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Effect of auxins and plant oligosaccharides on root formation and elongation growth of mung bean hypocotyls

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Abstract

The interaction of auxins – IAA, IBA or NAA – with galactoglucomannan oligosaccharides (GGMOs) on adventitious root formation and elongation growth of mung bean hypocotyl cuttings was studied. GGMOs induced adventitious roots in the absence of auxins; however, their effect was lower compared with IBA or NAA. On the other hand, in the presence of auxins, GGMOs inhibited adventitious root induction. Their effect depended on the concentration of oligosaccharides and the type of auxin used. The highest inhibition effect of GGMOs at a concentration of 10^{-8} M in the presence of IBA and NAA was observed. In the presence of IAA their inhibition was non-significant in regard to the concentration. The interaction of auxins with GGMOs resulted in the formation of adventitious roots on a shorter part of hypocotyls compared with the effect of auxins alone. However, roots were induced more extensively along the hypocotyls treated with GGMOs compared with the control. GGMOs inhibited the length of induced adventitious roots in the presence of IAA, while in combination with IBA or NAA they were ineffective. The elongation of hypocotyls induced by IAA or IBA was inhibited by GGMOs, too. However, in the presence of NAA or by endogenous growth they were without any significant effect on elongation growth. These findings suggest that GGMOs in certain concentrations might inhibit rooting and the elongation process dependant on auxin used.

Abbreviations: 2,4-D – 2,4-dichlorophenoxyacetic acid; GA_3 – gibberellic acid; GGMOs – galactoglucomannan oligosaccharides; GGM – galactoglucomannan; IAA – indole-3-acetic acid; IBA – indole-3-butyric acid; NAA – 1-naphthaleneacetic acid

Introduction

A variety of oligosaccharide signals have been identified that function in the regulation of plant development, defence, and other interactions of plants with the environment. The characteristic features of these regulatory molecules are that they are derivatives of cell wall polymers, and are biologically active at extremely low concentrations (John et al. 1997). Oligosaccharides control processes involved in plant growth and development under the regulation of phytohormones (Eberhard et al. 1989; Altamura et al. 1998). Xyloglucan oligosaccharides inhibit auxin or

gibberellic acid-induced elongation growth of pea epicotyls (York et al. 1984; McDougall and Fry 1988; Warneck and Seitz 1993). On the other hand, it was ascertained that xyloglucan oligosaccharides stimulate elongation growth of stem segments by modification of cell wall mechanical properties (McDougall and Fry 1990; Cuttilas-Iturralde and Lorences 1997; Takeda et al. 2002). The growth promotion effect of xyloglucan oligosaccharides has been attributed to the activation of cell wall enzymes responsible for xyloglucan breakdown (Kaku et al. 2004).

Adventitious root formation is important for the vegetative propagation of plants. Several natural and synthetic plant growth regulators have been tested for their rhizogenic activity (Smith and Thorpe 1975; Wightman and Thimann 1980; Blakely et al. 1988; Lloret and Pulgarín 1992; Balestri and Bertini 2003; Casimiro et al. 2003; Wang et al. 2003). IAA, IBA, and NAA are responsible for rhizogenesis in various plant materials (Eliasson 1980; Jarvis 1988; Blakesley 1994; Percival and Gerritsen 1998; Müller 2000; Wang et al. 2003). Besides auxins and ethylene (Mullins 1972; Coleman et al. 1980; Riov and Yang 1989; Biondi et al. 1990; Liu and Reid 1992), saccharides are the most important factors of root initiation and growth, since they are not only energy sources, but they are important also for constructing structural components of plant cells and cell walls (Jarvis 1986). Sucrose e.g., stimulates the elongation of hypocotyls and roots in wheat and *Arabidopsis* (Bingham and Stevenson 1993; Cano-Delgado et al. 2000). Sucrose, glucose, and fructose stimulate the induction of adventitious roots in *Arabidopsis*, but mannose doesn't influence this process (Takahashi et al. 2003). Likewise plant cell wall oligosaccharides are known to be active in induction and root growth process. Oligogalacturonides e.g., had shown root growth promoting activity in lettuce (Iwasaki and Matsubara 2000); however, they inhibited the auxin-induced formation of roots in tobacco explants (Bellincampi et al. 1993). Xylooligosaccharides were effective in rooting promotion of *Cryptomeria japonica* cuttings (Ishihara et al. 1991) and in black pine, and they also stimulated the rooting of *in vitro* grown shoots of birch and black pine (Ishii et al. 1992).

We were interested in the biological activity of galactoglucomannan oligosaccharides (GGMOs). Galactoglucomannan (GGM) is the structural constituent of both, primary and secondary cell walls of higher plants (Dey 1980; Akiyama et al. 1983; Lundqvist et al. 2002; Schröder et al. 2004). GGMOs derived from GGM showed an inhibition effect of 2,4-D-induced elongation growth of pea (*Pisum sativum* L. cv. Tyrkys) and spruce (*Picea abies* L. Karst) stem segments at very low concentrations (Auxtová et al. 1995; Auxtová-Šamajová et al. 1996). The inhibition effect of GGMOs is restricted not only to the elongation growth induced by 2,4-D, but the inhibition has been determined also in the presence of IAA- and GA_3-induced elongation as well (Kollárová et al. 2005). Besides elongation, GGMOs are able to influence some developmental processes and defence reactions in plant cells (Lišková et al. 1995; Slováková et al. 2000). However, their effect on root induction has not been studied yet. Mung bean hypocotyls are known to be highly responsive to exogenously applied auxins and other growth regulating compounds (Pan and Tian 1999; Tamimi 2003). Therefore, the aim of our work was to compare the effect of GGMOs, IAA, IBA, and NAA on root formation and growth, and the elongation of mung bean hypocotyl cuttings.

Materials and methods

Plant material

Seeds of mung bean (*Vigna radiata* (L.) Wilczek) (Breeding Station Co. Horná Streda, Slovakia) were soaked in water for 3 h and sown in cellulose wadding. The seeds were kept in the thermostat for 72 h at 27 ± 1 °C, 80% relative humidity in the dark. Uniform seedlings according to the length, hypocotyl diameter, size of leaves, and cotyledons were selected. Hypocotyls of 6–7 cm length were cut 5 cm below the cotyledons and roots were removed.

Chemicals

IAA, IBA, and NAA were purchased from Sigma–Aldrich Chemie Gmbh, Germany. GGMOs with d.p. 4–8 were obtained from spruce galactogluco-

mannan by partial acid hydrolysis as described previously (Capek et al. 2000). GGM consists of a backbone of (1 → 4)-linked β-D-mannopyranosyl and β-D-glucopyranosyl residues distributed at random, having single stubs of (1 → 6)-linked β-D-galactopyranosyl residues attached to both mannosyl and glucosyl residues, with slightly preferred substitution of mannosyl residues. Galactoglucomannan consists of galactose, glucose and mannose in the molar ratio 1:8:33 and trace amounts of pentose sugars i.e., D-xylose and L-arabinose.

Rooting, root length, and hypocotyl elongation

Hypocotyl cuttings were dipped for 24 h in glass vials containing a 3 cm column of distilled water (control), or the test solution. The test solution was prepared from GGMOs dissolved in distilled water to give concentrations ranging from 10^{-10} to 10^{-6} M. For interaction studies between auxins and GGMOs in the rooting process IAA at 10^{-6} M, IBA at 10^{-4} M, and NAA at 10^{-4} M concentrations were used either alone or in combination with GGMOs. Cuttings after the treatment were planted into the substrate (wet sand + peat in the ratio 3:1) and maintained under controlled conditions at 27 ± 1 °C, 60–70% relative humidity, under 12 h photoperiod at irradiance of 80 μmol m^{-2} s^{-1} and daily watering. The number, length, and position of adventitious roots on hypocotyls as well as hypocotyls length were determined after five days of treatment.

Statistical analysis

The data represent the mean of three separate experiments with 15 hypocotyls per treatment. The data were analyzed using ANOVA, comparisons between the mean values were made by LSD test (least significant difference), and standard error (SE) was calculated.

Results and discussion

Root formation and root length

Effect of auxins

IAA, NAA, and IBA for their most effective concentration on root induction and elongation in mung bean hypocotyl cuttings has been tested. IAA in the concentration 10^{-6} M showed the best induction of adventitious roots, and stimulated the elongation of hypocotyls, but with non-significant effect in regard to the concentrations tested (Table 1). The utmost stimulation of adventitious root formation by NAA at the concentration 10^{-4} M occurred (Table 2), but the elongation of hypocotyls wasn't significantly affected by any of the NAA concentrations. IBA tested previously by Šimonová et al. (2005) on mung bean hypocotyls showed the most effective concentration at 10^{-4} M.

All auxins used stimulated the formation of adventitious roots; however, the treatment with IBA was more effective in promoting adventitious root formation than that of the other two auxins. The number of adventitious roots decreased in the order of: IBA, NAA, and IAA (Figure 1). The same observation was recorded for optimal root regeneration using *Rosa* species, with IAA having

Table 1. Effect of IAA on root formation and length of mung bean hypocotyl cuttings.

IAA (M)	Root number per hypocotyl	Hypocotyl length (cm)
0	11.6 ± 0.98 a	5.73 ± 0.08 a
10^{-7}	13.3 ± 1.58 a	5.98 ± 0.09 b
10^{-6}	19.0 ± 0.85 b	5.99 ± 0.06 b
10^{-5}	13.9 ± 1.05 a	6.11 ± 0.05 b
10^{-4}	14.8 ± 1.17 a	6.01 ± 0.06 b
10^{-3}	Hypocotyl necrosis	

The values represent the means ± SE of three independent experiments with 15 hypocotyls per treatment. Data in each column followed by the same letter are not significantly different at 5% level according to LSD test.

Table 2. Effect of NAA on root formation and length of mung bean hypocotyl cuttings.

NAA (M)	Root number per hypocotyl	Hypocotyl length (cm)
0	11.6 ± 0.98 a	5.73 ± 0.08 a
10^{-7}	15.1 ± 1.26 a	5.65 ± 0.07 a
10^{-6}	17.7 ± 1.28 a	5.78 ± 0.04 a
10^{-5}	34.8 ± 3.18 b	5.82 ± 0.06 a
10^{-4}	45.5 ± 2.82 c	5.80 ± 0.06 a
10^{-3}	Hypocotyl necrosis	

The values represent the means ± SE of three independent experiments with 15 hypocotyls per treatment. Data in each column followed by the same letter are not significantly different at 5% level according to LSD test.

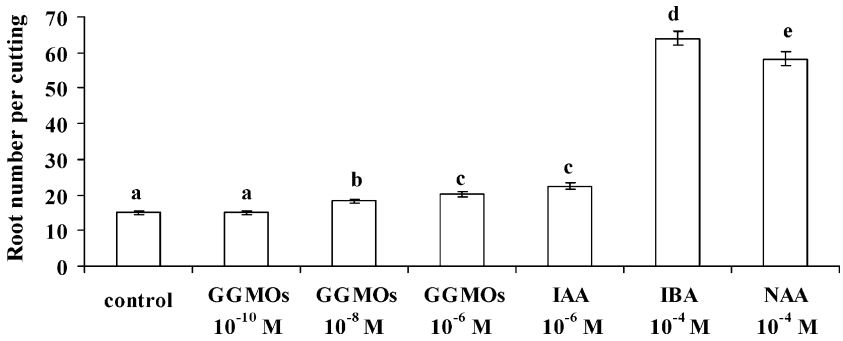

Figure 1. Effects of GGMOs, IAA, IBA, and NAA on adventitious root formation in mung bean hypocotyl cuttings. Vertical bars indicate SE of three independent experiments with 15 hypocotyls per treatment. Different letters above bars indicate significant differences among treatment at 5% level according to LSD test.

no root promoting effect (Fuchs 1986). It is assumed that the signal transduction pathway for IBA in the rooting process is at least partially different from that of IAA (Müller 2000; Wang et al. 2003). On the other hand NAA, in comparison with our results (Figure 1), inhibited root formation in various plant material (Percival and Gerritsen 1998).

Effect of GGMOs

GGMOs (10^{-8} and 10^{-6} M) induced adventitious root formation similar to IAA (Figure 1). Their effect was significantly lower compared with that of IBA and NAA in the concentrations tested. The roots in the control were induced only on the base of the hypocotyls. GGMOs treatment changed their position on the hypocotyls. With increasing concentrations of oligosaccharides, the roots were formed more extensively along the hypocotyl (Figures 2 and 3). GGMOs at 10^{-10} M concentration promoted the formation of longer adventitious roots, but at both higher concentrations the formation of shorter roots compared with the control were ascertained (Table 3). A similar effect is known for pectate oligosaccharides (d.p. 2–5) which exhibited root-growth-promoting activity in lettuce (Iwasaki and Matsubara 2000) and oligogalacturonic acids (d.p. 6–12) promoting root growth of cockscomb (*Celosia argentea* L.) and tomato seedlings (Suzuki et al. 2002). The biological activity of GGMOs in mung bean hypocotyls was weaker than that of oligogalacturonides in buckwheat (Lozovaya et al. 1993) which is probably related to their chemical structure and plant material used (Zabotina et al. 2002).

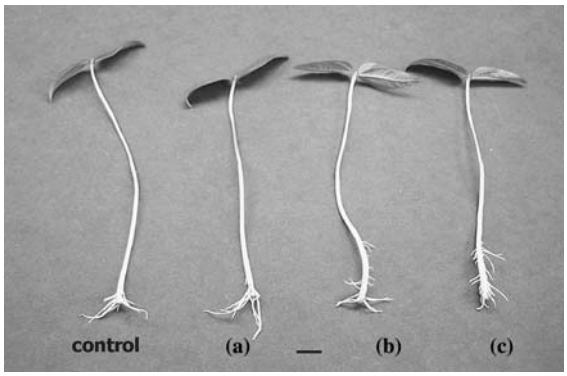

Figure 2. Effect of GGMOs on rooting of mung bean hypocotyl cuttings (bar = 1 cm). From left to right: Control = distilled water, (a) 10^{-10} M GGMOs, (b) 10^{-8} M GGMOs, (c) 10^{-6} M GGMOs.

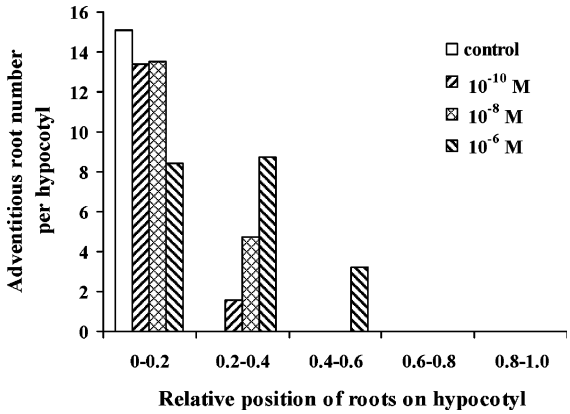

Figure 3. Position of GGMOs-induced adventitious roots on the hypocotyl cuttings. Positions are indicated by relative distance from the base of hypocotyl cuttings (0) to the cotyledons (1.0). Hypocotyl cuttings were treated with different concentrations of GGMOs. The values represent the means of three independent experiments with 15 hypocotyls per treatment.

Table 3. Effect of GGMOs, auxins, and their combinations on the length of adventitious roots.

Treatment	Root length (mm)
control	8.87 ± 0.27 a
10^{-10} GGMOs	10.13 ± 0.90 b
10^{-8} GGMOs	7.54 ± 0.23 c
10^{-6} GGMOs	7.17 ± 0.78 c
10^{-6} IAA	11.39 ± 0.30 d
10^{-6} IAA + 10^{-10} GGMOs	7.17 ± 0.31 c
10^{-6} IAA + 10^{-8} GGMOs	11.19 ± 0.61 bd
10^{-6} IAA + 10^{-6} GGMOs	10.94 ± 0.58 bd
10^{-4} IBA	7.05 ± 0.24 c
10^{-4} IBA + 10^{-10} GGMOs	6.50 ± 0.04 c
10^{-4} IBA + 10^{-8} GGMOs	6.42 ± 0.17 c
10^{-4} IBA + 10^{-6} GGMOs	6.95 ± 0.11 c
10^{-4} NAA	3.07 ± 0.24 e
10^{-4} NAA + 10^{-10} GGMOs	2.54 ± 0.10 e
10^{-4} NAA + 10^{-8} GGMOs	2.74 ± 0.44 e
10^{-4} NAA + 10^{-6} GGMOs	2.63 ± 0.38 e

The values represent the means ± SE of three independent experiments with 15 hypocotyls per treatment. Data followed by the same letter are not significantly different at 5% level according to LSD test.

Interaction of auxins and GGMOs

GGMOs inhibited adventitious root formation induced by all auxins (IAA, IBA, and NAA) used. The effect depended on the concentration of oligosaccharides and the type of auxin. The treatments with IBA or NAA in combination with GGMOs resulted in the formation of a significantly lower number of adventitious roots compared with the corresponding auxin. The highest inhibition effect of GGMOs at the concentration 10^{-8} M has been determined (Figure 4). In the presence of IAA, GGMOs inhibited the formation of adventitious roots similarly at all concentrations used. Oligogalacturonides inhibited root formation induced by IBA likewise in tobacco and caused the formation of roots on the basal end of thin-cell-layer explants (Eberhard et al. 1989). IAA-induced roots on tobacco leaf explants were also inhibited by oligogalacturonides and their inhibiting effect was dependent on their degree of polymerization (Bellincampi et al. 1993, 1996). The mechanism by which GGMOs affect the formation of adventitious roots induced by auxins is however, unknown.

Adventitious roots on mung bean hypocotyls induced by auxins were formed from the central region of the hypocotyl to its base (Figures 5 and 6). NAA stimulated the formation of roots more

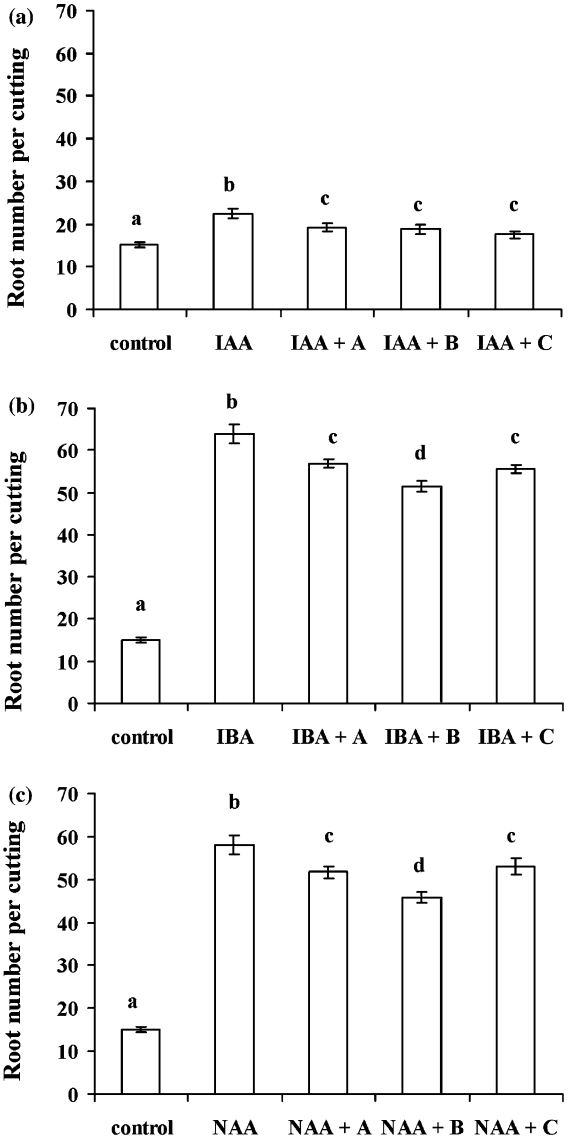

Figure 4. Effect of IAA at 10^{-6} M (a), IBA at 10^{-4} M (b), and NAA at 10^{-4} M (c) concentrations, and in combination with GGMOs at 10^{-10} (A), 10^{-8} (B) and 10^{-6} M (C) concentrations on the rooting of mung bean hypocotyl cuttings. Vertical bars indicate SE of three independent experiments with 15 hypocotyls per treatment. Different letters above bars indicate significant differences among treatment at 5% level according to LSD test.

extensively along the hypocotyl compared with the other two auxins (Figure 6). GGMOs shortened this rooting part.

Root length was affected differently by auxins compared with their effect on root induction. The length decreased in the order IAA, IBA, and NAA

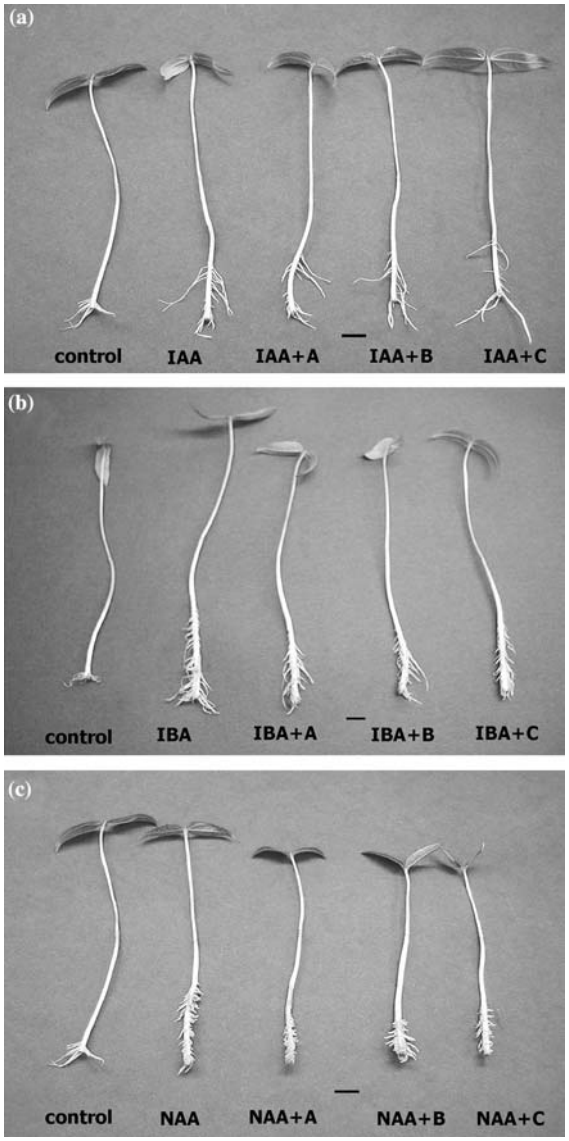

Figure 5. Effect of IAA at 10^{-6} M (a), IBA at 10^{-4} M (b), and NAA at 10^{-4} M (c) concentrations, and in combination with GGMOs at 10^{-10} (A), 10^{-8} (B) and 10^{-6} M (C) concentrations on the rooting of mung bean hypocotyl cuttings (bar = 1 cm).

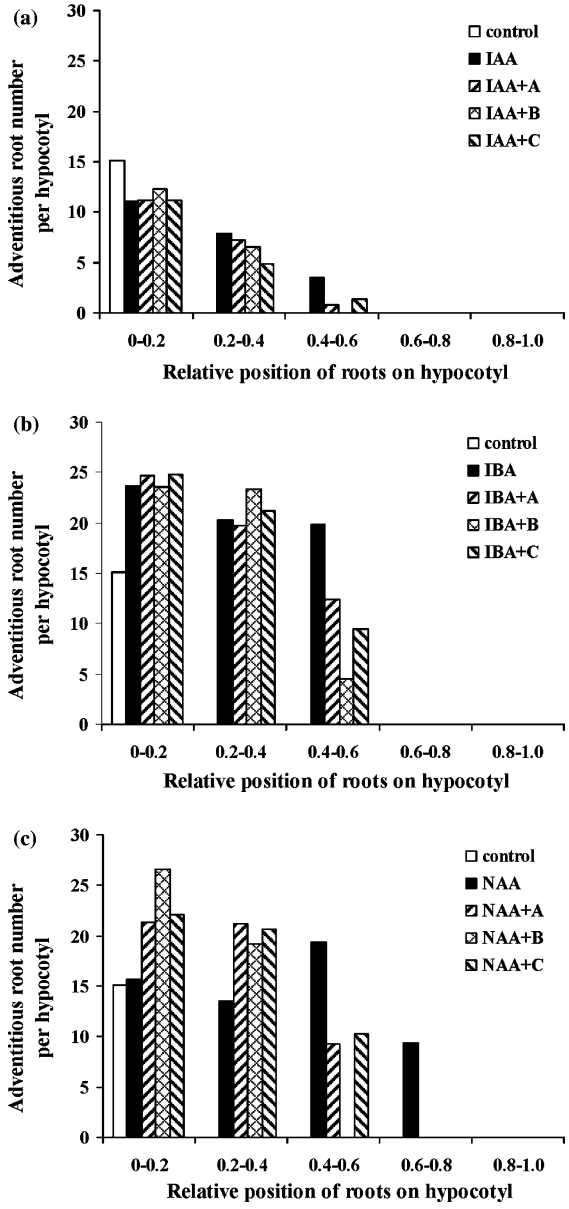

Figure 6. Position of adventitious roots on the hypocotyl cuttings induced by auxins (IAA (a), IBA (b) and NAA (c)) alone, or in combination with GGMOs at 10^{-10} (A), 10^{-8} (B) and 10^{-6} M (C) concentrations. Root positions are indicated by relative distance from the base of hypocotyl cuttings (0) to the cotyledons (1.0). The values represent the means of three independent experiments with 15 hypocotyls per treatment.

(Table 3). IBA and NAA were responsible for the formation of shorter roots compared with the control. In other plant material, e.g. branch cuttings of *Juniperus procera* NAA yielded relatively longer roots compared with other auxins (Berhe and Negash 1998). Different reactions of plant material to auxins indicate species specificity. GGMOs (10^{-10} M) inhibited the length of roots in the presence of IAA, but they were without significant effect on the roots length in the presence of IBA or NAA. It can be summarized that the type of auxin substantially influences the root length in certain plant material, and this effect of auxin is also reflected in the inhibition effect of oligosaccharides.

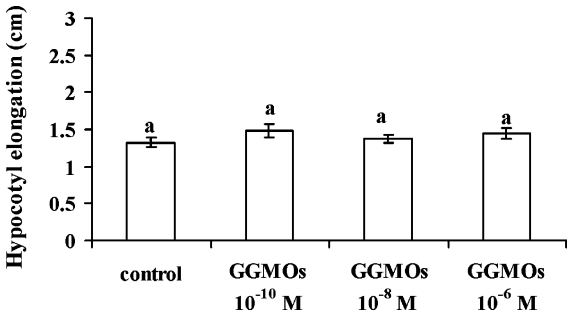

Figure 7. Effect of GGMOs on elongation growth of mung bean hypocotyl cuttings. Vertical bars indicate SE of three independent experiments with 15 hypocotyls per treatment. Different letters above bars indicate significant differences among treatment at 5% level according to LSD test.

Elongation of hypocotyls

GGMOs didn't affect the endogenous growth of hypocotyls (Figure 7) as determined previously for pea and spruce stem segments (Auxtová et al. 1995), but they inhibited their elongation induced by IAA and IBA respectively, with the highest inhibition achieved at the GGMOs concentration 10^{-8} M (Figure 8). The hypocotyls elongation induced by NAA was not significantly influenced by GGMOs. This result probably is connected with the weak stimulation of hypocotyls elongation by NAA.

On the basis of our results, it is evident that the type of auxin plays an important role in the elongation process, which is in accordance with our previous observations (Auxtová et al. 1995; Kollárová et al. 2005). GGMOs were without any significant effects on the endogenous growth of these stem segments. The mechanism and/or mechanisms by which GGMOs inhibit the hypocotyl elongation induced by auxins are unknown, and maybe they are different from that of adventitious root formation and elongation.

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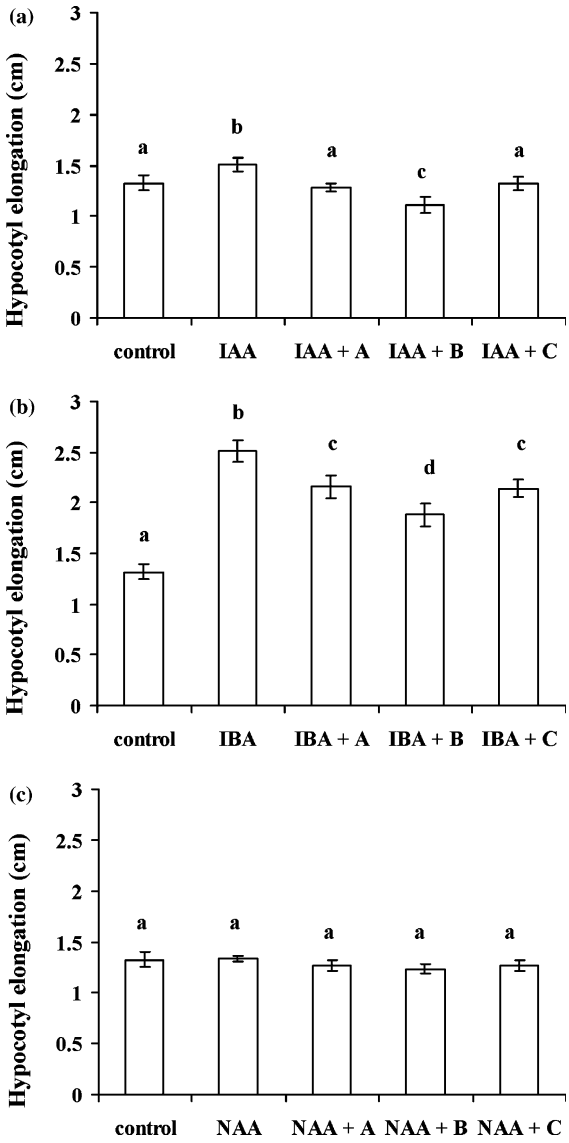

Figure 8. Effect of IAA at 10^{-6} M (a), IBA at 10^{-4} M (b), and NAA at 10^{-4} M (c) concentrations, and in combination with GGMOs at 10^{-10} (A), 10^{-8} (B) and 10^{-6} M (C) concentrations on elongation growth of mung bean hypocotyl cuttings. Vertical bars indicate SE of three independent experiments with 15 hypocotyls per treatment. Different letters above bars indicate significant differences among treatment at 5% level according to LSD test.

References

Akiyama Y., Eda S., Mori M. and Kato K. 1983. A galactoglucomannan from extracellular polysaccharides of suspension-cultured cells of *Nicotiana tabacum*. Phytochemistry 22: 1177–1180.

Altamura M.M., Zaghi D., Salvi G., De Lorenzo G. and Bellincampi D. 1998. Oligogacturonides stimulate pericycle cell wall thickening and cell divisions leading to stoma formation in tobacco leaf explants. Planta 204: 429–436.

Auxtová O., Lišková D., Kákoniová D., Kubačková M., Karácsonyi Š. and Bilisics L. 1995. Effect of galactoglucomannan-derived oligosaccharides on elongation growth of pea and spruce stem segments stimulated by auxin. Planta 196: 420–424.

Auxtová-Šamajová O., Lišková D., Kákoniová D., Kubačková M., Karácsonyi Š. and Bilisics L. 1996. Inhibition of auxin stimulated short-term elongation growth of pea stem segments by galactoglucomannan-derived oligosaccharides. J. Plant Physiol. 147: 611–613.

Balestri E. and Bertini S. 2003. Growth and development of *Posidonia oceanica* seedlings treated with plant growth regulators: possible implications for meadow restoration. Aquatic Bot. 76: 291–297.

Bellincampi D., Salvi G., De Lorenzo G., Cervone F., Marfà V., Eberhard S., Darvill A.G. and Albersheim P. 1993. Oligogacturonides inhibit the formation of roots on tobacco explants. Plant J. 4: 207–213.

Bellincampi D., Cardarelli M., Zaghi D., Serino G., Salvi G., Gatz C., Cervone F., Altamura M.M., Costantino P. and Lorenzo G. 1996. Oligogalacturonides prevent rhizogenesis in *rolB*-transformed tobacco explants by inhibiting auxin-induced expression of the *rolB* gene. Plant Cell 8: 477–487.

Berhe D. and Negash L. 1998. Asexual propagation of *Juniperus procera* from Ethiopia: A contribution to the conservation of African Pencil cedar. Forest Ecol. Manag. 112: 179–190.

Bingham I.J. and Stevenson E.A. 1993. Control of root growth: effects of carbohydrates on the extension, branching and rate of respiration of different fractions of wheat roots. Physiol. Plant 88: 149–158.

Biondi S., Diaz T., Iglesias M., Gamberini G. and Bagni N. 1990. Polyamines and ethylene in relation to adventitious root formation in *Prunus avium* shoot cultures. Physiol. Plant 78: 474–483.

Blakely L.M., Blakely R.M., Colowit P.M. and Elliott D.S. 1988. Experimental studies on lateral root formation in radish seedling roots. Plant Physiol. 87: 414–419.

Blakesley D. 1994. Auxin metabolism and adventitious root initiation. In: Davis T.D. and Haissing B.E. (eds), Biology of Adventitious Root Formation. Plenum Press, New York, pp. 143–154.

Cano-Delgado A.I., Metzlaff K. and Bevan M.W. 2000. The eli1 mutation reveals a link between cell expansion and secondary cell wall formation in *Arabidopsis thaliana*. Development 127: 3395–3405.

Capek P., Kubačková M., Alföldi J., Bilisics L., Lišková D. and Kákoniová D. 2000. Galactoglucomannan from the secondary cell wall of *Picea abies* L. Karst. Carbohydr. Res. 329: 635–645.

Casimiro I., Beeckman T., Graham N., Bhalerao R., Zhang H., Casero P., Sandberg G. and Bennett M.J. 2003. Dissecting *Arabidopsis* lateral root development. Trends Plant Sci. 8: 165–171.

Coleman W.K., Huxter T.J., Reid D.M. and Thorpe T.A. 1980. Ethylene as an endogenous inhibitor of root regeneration in tomato leaf discs cultured *in vitro*. Physiol. Plant 48: 519–525.

Cutillas-Iturralde A. and Lorences E.P. 1997. Effect of xyloglucan oligosaccharides on growth, viscoelastic properties, and long-term extension of pea shoots. Plant Physiol. 113: 103–109.

Dey P.M. 1980. D-Galactoglucomannans. Adv. Carbohydr. Chem. Biochem. 37: 337–339.

Eberhard S., Doubrava N., Marfà V., Mohnen D., Southwick A., Darvill A.G. and Albersheim P. 1989. Pectic cell wall fragments regulate tobacco thin-cell-layer explants morphogenesis. Plant Cell 1: 747–755.

Eliasson L. 1980. Interaction of light and auxin in regulation of rooting in pea stem cuttings. Physiol. Plant 48: 78–82.

Fuchs H.W.M. 1986. Root regeneration of rose plants as influenced by applied auxins. Acta Horticult. 189: 101–107.

Ishihara M., Nagao Y. and Shimizu K. 1991. Physiological activity of xylooligosaccharides. Res. Rep. Biomass Conv. Program 27: 20–32.

Ishii K., Kinoshita I., Shigenaga H., Ishihara M., Shimizu K., Nishihara H. and Tanaka K. 1992. The effects of oligosaccharides on tissue culture of white birch and black pine. Trans. Japan Forestry Soc. 103: 485–486.

Iwasaki I. and Matsubara Y. 2000. Purification of pectate oligosaccharides showing root-growth-promoting activity in lettuce using ultrafiltration and nanofiltration membranes. Biosci. Bioeng. 89: 495–497.

Jarvis B.C. 1986. Endogenous control of adventitious rooting in non-woody cuttings. In: Jackson M.B. (ed.), New Root Formation in Plants and Cuttings. Nijhoff, Hingham, Mass, pp. 191–222.

Jarvis B.C. 1988. Adventitious root formation with respect to auxin distribution. In: Kutacek M., Bandurski R.S. and Krekule J. (eds), Physiology and Biochemistry of Auxins in Plants. Academia, Praha, pp. 295–303.

John M., Röhrig H., Schmidt J., Walden R. and Schell J. 1997. Cell signalling by oligosaccharides. Trends Plant Sci. 2: 111–115.

Kaku T., Tabuchi A., Wakabayashi K. and Hoson T. 2004. Xyloglucan oligosaccharides cause cell wall loosening by enhancing xyloglucan endotransglucosylase/hydrolase activity in azuki bean epicotyls. Plant Cell Physiol. 45: 77–82.

Kollárová K., Lišková D. and Capek P. 2005. Further biological characteristics of galactoglucomannan oligosaccharides. Biol. Plant (in press).

Liu J.H. and Reid D.M. 1992. Auxin and ethylene-stimulated adventitious rooting in relation to tissue sensitivity to auxin and ethylene production in sunflower hypocotyls. J. Exp. Bot. 43: 1191–1198.

Lišková D., Auxtová O., Kákoniová D., Kubačková M., Karácsonyi Š. and Bilisics L. 1995. Biological activity of galactoglucomannan-derived oligosaccharides. Planta 196: 425–429.

Lloret P.G. and Pulgarín A. 1992. Effect of naphthaleneacetic acid on the formation of lateral roots in the adventitious root of *Allium cepa*: number and arrangement of laterals along the parent root. Can. J. Bot. 70: 1891–1896.

Lozovaya V.V., Zabotina O.A., Rumyantseva N.I., Malihov R.G. and Zihareva M.V. 1993. Stimulation of root development on buckwheat thin cell-layer explants by pectic fragments from pea stem cell walls. Plant Cell Rep. 12: 530–533.

Lundqvist J., Teleman A., Junel L., Yacchi G., Dahlman O., Tjerneld F. and Stalbrand H. 2002. Isolation and character-

ization of galactoglucomannan from spruce (*Picea abies*). Carbohydr. Polym. 48: 29–39.

McDougall G.J. and Fry S.C. 1988. Inhibition of auxin-stimulated growth of pea stem segments by a specific nonasaccharide of xyloglucan. Planta 175: 412–416.

McDougall G.J. and Fry S.C. 1990. Xyloglucan oligosaccharides promote growth and activate cellulase: evidence for a role of cellulase in cell expansion. Plant Physiol. 93: 1042–1048.

Mullins M.G. 1972. Auxin and ethylene in adventitious root formation in *Phaseolus aureus* (Roxb.). In: Carr D.J. (ed.), Plant Growth Substances. Springer-Verlag, Berlin, pp. 526–533.

Müller J.L. 2000. Indole-3-butyric acid in plant growth and development. Plant Growth Regul. 32: 219–230.

Pan R.C. and Tian X. 1999. Comparative effect of IBA, BSAA and 5,6-Cl_2-IAA-Me on the rooting of hypocotyl in mung bean. Plant Growth Regul. 27: 91–98.

Percival G. and Gerritsen J. 1998. The influence of plant growth regulators on root and shoot growth of containerized trees following root removal. J. Hort. Sci. Biotech. 73: 353–359.

Riov J. and Yang S.F. 1989. Ethylene and ethylene-auxin interaction in adventitious root formation in mung bean (*Vigna radiate*) cuttings. J. Plant Growth Regul. 8: 131–141.

Schröder R., Wegrzyn T.F., Bolitho, K.M. and Redgwell R.J. 2004. Mannan transglycosylase: a novel enzyme activity in cell walls of higher plants. Planta 219: 590–600.

Slováková L., Lišková D., Capek P., Kubačková M., Kákoniová D. and Karácsonyi Š. 2000. Defence responses against TNV infection induced by galactoglucomannan-derived oligosaccharides in cucumber cells. Eur. J. Plant Pathol. 106: 543–553.

Smith D.R. and Thorpe T.A. 1975. Root initiation in cuttings of *Pinus radiata* seedlings. II. Growth regular interactions. J. Exp. Bot. 26: 193–202.

Suzuki T., Tomita-Yokotani K., Tsubura H., Yoshida S., Kusakabe I., Yamada K., Yoichi M. and Hasegawa K. 2002. Plant growth-promoting oligosaccharides produced from tomato waste. Bioresource Technol. 81: 91–96.

Šimonová E., Henselová M. and Zahradník P. 2005. Benzothiazole derivatives substituted in position 2 as biologically active substances with plant growth regulation activity. Plant Soil Environ. 51: 496–505.

Takahashi F., Sato-Nara K., Kobayashi K., Suzuki M. and Suzuki H. 2003. Sugar-induced adventitious roots in *Arabidopsis* seedlings. J. Plant Res. 116: 83–91.

Takeda T., Furuta Y., Awano T., Mizuno K., Mitsuishi Y. and Hayashi T. 2002. Suppression and acceleration of cell elongation by integration of xyloglucans in pea stem segments. Proc. Nat. Acad. Sci. USA 99: 9055–9060.

Tamimi S.M. 2003. Stimulation of adventitious root formation in non-woody stem cuttings by uridine. Plant Growth Regul. 40: 257–260.

Wang S., Taketa S., Ichii M., Xu L., Xia K. and Zhou X. 2003. Lateral root formation in rice (*Oryza sativa* L.): differential effects of indole-3-acetic acid and indole-3-butyric acid. Plant Growth Regul. 41: 41–47.

Warneck H. and Seitz H.U. 1993. Inhibition of gibberellic acid-induced elongation-growth of pea epicotyls by xyloglucan oligosaccharides. J. Exp. Bot. 44: 1105–1109.

Wightman F. and Thimann K.V. 1980. Hormonal factors controlling the initiation and development of lateral roots. I. Sources of primordia-inducing substances in the primary root of pea seedlings. Physiol. Plant 49: 13–20.

York W.S., Darvill A.G. and Albersheim P. 1984. Inhibition of 2,4-dichlorophenoxyacetic acid-stimulated elongation of pea stem segments by a xyloglucan oligosaccharide. Plant Physiol. 75: 295–297.

Zabotina O.A., Ibragimova N.N., Zabotin A.I., Trofimova O.I. and Sitnikov A.P. 2002. Biologically active oligosaccharides from pectins of *Pisum sativum* L. seedlings affecting root generation. Biochem. (Moscow) 67: 227–232.