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Article

Comparison of Plant Growth Promoting *Methylobacterium* spp. and Exogenous Indole-3-Acetic Acid Application on Red Pepper and Tomato Seedling Development

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A comparative study was performed in gnotobiotic and greenhouse conditions to evaluate the effect of exogenous application of indole-3-acetic acid (IAA) and inoculation of *Methylobacterium* spp. possessing 1-aminocyclopropane-1-carboxylate deaminase (ACCD) and IAA activity on red pepper and tomato seedling growth and development. Application of 1.0 μg mL^{-1} IAA positively influenced root growth while high concentrations (>10.0 μg mL^{-1}) suppressed root growth of red pepper and tomato under gnotobiotic condition. On the other hand, inoculation of *Methylobacterium* strains with ACCD activity and IAA or without IAA enhanced root growth in both plants. Similarly, under greenhouse condition the inoculation of *Methylobacterium* sp. with ACCD activity and IAA enhanced plant fitness recorded as average nodal length and specific leaf weight (SLW) but the effect is comparable with the application of low concentrations of IAA. Seedling length was significantly increased by *Methylobacterium* strains while total biomass was enhanced by *Methylobacterium* spp. and exogenous applications of < 10.0 μg mL^{-1} IAA. High concentrations of IAA retard biomass accumulation in red pepper and tomato. These results confirm that bacterial strains with plant growth promoting characters such as IAA and ACCD have characteristic effects on different aspects of growth of red pepper and tomato seedlings which is comparable or better than exogenous applications of synthetic IAA.

Key words: *Methylobacterium* spp., indole-3-acetic acid, 1-aminocyclopropane-1-carboxylate deaminase, plant growth, plant performance

Introduction

Beneficial plant growth promoting (PGP) bacteria that are able to colonize plants effectively can accelerate seedling emergence, promote plant establishment and enhance plant growth (Chanway, 1997; Bent and Chanway, 1998). Beneficial PGP bacteria are believed to elicit plant growth promotion directly or indirectly. Indirect effects may be by helping plants acquire nutrients, e.g. via nitrogen fixation, phosphate solubilization (Wakelin et al., 2004) or iron chelation (Costa and Loper, 1994); by preventing pathogen infections via antifungal or antibacterial agents, by out competing pathogens for nutrients by siderophore production, or by establishing the plant's systemic resistance (Van Loon et al., 1998; Strobel et al., 2004). On the other hand, these can directly affect plant growth by producing phytohormones such as auxin or cytokinin (Madhaiyan et al., 2006), or by producing the enzyme 1-aminocycloropane-1-carboxylate (ACC) deaminase, which lowers plant ethylene levels (Glick, 1995; Madhaiyan et al., 2007). A particular bacterium may affect plant growth and development using one or more of the above mechanisms and may use different ones at various times during the life cycle of the plant. Many studies have documented the interactions between PGP rhizobacteria and host plants (Glick et al., 2007; Long et al., 2008; Madhaiyan et al., 2007; Poonguzhali et al., 2008). Glick et al. (1998) explained the role of bacterial ACC deaminase and IAA in promoting plant growth. Ethylene and IAA are implicated in virtually all aspects of plant growth and development, ranging from seed germination to shoot growth and leaf abscission (Woodward and Bartel, 2005). Therefore, production of ACC deaminase and IAA is likely an important and efficient way for beneficial PGP to

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manipulate their plant hosts. Among the different IAA producing PGP bacteria, the production of IAA by ubiquitous *Methylobacterium* spp. is remarkable (Abanda-Nkpwatt et al., 2006; Madhaiyan et al., 2006).

Bacteria belonging to the genus *Methylobacterium* spp. are ubiquitous in nature and colonize probably all land plants (Koenig et al., 2002; Holland and Palacco 1992; Chanprame et al., 1996; Shepelyakovskaya et al., 1999). In the case of symbiosis with nitrogen-fixing *Methylobacterium* strains, the benefit for the plant is evident, but this is not the case for looser forms of association, although it has been suggested that plants benefit from the production of plant hormones, such as cytokinins and auxins, by the epiphytic methylotrophs (Ivanova et al., 2000; Omer et al., 2004b; Madhaiyan et al., 2007). Much investigation has been done to predict the role of different PGP traits on plant growth with respect to the effect of bacterial hormones (Glick et al., 2007; Raaijmakers et al., 2009; Madhaiyan et al., 2007). Thus the aim of the present study was to compare the effect of exogenous application of IAA and inoculation of *Methylobacterium* spp. with ACCD activity and IAA on seedling growth and development of red pepper (*Capsicum annum* L.) and tomato (*Lycopersicon esculentum* L.) under gnotobiotic and greenhouse conditions.

Materials and Methods

Bacterial strains, media and bacterial inocula The *Methylobacterium* spp. used in this study are listed in Table 1. The strains possessed more than one plant growth promoting characteristic. Stock cultures were stored at -80℃ in 50% glycerol. All the strains were maintained in ammonium mineral salt (AMS) media. Bacterial inocula for seed bacterization was prepared by growing the strains in AMS broth for 72 h. Cell pellets were collected by centrifugation (10,000 rpm, 10 min, 4℃) and washed twice in distilled water. Bacteria in sterile distilled water suspension ($OD_{600} = 0.8$) were used for seed inoculation.

Test plants Tomato (*Lycopersicon esculentum* Mill) and red pepper (*Capsicum annum* L.) were used as test plants in gnotobiotic condition. Red pepper was further used in a greenhouse experiment.

Preparation of gnotobiotic growth pouch and IAA amendment Growth pouches (CY9 seed germination pouch, Mega International) were prepared for gnotobiotic assays to check root elongation. This was done by adding 20 mL of distilled water to each growth pouch, wrapping them in aluminum foil in groups of 10 in an upright position to prevent water loss then autoclaving these at 121℃ for 15 minutes. Three different doses (1.0 µg mL^{-1}, 10.0 µg mL^{-1} and 20.0 µg mL^{-1}) indole-3-acetic acid concentrations were maintained in each growth pouch to test the effect of IAA on root growth and overall seedling development.

Seed sterilization Seeds of red pepper and tomato were surface sterilized before treatment with the bacterial suspension. The seeds were first washed with sterile distilled water twice then treated with 70% ethanol for 1 min. This was followed by treatment with 2% sodium

Table 1. *Methylobacterium* strains used in the study and their characteristics.

Strain ID	Name of the bacteria	Source of isolation	NCBI accession No.	Biological character		References
				IAA[#]	ACCD[§]	
CBMB20	*Methylobacterium oryzae*	Rice stem	AY683045	+	++	Madhaiyan et al. 2004, 2006 Poonguzhali et al. 2007; Lee et al. 2006
CBMB12	*Methylobacterium sp.*	Rice stem	EF126740	-	++	Madhaiyan et al., 2004,
CBMB15	*Methylobacterium sp.*	Rice leaf	EF126745	-	++	Madhaiyan et al., 2004,
KACC 10744	*M. fujisawaense*	Rhizoplane / *M. sativa*	KACC 10744	++	+	Green et al. 1988

++ = present; - = absent;

[#] IAA: + = < 5.0 mg ml^{-1}; ++ = >5 mg ml^{-1} but <10 mg ml^{-1}

[§] ACCD activity: + = >50 nmol α-keto butyrate mg^{-1} protein h^{-1} but <100 nmol α-keto butyrate mg^{-1} protein h^{-1}
++ = >100 nmol α-keto butyrate mg^{-1} protein h^{-1}.

hypochlorite solution for 30 seconds. Finally, the treated seeds were thoroughly rinsed for more than five times with sterile distilled water.

Seed bacterization Surface sterilized seeds were immersed in the bacterial cell suspension prepared as mentioned above for 4 h at 60 rpm. After decanting the suspension, the dried seeds were transferred to growth pouches (six seeds per pouch), with six replication per treatment. Two empty pouches were placed at the ends of each rack so that plants at the end of a rack are not subjected to extremes of light or air circulation. The racks were placed in a plastic tray containing sterile distilled water. The pouches were then incubated in a growth chamber at 20℃ with 12 h day -night photoperiod for 14 days.

Measurement of seedling development The effect of *Methylobacterium* spp. and exogenous IAA treatments on root elongation was determined after 14 days in gnotobiotic condition and after 20 days from seed germination in greenhouse condition by measuring the root length from the base of the plants to the root tip. Seedling length was measured from the root tip to the tip of the plant. Total dry matter accumulation was measured after drying the seedlings in an oven at 70℃ until a constant weight was obtained.

Greenhouse experiment Surface-sterilized red pepper seeds were sown in plastic pots (9 cm x 8 cm x 6 cm) containing approximately 250 g of vermiculite soil from Seoul Bio (peatmoss 13-17%, perlite 5-8%, cocopeat 65-70%, zeolite 3-5%, vermiculite 6-8%), pH 5.5-7.0, NH_4-N 200 mg L^{-1}, EC (1:5 water suspension) 0.7 dS m^{-1} ±0.3, CEC: 40-60 $cmol_c$ Kg^{-1}; NO_3-N: 130-350 mg L^{-1}, P_2O_5: 0.14-0.21 mg L^{-1}. The media was moistened and allowed to stabilize. The pots were held in a rack (20 pots per rack) with five replications in each treatment and grown under greenhouse conditions and watered regularly. One seed was sown in each pot with 5 replications in each treatment. The experiment was laid out in a completely randomized design. To maintain the IAA concentration under *in situ* soil condition at 1.0 μg mL^{-1}, 10 mL of water with different concentrations of IAA was supplemented at 5 day intervals for 20 days.

The length of seedlings was measured after uprooting. Total dry biomass of the plants was determined after drying the plants in an oven at 70 ℃ for 48 h. The specific leaf weight and average nodal length was calculated as performance of the plant species according to Gardiner et al. (1987).

Chlorophyll content The chlorophyll content of the inoculated and control red pepper plants grown under greenhouse condition were measured as SPAD indices. The chlorophyll content of fully expanded leaves of the plant was measured using a chlorophyll analyser (SPAD-501, Japan, Minolta).

Statistics Data generated were normalized and mean standard error (SE) was determined. Analysis of variance and testing of means by Duncan's Multiple Range Test at $P<0.05$ were calculated using SAS package, Version 9.1 (SAS Institute Inc., Cary, NC, USA).

Result

Effect of *Methylobacterium* spp. and exogenous IAA application on root elongation Under gnotobiotic condition, tomatoes inoculated with *Methylobacterium* CBMB15, CBMB20 and CBMB12, together with exogenous application of 1.0 μg mL^{-1} IAA have significantly longer roots compared to control. While KACC10744 and application of 10 μg mL^{-1} did not significantly increase root length, application of 20 μg mL^{-1} retarded it (Fig. 1).

In red pepper, 1.0 μg mL^{-1} IAA significantly promoted root growth. Increased root length was also observed in plants inoculated with CBMB12, CBMB15 and CBMB20. Similar to the observations in tomatoes, KACC10744 and 10 μg mL^{-1} did not promote root length while 20 μg mL^{-1} IAA significantly suppressed root growth. Although there was evidence of emergence of plumule and radicle at 10 μg mL^{-1} and 20 μg mL^{-1} concentrations in red pepper, the radicles are rudimentary and no basal root emergence was observed (Fig. 2).

Effect of *Methylobacterium* spp. and exogenous IAA application on seedling length and dry biomass The effect of the different *Methylobacterium* strains and exogenous application of IAA on seedling length and dry matter accumulation of red pepper and tomato is summarized in Table 2. All the bacterial strains and 1.0 μg mL^{-1} of applied IAA significantly enhanced seedling

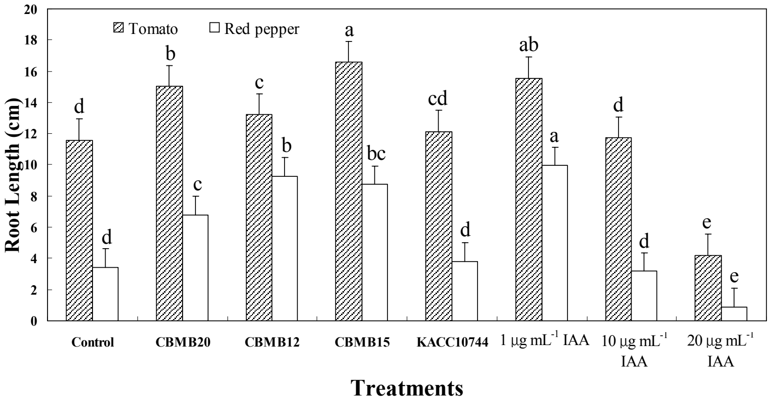

Fig. 1. Effect of *Methylobacterium* spp. and exogenous IAA application on root growth of tomato and red pepper under gnotobiotic condition.

Values are means of five individual observations error bars = standard error means of observed values Identical columns followed by similar letters are not significantly different from each other according to Duncan's Multiple Range Test (DMRT).

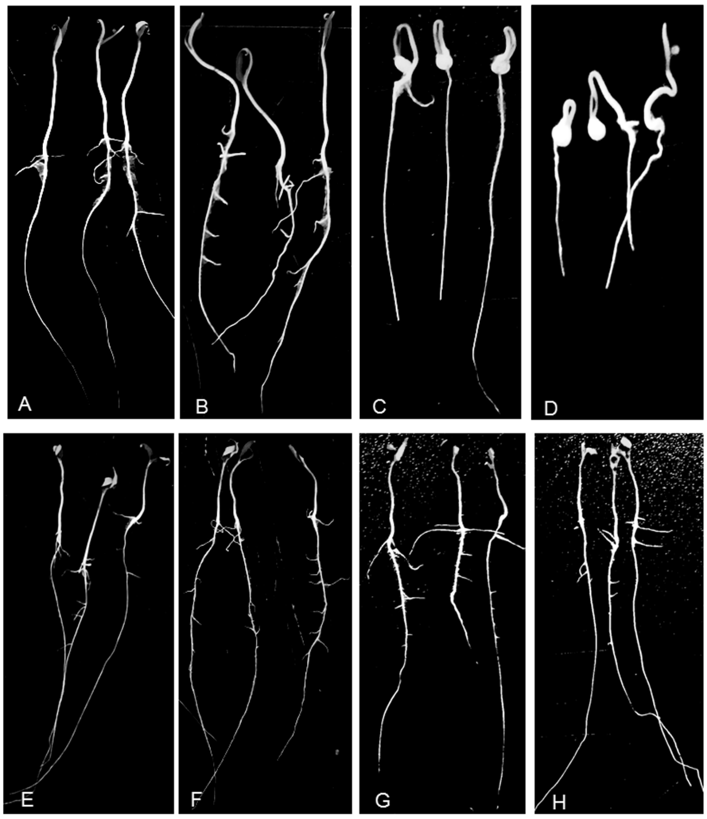

Fig. 2. Effect of *Methylobacterium* spp. and exogenous IAA application on germination and root length of red pepper under gnotobiotic condition.

A. Control; B. 1.00 µg mL^{-1} IAA; C. 10.00 µg mL^{-1} IAA; D. 20.00 µg mL^{-1} IAA; E. CBMB20; F. CBMB 12; G. CBMB15 and H. KACC10744

length of tomato and red pepper compared to uninoculated control. The longest tomato seedlings were those inoculated with CBMB15 (30.8%) while the shortest plants were tomatoes treated with 20 µg mL^{-1} IAA. IAA concentration of 10 µg mL^{-1} similarly did not enhance seedling growth of tomatoes. In red pepper, inoculation with CBMB12 (178.8%) gave the longest seedlings. As with tomatoes, growth was also retarded in red pepper when inoculated with 20 µg mL^{-1} IAA.

All *Methylobacterium* strains significantly increased biomass of tomato and red pepper, though in different degrees. Moreover, 1 µg mL^{-1} IAA enhanced plant

Table 2. Effect of *Methylobacterium* spp. and exogenous IAA application on growth and biomass accumulation of tomato and red pepper grown in pouch.

Treatments	Plant length (cm)		Plant dry biomass (mg)	
	Tomato	Red pepper	Tomato	Red pepper
Control	16.84 ± 0.34c	5.32 ± 0.65d	10.33 ± 1.52d	17.00 ± 1.00c
CBMB20	20.02 ± 0.68b	12.59 ± 0.47b	18.33 ± 2.01a	24.00 ± 1.73a
CBMB12	18.32 ± 0.22c	14.83 ± 0.32a	17.33 ± 1.52ab	23.67 ± 2.93a
CBMB15	22.02 ± 0.67a	13.55 ± 0.21ab	13.67 ± 2.30c	23.00 ± 2.21a
KACC10744	18.22 ± 1.20c	10.07 ± 0.25c	15.67 ± 2.62b	22.33 ± 2.02a
1.0 μg mL^{-1} IAA	19.98 ± 0.89b	12.18 ± 0.82b	16.67 ± 2.02ab	20.33 ± 1.51b
10.0 μg mL^{-1} IAA	15.56 ± 0.68d	6.36 ± 0.65d	11.67 ± 2.31cd	16.33 ± 2.89c
20.0 μg mL^{-1} IAA	7.56 ± 0.49e	0.9 ± 0.20e	5.67 ± 1.55e	8.67 ± 2.08d

Values are means of five individual experiments with 5 replications each; ± = standard deviation of observed values. Values in a column followed by similar letters are not significantly different from each other according to Duncan's Multiple Range Test (DMRT).

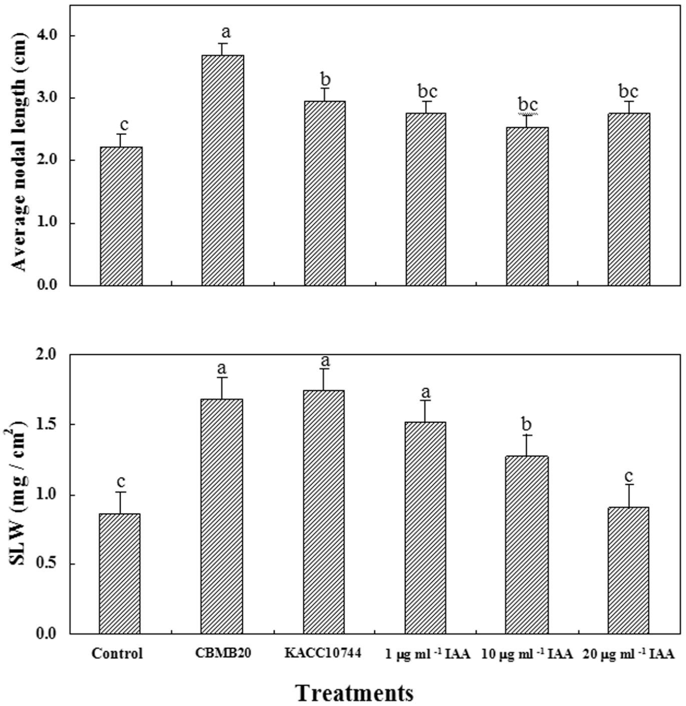

Fig. 3. Effect of *Methylobacterium* strains CBMB20 and KACC10744 and exogenous IAA application on average nodal length and specific leaf weight (SLW) of red pepper grown under greenhouse condition.

Values are means of five individual observationserror bars = standard error means of observed values Columns followed by similar letters are not significantly different from each other according to Duncan's Multiple Range Test (DMRT).

biomass of both test plants while 10 μg mL^{-1} IAA enhanced tomato biomass in a significantly lesser degree.

Effect of *Methylobacterium* spp. and exogenous IAA application on growth of red pepper under greenhouse condition To compare the effect of inoculation of *Methylobacterium* spp. and exogenous application of IAA on red pepper growth under green house condition, *Methylobacterium* strains CBMB20 and KACC10744 were selected. The average nodal lengths, specific leaf weight (SLW) (Fig. 3) and percentage of SPAD index (Fig. 4) were considered as effects of *Methylobacterium* spp. and IAA on the performance of the red pepper seedlings. Plant height and biomass accumulation were considered as the ultimate effect of *Methylobacterium* spp. and IAA on red pepper growth.

Methylobacterium CBMB20 and *Methylobacterium*

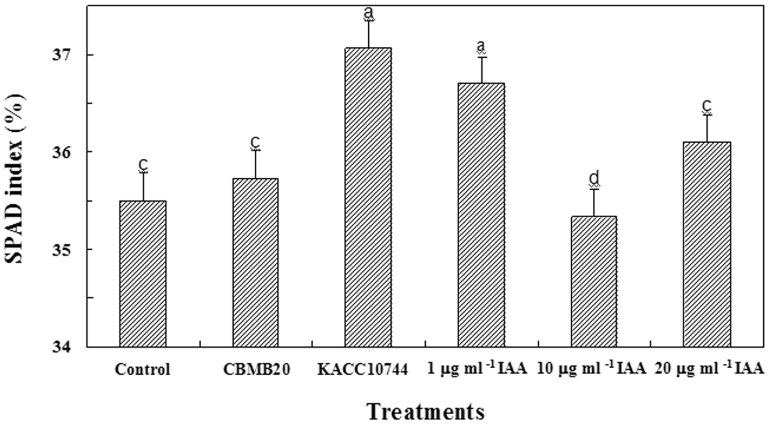

Fig. 4. Effect of *Methylobacterium* strains CBMB20 and KACC10744 and exogenous IAA application on SPAD index of red pepper grown under greenhouse condition.

Values are means of five individual observationserror bars = standard error means of observed values Columns followed by similar letters are not significantly different from each other according to Duncan's Multiple Range Test (DMRT).

KACC10744 significantly enhanced nodal length of red pepper seedlings under greenhouse condition. However, IAA treated plants have appreciably higher increment in nodal length compared to untreated control. The highest increment in nodal length was found in red pepper inoculated with CBMB20 (65.7%) and followed by KACC10744 (13.4%). No dose-dependent effect of exogenous application of IAA was observed on the nodal length of red pepper seedlings.

Methylobacterium inoculated seedlings have enhanced SLW; CBMB20 with 95.4% and KACC10744 with 102.7% compared to control. On the other hand, a dose-dependent effect on SLW was observed in seedlings exogenously applied with IAA. Exogenous application of beyond 1.0 µg mL^{-1} IAA concentration on red pepper showed no significant enhancement on SLW.

Effect of *Methylobacterium* spp. and exogenous IAA application on SPAD index of red pepper grown under greenhouse condition The effect of inoculation of *Methylobacterium* spp. and exogenous application of IAA on pigment synthesis of red pepper seedlings was determined as percentage of SPAD index (Fig. 4). Red pepper with KACC10744 (37.1%) and 1.0 µg mL^{-1} of IAA (36.7%) showed significantly high SPAD indices compared to untreated control. Chlorophyll content of inoculated red pepper seedlings was 0.7 to 4.6% higher compared to the control.

Effect of *Methylobacterium* spp. and exogenous IAA application on plant height and total dry biomass grown under greenhouse condition Similar to the gnotobiotic study, there was a dose-dependent effect of exogenously applied IAA on plant height and biomass accumulation of red pepper seedlings grown under greenhouse condition (Table 3). Among the treatments, red pepper seedlings inoculated with *Methylobacterium* CBMB20 and KACC10744 significantly enhanced plant height and biomass accumulation compared to the control. The highest increment in height was observed in seedlings inoculated with CBMB20 (43.8%) and lowest in seedlings applied with 20.0 µg mL^{-1} IAA (10.9%). The highest

Table 3. Effect of *Methylobacterium* strains CBMB20 and KACC10744 and exogenous IAA application on growth and biomass accumulation of red pepper grown under greenhouse condition at 20 days after sowing.

Treatments	Plant height (cm)	Total dry biomass (mg $plant^{-1}$)
Control	11.54±1.67b	56.43±7.03c
CBMB20	16.59±1.08a	84.53±7.86b
KACC10744	15.80±2.18a	94.87±7.25a
1.0 µg mL^{-1} IAA	13.33±0.48b	84.50±2.21b
10.0 µg mL^{-1} IAA	13.33±0.57b	82.73±7.51b
20.0 µg mL^{-1} IAA	12.79±1.33b	44.23±3.82c

Values are means of five individual experiments with 5 replications each; ±= standard deviation of observed values values in a column followed by similar letters are not significantly different from each other according to Duncan's Multiple Range Test (DMRT).

biomass was with seedlings inoculated with KACC10744 (68.0%) followed by CBMB20, 1.0 μg mL^{-1} IAA and 10.0 μg mL^{-1} treated seedlings. Retardation of biomass accumulation was observed in seedlings applied with 20.0 μg mL^{-1} IAA (-21.0%).

Discussion

The effect of four *Methylobacterium* spp. having ACC deaminase activity and with or without IAA production along with exogenous application of synthetic IAA was compared in root growth and plant fitness of red pepper and tomato under gnotobiotic condition. The same was compared only for red pepper under greenhouse condition. The effect of *Methylobacterium* spp. is known for plant growth promotion and fitness of their host by modulating ethylene and IAA homeostasis and by producing phytohormones such as cytokinins or auxins, or by degrading hormone precursors, such as ACC by ACC deaminase (Madhaiyan et al., 2007; Ryu et al., 2006; Kim et al., 2009). The relatively widespread production of IAA by plant-associated bacteria suggests that bacterial IAA stimulates root development of host plants (Glick and Pasternak, 2003; Spaepen et al., 2007). In the present investigation, it was observed that IAA-producing isolates stimulated root growth, but only when they released low quantities of IAA (<5.0 μg mL^{-1}). Similar result was observed for greenhouse condition. The present findings were in agreement with the works of Long et al. (2008) and Madhaiyan et al. (2007). Madhaiyan et al. (2007) while working on the interaction of auxins and ACCD regulations of ethylene in *M. oryzea*-inoculated canola, reported that IAA inhibit the root growth by 52.5%. Similarly, while establishing the relationship of IAA and ACCD on root growth of *Solanum nigrum* and *Nicotiana attenuate*, Long et al. (2008) reported that application of IAA at 1.0 μg mL^{-1} to seed significantly increased the root growth and seeds treated with 10 μg mL^{-1} to 100 μg mL^{-1} retarded the root elongation.

Plant growth promoting rhizobacteria living in the rhizosphere are generally believed to be beneficial to all plant species they associate with because of their conserved influence of phytohormones on plant growth (Cakmakci et al., 2007). Given that hormonal regulation is conserved among plants, it was anticipated that IAA and ACCD effects on root growth would be similar in tomato and red pepper. However, no similar effect on the root growth of the tested crops was observed due to high concentration of exogenous IAA application. These suggest the possible explanation for the discrepancy in the bacterial ACC deaminase and IAA as well as the mutual effects on root growth. Some models describe how ACC deaminase counteracts ethylene-repressed auxin-response factors involved in root growth (Madhaiyan et al., 2007; Glick et al., 2007). The presence of ACC deaminase-producing rhizobacteria in the rhizosphere can depress the expression of auxin response genes in the shoots which ultimately affect the plant root growth (Long et al., 2008).

Methylobacterium and low concentration of IAA consistently enhanced plant fitness. This was also supported by appreciably higher SPAD index along with a significant increment in plant height and biomass accumulation in *Methylobacterium* CBMB20 and KACC10744 inoculated seedlings.

These findings demonstrated that *Methylobacterium* spp. with low IAA but high ACCD as well as low concentrations of exogenous IAA positively influenced root growth while high concentrations of IAA have inhibiting effects on root growth. The effect of *Methylobacterium* spp. on plant fitness and high biomass accumulation could be the cumulative effect of ACCD and IAA. The potential of *Methylobacterium* spp. should be further investigated in their ecological context to maximize their utilization for sustainable agricultural crop production.

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식물생장촉진 세균 *Methylobacterium* spp. 와 IAA 처리가 고추와 토마토 유묘의 생육에 미치는 영향

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무균 및 온실조건에서 indole-3-acetic acid (IAA)의 처리와 1-aminocyclopropane-1-carboxylate deaminase (ACCD) 및 IAA 활성을 갖는 *Methylobacterium* 균주 접종 시 토마토와 고추의 생장을 비교 평가하였다. 무균조건에서 1.0 ㎍ mL^{-1}의 IAA는 고추와 토마토의 뿌리생장을 촉진시키는데 비해 10.0 ㎍ mL^{-1} 이상의 높은 농도에서는 뿌리생장이 억제되었다. 그러나 높은 ACCD 활성을 갖고, IAA 활성은 낮거나 가지고 있지 않은 *Methylobacterium* 균주들을 접종하였을 때에는 고추와 토마토 모두 IAA 처리구 보다 뿌리생장이 증진되는 것을 확인하였다. 마찬가지로 온실조건에서 *Methylobacterium* 균주들을 접종했을 때, 마디길이와 잎의 크기 그리고 단위 면적당 잎의 무게 (SLW)에서 유의성 있는 증진효과를 보였다. 전반적인 식물 생장에서 저농도의 IAA 처리 효과는 *Methylobacterium*의 효과와 비슷한 경향을 나타냈다. 유묘의 지상부 길이는 ACCD 활성과 IAA 생산능을 갖는 *Methylobacterium* 균주 처리구에서 유의성 있는 증가를 확인할 수 있었으며, 전체 건물중 또한 *Methylobacterium* 처리 시 유의성 있는 증진 효과를 확인 할 수 있었다. 하지만 고농도의 IAA는 고추와 토마토의 생물량을 억제시켰다. 이러한 결과는 접종 균주의 IAA와 ACCD가 고추와 토마토 유묘의 생장 증진에 영향을 끼친다는 것을 증명한다.