植物組織培養用寒天に含まれる野菜の根の伸長促進物質

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Stimulation of Root Growth of Several Vegetables by Extracts from a Commercial Preparation of Agar

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Summary

Commercial preparations of agar, agarose, cellulose, gellan gum, pectin, sodium alginate, and starch were immersed in water and assayed for root growth-promoting activity. Agar greatly stimulated root growth of cucumber (*Cucumis sativus* L.), Japanese radish (*Raphanus sativus* L.), lettuce (*Lactuca sativa* L.), rice (*Oryza sativa* L.), spinach (*Spinacia oleracea* L.), tomato (*Lycopersicon esculentum* Mill.), and Welsh onion (*Allium fistulosum* L.). Cellulose, gellan gum, and starch also stimulated root growth to a lesser degree. The most consistent results were obtained with lettuce; thus it was chosen for further experimentations. Water extract of agar stimulated root growth of lettuce whereas an inorganic ion solution whose composition was equivalent to the agar extract was less stimulating. Thus, the stimulating activity of the agar extract is not attributable to inorganic ions in the extract. To examine properties of root growth-stimulating substances in the agar extract, the extract was fractionated on columns of Sephadex G-25, Bio-Gel P-2 and Shodex C18. Activities were found in several low molecular weight fractions isolated with Bio-Gel P-2. When the active fractions separated by Bio-Gel P-2 were subjected to Shodex C18, an active fraction was concentrated in a single major peak, which eluted faster than glucose. These results indicate that commercial preparations of agar contain several root growth-stimulating, highly hydrophilic substances of low molecular weight.

Key Words: agar, agarose, lettuce, polysaccharide, root growth.

Introduction

Agar is generally used as a gelling agent in plant tissue culture, but it has several disadvantages, such as the need for subculturing and regenerated roots do not always grow normally in agar. Furthermore, agar seems to have some inhibitors of differentiation and growth of explants (Kohlenbach and Wernicke, 1977; Tyagi et al., 1980; Wernicke and Kohlenbach, 1976).

Supports made of polyester, ceramic or wood pulp fiber have been substituted for agar and found to be superior (Cheng and Voqui, 1977; Doi et al., 1992; Nagaoka et al., 1987; Oishi and Sasaki, 1989). Ichimura et al. (1995) reported that more adventitious shoots from tomato tissues were regenerated on supports derived from plant tissues such as wood pulp or on agar medium than were regenerated on supports made of polyester and ceramic. Ichimura et al. (1995) and Ichimura and Oda (1995b) attributed these positive effects to compounds extracted from these substances. Furthermore, Ichimura and Oda (1995a) found that the pulp extracts had root growth-stimulating activities for several plants. From these findings, we speculate that plant polysaccharides contain common unidentified biologically active compounds that stimulate shoot regeneration and/or root growth. In this study, we examined the effects of various kinds of commercial polysaccharides derived from plants on the root growth of lettuce and found that only agar greatly stimulated the root growth. Hence, we tried to characterize the chemical properties of these root growth-stimulating compounds in agar.

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Materials and Methods

1. Plant materials

Seeds of cucumber (*Cucumis sativus* L. cv. Sagamihanjiro), Japanese radish (*Raphanus sativus* L. cv. Moriguchi), lettuce (*Lactuca sativa* L. cv. Great lakes 366), rice (*Oryza sativa* L. cv. Tanginbouzu), spinach (*Spinacia oleracea* cv. Okame), tomato (*Lycopersicon esculentum* Mill. cv. Zuiken), and Welsh onion (*Allium fistulosum* L. cv. Iwatsuki) were sown on moistened filter paper in Petri dish at 30°C. When the main roots of the seedlings grew 3 to 5 mm, they were used as test materials.

2. Commercial plant polysaccharides and their sources

Plant polysaccharides used in the present study were

as follows; agar-BA-10 (BA-10, Funakoshi Co., Ltd.), agar-BA-30 (BA-30, Funakoshi Co., Ltd.), agar-BC (for bacteria culture, Wako Pure Chemical Industries, Ltd.), agar-EP (Extra pure, Nacalai tesque Inc.), agar-FG (1st grade, Katayama Kagaku Kogyo Co., Ltd.), agar-P (purified, Sigma Chem. Co.), agar-PC (for plant culture, Wako Pure Chemical Industries, Ltd.), agar-TE (Type E, Sigma Chem. Co.), agarose-Type I (Low EFO, Sigma Chem. Co.), agarose-Type III (High EFO, Sigma Chem. Co.), agarose-Type VIII (Sigma Chem. Co.), cellulose (cellulose powder B, Toyo Roshi Kaisha, Ltd.), gellan gum (Gelrite, Sanei Chemical Industries Co., Ltd.), pectin (from apple, Wako Pure Chemical Industries, Ltd.), sodium alginate (Nacalai tesque Inc.) and starch (Special grade, Katayama Kagaku Kogyo Co., Ltd.).

3. Extraction of agar

In a preliminary experiment, we confirmed that root growth-stimulating substances were easily extracted from agar with water at room temperature. Agar BA-10 was immersed in twenty times its volume of distilled water and gently stirred for 1 hr at room temperature. The suspension was filtered through a glass filter (No. 2, Toyo Roshi Kaisha, Ltd.). The filtrate was then concentrated *in vacuo* with a rotary evaporator kept below 50°C and the residue stored at -30°C until used.

4. Root growth assay

For experiments with lettuce seedlings, 45 ml of polysaccharide suspension equivalent to 10 g · liter^{-1} or a test solution diluted with distilled water was poured into an acryl vessel (6×120×70 mm). For the experiment with the other plants, 200 ml of agar suspension equivalent to 10 g · liter^{-1} was poured into a polycarbonate vessel (62×62×98 mm). A styrofoam plate with 12 holes (2 or 3 mm diam.) was floated on the suspension or solution, and the germinated seeds were placed in the holes to keep them floating. Top of the vessel was, then, covered with a transparent plate to prevent loss of solution by evaporation. Each vessel containing the seedlings, was held at 25°C under a 12-hr photoperiod. The light intensity at plant height was about 100 μmole · m^{-2} · s^{-1}. After 4 days, the lengths of 8 main roots were measured.

5. Determination of inorganic ion contents in agar extract

The inorganic ion contents in agar extracts were determined by HPLC, equipped with an electroconductivity detector and a Shodex IC Y-421D column (Shoko Co., Ltd.) to separate the cations. The column was eluted with a solution of 5 mM tartaric acid and 1 mM dipicolinic acid at a flow rate of 1 ml · min^{-1} at 40°C. Anions were separated with a Shodex IC I-524A column (Shoko Co., Ltd.) by eluting with a 2.5 mM phthalic acid solution (pH 4.0) at a flow rate of 1 ml · min^{-1} at 40°C.

6. Chromatography conditions

Sephadex G-25 (fine; 4×90 cm) column was equilibrated and eluted with distilled water at room temperature at a flow rate of 100 ml · hr^{-1}; 12-ml fractions were collected. Bio-Gel P-2 (fine; 2×100 cm) column was equilibrated and eluted with distilled water at room temperature at a flow rate of 20 ml · hr^{-1}; 3-ml fractions were collected. The column was calibrated with blue dextran and glucose oligomer (Seikagaku Corp.) whose degree of polymerization was from 20 to 1. The sugar concentration of each fraction was determined by the method of Dubois et al. (1956).

After gel filtration, active fractions were subjected to HPLC, equipped with a refractive index detector on a Shodex C18 column (5E; Shoko Co., Ltd.). The column was eluted with water at a flow rate of 2 ml · min^{-1} at room temperature.

Results

1. Effect of commercial polysaccharides on the root growth of lettuce seedlings

Agar (BA-10), immersed in water, greatly stimulated the root growth of lettuce seedlings. The pH of the solution with agar before and after the assay were 5.8 and 5.4, respectively; whereas, the value of the control solution after the assay was 5.1; cellulose, gellan gum and starch stimulated root growth to a lesser degree. On the contrary, pectin and sodium alginate inhibited root growth (Table 1). When 8 other commercial agars on root growth were assayed, all were found to stimulate the root growth of lettuce (Table 2).

When agarose, a main component of agar, was examined, it was found that all agaroses stimulated root growth as did others, although the stimulating effect was less than that of agar (Table 3).

2. Root growth of several plants in water with agar

When the effects of agar BA-10 extracts were expanded to 7 species across 7 families, they stimulated

Table 1. Effect of commercial plant polysacchrides on root growth of lettuce seedings. Polysacchrides equivalent to 10 g·liter^{-1} were immersed in water,and root length in the mixture was measured.Values are means of 8 replications ± standard errors.

Polysaccharide	Root length (mm)		
Water	10.3	±	0.5
Agar(BA-10)	56.1	±	2.1
Cellulose	15.1	±	0.6
Gellan gum	18.0	±	0.5
Pectin	4.9	±	0.1
Sodium alginate	6.3	±	0.2
Starch	15.6	±	0.3

root growth of all species. However, the greatest stimulating effect was obtained on lettuce. Root growth of Japanese radish, tomato, spinach, and Welsh onion were also markedly stimulated by agar (Table 4). Because lettuce seedlings are easy to obtain and handle, they were chosen for further experiments.

3. *Effect of agar extract on the root growth of lettuce seedlings*

Root growth was promoted by increasing the concentration of the agar extract; maximum root length was obtained at 100 g agar equivalent · liter^{-1} (Fig. 1). Because 1 g of agar yields 15 mg of dry extract, an agar equivalent to 0.1 g · liter^{-1} is estimated to be 1.5 mg · liter^{-1}, a concentration at which maximum root growth was obtained. Thus the active substance is shown to be effective at a relatively low concentration.

Table 2. Effect of commercial plant polysacchrides (agar) on root growth of lettuce seedings. Agars equivalent to 10 g·liter^{-1} were immersed in water,and root length in the mixture was measured.Values are means of 8 replications ± standard errors.

Agar	Root length (mm)		
Water	11.4	±	0.6
BA-10	61.1	±	1.0
BA-30	58.4	±	1.7
BC	37.9	±	1.7
EP	58.3	±	1.8
FG	62.1	±	1.1
P	21.3	±	0.3
PC	59.8	±	1.7
TE	41.6	±	0.6

Table 3. Effect of commercial plant polysacchrides (agarose) on root growth of lettuce seedings. Agars equivalent to 10 g·liter^{-1} were immersed in water,and root length in the mixture was measured.Values are means of 8 replications ± standard errors.

Agarose	Root length (mm)		
Water(control)	11.3	±	0.6
Type-Ⅰ	17.1	±	0.2
Type-Ⅲ	19.3	±	0.5
Type-Ⅷ	36.4	±	0.8

Table 4. Effect of agar (BA-10) on root growth of several plants. Agar equivalent to 10 g·liter^{-1} was immersed in water,and root length in the mixture was measured.Values are means of 8 replications ± standard errors.

Plant	Root length (mm)		Ratio[z] (%)
	Control	Agar	
Lettuce	7.9 ± 0.3	59.3 ± 1.3	751
Japanese radish	15.4 ± 0.7	89.5 ± 5.0	581
Tomato	17.1 ± 1.9	97.8 ± 1.9	572
Spinach	10.3 ± 0.5	48.8 ± 7.4	474
Welsh onion	6.5 ± 0.3	30.8 ± 3.5	474
Rice	39.9 ± 1.1	64.6 ± 4.2	162
Cucumber	11.0 ± 0.2	14.6 ± 0.5	133

[z] Percentage of root length exposed to agar to that of control.

4. *Inorganic ion contents of agar extract*

As some inorganic ions are known to promote root growth, the mineral of the agar extract was determined with HPLC. The extract from 1,000 g agar contained inorganic ions as follows in mg : Na^+, 334; K^+, 20; Ca^{2+}, 117; Mg^{2+}, 138; Cl^-, 174; SO_4^{2-}, 1326.

To test whether the above ions were involved in root growth-stimulating activity, comparable nutrient solutions were made. The composition of the solution recovered from 1.0 kg agar was as follows in mg · liter^{-1} : Na_2SO_4 · $10H_2O$, 2335.9; $MgSO_4$ · $7H_2O$, 1399.7; $CaCl_2$, 272.0; $CaSO_4$ · $2H_2O$, 81.66; K_2SO_4, 52.9. The unadjusted pH of the solution was about 6, a value similar to that of the agar extract. The synthetic ion solution did not stimulate root growth any more than did agar extract at any concentrations (Fig. 2), so that the root growth-stimulating substances are not likely to be these ions or their combinations.

5. *Fractionation of root growth stimulating substances of agar extract*

Extract obtained from 620 g of agar BA-10 was concentrated *in vacuo* with a rotary evaporator below 50°C to 114 ml. The concentrate was suspended with 342 ml of ethanol and kept at room temperature for 1 hr. The suspension was then centrifuged at 3,000×g for 5 min to remove large amount of polysaccharide-like substance in agar extract. The supernatant was concentrated to 43 ml as above and then transferred to a Sephadex G-25 column. The elution profile showed that the extract still contained a large amount of polysaccharide-like substances. The column fractions were pooled,

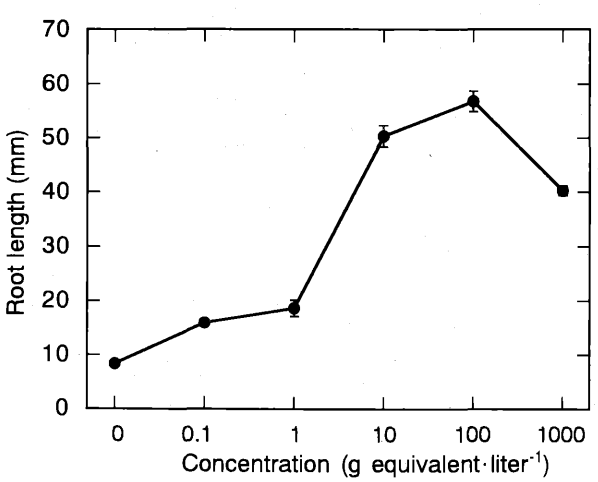

Fig. 1. Effect of agar extract on root growth of lettuce. Values are means of 8 replications±standard errors.

labeled (Fig. 3), and assayed for root growth-stimulating activity. High activity was found in the low molecular weight fraction. The active pooled fractions, G-4 and G-5 were combined and concentrated to 9 ml, and the concentrate was then subjected to Bio-Gel P-2 column. Activities two times higher than control were found in 7 pooled fractions, II, IV, V, VI, VII, IX, and X (Fig. 4). The molecular weights of pooled fraction V and VI were equivalent to di- and monosaccharide, respectively. According to estimation of dry weight, fraction V at 20 mg · liter^{-1} promoted root growth by about 300% of the control, whereas fraction IX at 10 mg · liter^{-1} enhanced growth by 400% of the control .

Among these active fractions, pooled fractions V, VI, IX, and X were respectively fractionated using HPLC on a Shodex C18 column. When fraction V was fractionated on Shodex C18, a single major peak was detected. This major peak (Fig. 5) corresponded to the growth responses, whereas other minor peaks had none. Similarly, when fraction VI, IX, and X were separately fractionated by Shodex C18, activity was found in single major peak in each fraction (data not shown). All of these peaks eluted faster than that of glucose, which eluted at 6.2 min under this experimental condition, indicating that root growth-stimulating substances are highly hydrophilic compounds.

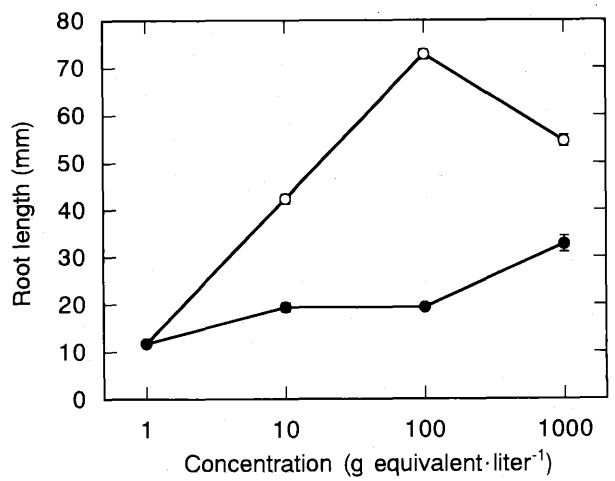

Fig. 2. Comparison of the root growth of lettuce exposed to agar extract (○) and inorganic ion solution whose composition was equivalent to the agar extract (●) at each concentration. Values are means of 8 replications±standard errors.

Discussion

Previously, we reported that extracts of wood pulp and commercial filter paper greatly stimulated root growth of several plants (Ichimura and Oda, 1994; 1995a). These findings indicate that substances related to plant polysaccharides have some biologically active substances. Thus, in this study, we examined the effects of several commercial polysaccharides on root growth of lettuce. Only agars greatly stimulated root growth of lettuce.

A water extract of agar also stimulated root growth (Fig. 1) whereas agaroses were less effective (Table 1 and 2). In addition, when the agar extract was subjected to gel filtration, activity was found in the low

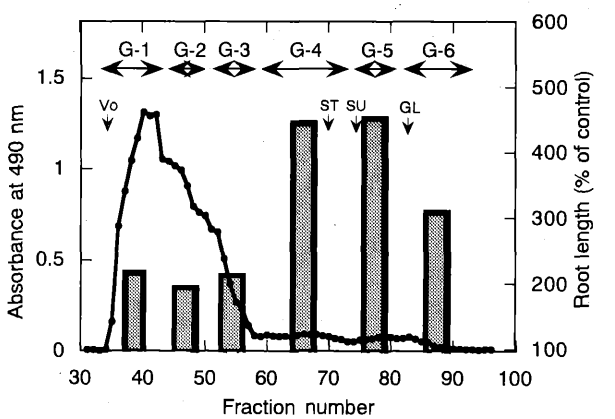

Fig. 3. Sephadex G-25 elution profile of agar extract on root growth-stimulating activity. Curve represents sugar content expressed as absorbance at 490 nm and vertical columns root length. Twelve-ml fractions were collected and a 10-μl aliquot of each column fraction was assayed for sugar content. The column fractions were pooled and labeled as G-1, G-2, G-3, G-4, G-5 and G-6, and one-200th of each pooled fraction was used for root growth assay. Void volume (Vo) was determined by blue dextran. Elution positions of stachyose tetrahydrate (ST), sucrose (SU) and glucose (GL) are also indicated. Length of control root exposed to water was 7.3 mm.

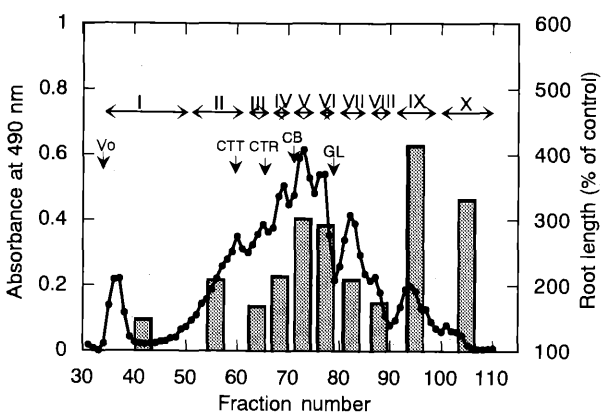

Fig. 4. Bio-Gel P-2 elution profile of agar extract and root growth-stimulating activity. Curve represents sugar content expressed as absorbance at 490 nm and the columns root length. Three-ml fractions were collected and a 20-μl aliquot of each fraction was assayed for sugar content. Fractions were pooled and labeled as I, II, III, IV, V, VI, VII, VIII, IX and X and one-100th of each pooled fraction was used for root growth assay. Void volume (Vo) was determined by blue dextran. Elution positions of cellotetraose (CTT), cellotriose (CTR), cellobiose (CB) and glucose (GL) are also indicated. Length of control root exposed to water was 8.7 mm.

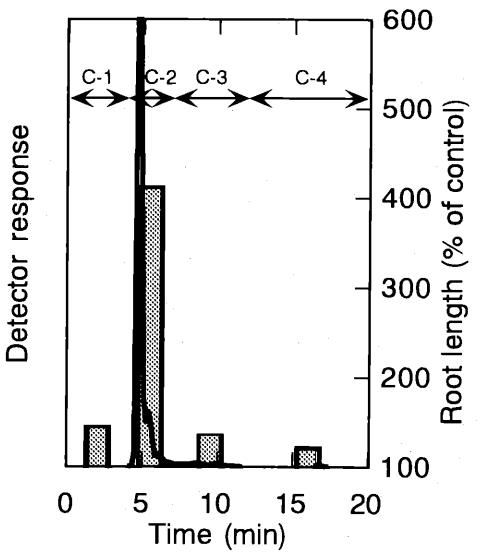

Fig. 5. Shodex C18 elution profile of agar extract and root growth-stimulating activity. Curve represents detector response and the columns root length. One ml fractions were collected, pooled and labeled as C-1, C-2, C-3 and C-4; one-100th of each pooled fraction was used for root growth assay. Length of control root exposed to water was 8.7 mm.

molecular weight fraction (Fig. 3). These results show that root growth-stimulating substance contained in commercial agar is not agar nor agarose but some low molecular weight contaminants which are water soluble. Agar BA-10 is made from *Gelidium elegans,* which is also the raw material of commercial agar (personal communication). Therefore, the active compounds could be either components originally contained in *Gelidium elegans* or artifacts produced from original components of the plant during the manufacture of agar.

Root growth was affected by pH in the medium (Tanimoto and Watanabe, 1986), but the pH was changed little by agar. Therefore, root growth-stimulating activity seems not to be involved in changes in pH.

Many compounds such as helminthosporol (Tamura and Sakurai, 1964), L-β-phenyllactic acid (Tamura and Chang, 1965), caulerpin (Raub et al., 1987), 3-(hydroxy)indole (Bernart and Gerwick, 1990), and BSF-A (Kimura et al., 1993) have been reported to promote root growth of lettuce. However, the root growth-stimulating substances in agar extract were shown to be highly hydrophilic (Fig. 5), suggesting that the substances are not these compounds. The root growth-stimulating substances also seem to be different from known phytohormones such as indole acetic acid (IAA), gibberellic acids (GA), zeatin, and abscisic acid (ABA) because they have little or no effect on root growth of lettuce (data not shown).

Eluates of Bio-Gel P-2 column contain at least several root growth-stimulating substances. Fractions V and VI were eluted at the same position as di- and monosaccharide, respectively and gave a positive reaction to phenol-sulfuric acid (Fig. 4) which suggests that they are possibly sugars or sugar derivatives. Oligosaccharides, digested from pectin and xyloglucan, have biological activities on various physiological responses (Darvill et al., 1985; Ryan and Farmer, 1991). Tomoda et al. (1994) also reported that alginate lysate stimulated root growth of barley under hypoxic conditions. The active substances of agar extract seem to be different from these oligosaccharides because their molecular weight is lighter and their sources differ.

Agar has been found to contain compounds that affect differentiation and development of cultured tissue. In anther culture, addition of activated charcoal to agar medium increased the frequency of plant regeneration (Anagnostakis, 1974; Kohlenbach and Wernicke, 1977; Nakamura and Itagaki, 1973; Tyagi et al., 1980; Wernicke and Kohlenbach, 1976), indicating that agar contains inhibitor(s) of plant regeneration which is absorbed by activated charcoal, whereas Ichimura and Oda (1995b) found that the active substance in agar extract which stimulated shoot regeneration of tomato is a thermostable, highly hydrophilic compound. However, whether root growth simulating substances shown in this study are identical to shoot regenerating substances remains unsolved.

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植物組織培養用寒天に含まれる野菜の根の伸長促進物質

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摘　要

市販の植物多糖である寒天，アガロース，セルロース，ジェランガム，ペクチン，アルギン酸ナトリウムおよびデンプンの浸漬液がレタスの根の伸長に及ぼす影響を調べたところ，寒天の促進効果が最も大きかった．寒天による根の伸長促進効果はキュウリ，ダイコン，イネ，ホウレンソウ，トマトおよびネギと比べて，レタスで最も大きかった．それに加えて，レタスでの促進効果は変動が小さく，取り扱いが容易であったため，以下の実験にはすべてレタスを用いた．根の伸長は寒天抽出液によっても促進された．寒天抽出液に含まれる無機イオンと同じ組成に調製した溶液は寒天抽出液より根の伸長促進効果は小さかった．これより，寒天抽出液に含まれる根の伸長促進物質は無機イオンとは異なる物質であると考えられた．寒天抽出液を Sephadex G-25 カラムおよび Bio-Gel P-2 カラムを用いて分画したところ，根の伸長促進活性は低分子領域の数画分に認められた．これらの活性画分を Shodex C18 カラムで分画したところ，グルコースより早く溶出した．これらの結果より，寒天に含まれる根伸長促進物質は数種類存在しており，これらはいずれも低分子で，親水性の高い物質であると示唆された．

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