Musa paradisiaca*	1 y 5 mg L^{-1} OGAs	*Provides better adaptation to ex vitro conditions*	(9)
Cassava *Manihotesculenta*	5 mg L^{-1} OGAs	Stimulates the growth of meristems	(36)
Yam *Dioscorea rotundata* Poir	6 mg L^{-1} OGAs	Stimulates the micropropagation phase and the acclimatization phase	(26)
Potato *Solanum tuberosum*	3,2 mg L^{-1}OGAs +0,1 mg L^{-1} AUX	It favors the obtaining of somatic embryos	(33)
Sugar cane *Saccharum officinarum*	5 mg L^{-1} OGAs + 1,5 mg L^{-1} AUX	Induction of somatic embryo differentiation processes	(18)
Papaya *Carica papaya*	9 mg L^{-1} OGAs + 2 mg L^{-1} AUX	It positively influences the rooting and the *in vitro* acclimatization of the sprouts	(25)
Ex vitro			
African violet *Saintpauliaionantha*	10 mg L^{-1} OGAs	Advance the rooting process	(23)
Kidney bean *Vigna unguiculata* L	10 mg L^{-1} OGAs	Increase performance	(31)
Guava *Psidium guajava*	20 mg L^{-1} OGAs	Promotes the formation of adventitious roots	(24)
Tomato *Solanum lycopersicum*	10 mg L^{-1} OGAs	Increase yield and improve the quality of the fruits	(40)
Lettuce *Lactuca sativa*	10 mg L^{-1} OGAs	Increase the size of the leaflets and the radical length	(27)
Radish *Raphanus raphanistrum*	10 mg L^{-1} OGAs	Favors the growth of stems and roots	(27)
Bean *Phaseolus vulgaris*	10 mg L^{-1} OGAs	Increase the stomatal index	(39)

The Pectimorf® also positively influences the rooting and acclimatization of papaya plants (*Carica papaya*). The concentration of 9 mg L^{-1} of Pectimorf® combined with 2 mg L^{-1} of auxin (AIB) guaranteed a greater foliar area, fresh mass, greater value in the number of roots, a high photosynthetic rate and stomatal conductance, a high percentage of rooting (84.2 %) and a lower percentage of open stomata with respect to control without Pectimorf® (25).

According to studies with OGAs in *Arabidopsis thaliana* and in the tobacco cell line BY-2, root elongation occurs through an increase in cell division in the meristems of the apical roots together with a positive effect on cell elongation. Some authors suggest that OGAs induce the shortening of the cell cycle in the primary root as a consequence of the shortening or elimination of the G1 phase, while the other phases remain relatively constant, although they cannot assure that the G1 phase is completely eliminated from the cell (38).

These results give great importance to this mixture of OGAs in the development of *in vitro* culture, although the mechanisms that explain the stimulation of OGAs in cell division in higher plants are still unknown.

OGAs IN THE *EX VITRO* CULTURE

In recent years, research with this product in the *ex vitro* culture has been aimed at determining the best concentration and application form to which plants show a greater physiological and biochemical response aimed at improving development, in addition to increasing yield and the quality of the crop (Table).

It has been shown that Pectimorf® has a positive effect on the growth activation of ornamental plants such as areca (*Areca catechu*), anthurium (*Anthurium*) and orchids (*Orchidaceae*), as well as edible plants, mainly legumes and solanaceae. According to studies, the growth of ornamental plants is favored by foliar spraying at different concentrations and times of application (5).

In legumes this mixture of OGAs also increases leaf development and yield mainly in the cultivation of beans (*Phaseolus vulgaris*) and in soybeans (*Glycine max*) (31). Root formation contributes to the development of roots from early stages of the crop with the possibility of ensuring an efficient supply of water and mineral salts and, therefore, greater success in the development of the plant.

The rooting effect of the OGAs is also evident in African violet petioles (*Saintpauliaionantha*), where two concentrations (10 and 20 mg L^{-1}) were used, this product being able to stimulate root emission, its length, as well as how he managed to advance in a week the appearance of them (23). It also caused this same effect in cucumber seedlings (*Cucumis sativus*) in combination with auxins (17); in cuttings of guava (*Psidium guajava*) var. Enana roja cubana at concentrations of 20 mg L^{-1} (24) and in ornamental plants (25).

Investigations in bean plants sprinkled with 10 mg L^{-1} of Pectimorf® at the beginning of the second stage of the vegetative phase of culture revealed that this mixture of OGAs causes an increase in the stomatal index without altering the structure of the epidermal cells in both foliar surfaces; nor modify the size of the stomatal cells. On the abaxial surface, the occlusive cells were narrower and shorter, which evidenced that the leaves with the highest stomatal index showed smaller stomata. These modifications in the distribution patterns and stomatal morphogenesis could favor the adequate growth of bean plants in unfavorable environments (39).

The OGAs are also involved in the process of maturation of the fruits (19) also can improve their quality. In tomato plants treated with this mixture of OGAs, results were obtained in which the yield of the fruit per plant was increased by 40 %, the titratable acidity was improved by 0.04 %, total solids by 13 %; as well as the firmness of the fruit in 27 % with respect to the control (40). Also in studies carried out in wild strawberry plants treated with OGAs ripe fruits were obtained with an increase in size (17).

In table grape varieties Flame Seedless and Red Globe, the application of OGAs of 3-20 GP caused an increase in their coloration, which constitutes an indicator of quality. One possible explanation is that OGAs increase the level of ethylene in fruits and in turn over-regulate genes related to the synthesis of anthocyanins such as chalcone synthase, flavonone 3-hydroxylase and UDP glucose flavonoid-3-glucosyltransferase (41,42), leucoanthocyanidin dioxygenase, as well as lignin (42). The application of OGAs increased the antioxidant capacity of the grapes due to the accumulation of phenolic compounds (41). The color improvement and the increase in anthocyanin content may be the result of the inducing action exerted by OGAs on the synthesis of RNAm of the phenylalanine Ammonium Liase (PAL) (42).

In vegetables such as lettuce (*Lactuca sativa*) and radish (*Raphanus raphanistrum* subsp. sativus) OGAs cause morphological changes. In the case of lettuce they increase the size of the leaflets and in radish plants it favors the growth of stems, roots and radishes (27). In the kidney bean (*Vigna unguiculata* L.) var. Lina managed to increase its yield to 4.7 kg m^2 from the combination of two forms of application, seed imbibition + foliar application at a concentration of 10 mg L^{-1} at the beginning of flowering (31).

There are authors who suggest that a possible way in which OGAs increase the growth of plants is because these molecules can stimulate photosynthetic activity; which causes a greater gain of carbon skeletons that can be used for the synthesis of new compounds, such as proteins (43).

From the analysis of the results obtained in vegetables, fruit trees and ornamental plants it can be stated that this mixture of OGAs promotes the process of growth and development of different organs in the plants and physiological processes at concentrations between 5 and 20 mg L^{-1} in the treatment of seeds, cuttings and by foliar spray and the combination of these forms of application; although several authors attribute its rooting power to it as a main effect (23,24,27,44).

Oligogalacturonides as mitigating the abiotic stress

The stress caused in plants by water deficit inhibits photosynthesis, causes changes in the chlorophyll content and damages the photosynthetic apparatus. Under these conditions the dry and fresh weight of the plants decreases and the content of proline, carbohydrates and proteins increase as survival mechanisms adopted by the plant itself (45).

The property of the OGAs to stimulate the growth of the radical system, allows the plant a better exploration and radical activity, translated into a greater capacity of absorption of water and nutrients, so it represents an appropriate option to address water stress problems (30).

It is also known that the gelling effect of OGAs allows the absorption of water from the medium, although it is scarce, facilitating the processes involved in the germination and emergence of the seeds. These molecules are capable of triggering in plant cells a series of stimuli that promote faster metabolism and greater enzymatic activity, depending on the plant species, the concentrations used and the degree of polymerization (30).

In a study of basil plants (*Ocimum basilicum*) in the germination, emergence and initial growth stage subjected to water stress, to which Pectimorf® was applied at a concentration of 10 mg L^{-1}, an increase was obtained in both the rate as in the germination percentage.

Stressed plants treated with the mixture of OGAs showed a higher concentration of foliar reducing carbohydrates, protein and proline content in leaves and root, than plants subjected to stress that were not treated (30).

This result is related to the increase of photosynthesis and to the direct stimulation that OGAs have in cellular metabolism, product of their participation in the synthesis of antioxidant agent precursor molecules, capable of counteracting some of the negative effects of water stress (30).

The OGAs have also been studied with the aim of reducing the negative effects caused by heavy metals (13). As a result of the presence of these ions in the soil the roots of plants shorten and swell, because metal ions act directly on the metabolism, interfering in the transfer of ions through cell membranes, which affects the absorption of water and nutrients from the soil by the plant (46). From studies, it was found that when applying a dose of 60 kg ha^{-1} of Pectimorf® to a soil with high levels of Cu^{2+} cultivated with tomato plants of the cultivar Amalia, the elongation of the main root is stimulated and levels are achieved of extraction of Cu^{2+} ions of 25, 47 mg kg^{-1} (47).

They have good properties as copper ion absorbers in aqueous solution because they form stable complexes in a pH range of 3-7, although the metal complexes obtained are less thermally stable than the mixture of starting OGAs (13). This feature gives it great importance in the processes of phytoextraction.

CONCLUSIONS

- The OGAs are an ecologically and economically viable alternative to increase crop yields. Its capacity as mitigating factors of abiotic stress allows enhancing agriculture in unfavorable conditions.
- Despite the fact that Pectimorf® research has increased in recent years and that very good morphoagromic results have been obtained, the biochemical and molecular mechanisms by which this product exerts its action are not known. So it would be valid to conduct studies aimed at determining which indicators of carbon and nitrogen metabolism are stimulated with their application. On the other hand, the ability of OGAs to have biological activity at low concentrations and replace some traditional hormones is an element to consider in order creating new biostimulants for the benefit of agriculture.

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