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Influence of L-tryptophan and auxins applied to the rhizosphere on the vegetative growth of *Zea mays* L.

MUHAMMAD SARWAR and W.T. FRANKENBERGER, Jr.[1]
Department of Soil and Environmental Sciences, University of California, Riverside, CA 92521, USA.
[1]*Corresponding author*

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Abstract

Glasshouse experiments were conducted to evaluate the influence of L-TRP in comparison with indole-3-acetamide (IAM), tryptophol (TOL) and indole-3-acetic acid (IAA) on the growth of *Zea mays* L. var. Early Sunglow. L-TRP (25 to 2.5×10^{-5} mg kg^{-1} soil), IAM (22 to 2.2×10^{-5} mg kg^{-1} soil), TOL (20 to 2.0×10^{-5} mg kg^{-1} soil), and IAA (22 to 2.2×10^{-5} mg kg^{-1} soil) were applied as a soil drench to established uniform seedlings. All treatments were applied in a completely randomized design with 10 replicates. IAM had no significant effect on the plant growth parameters. Shoot height, uppermost leaf collar base distance, internodal distance, and shoot dry and fresh weights were significantly improved upon the addition of TOL (2.0×10^{-2} mg kg^{-1} soil), however, the highest concentration (20 mg kg^{-1} soil) caused a 14.6% reduction in leaf width. L-TRP (2.5×10^{-3} mg kg^{-1} soil) also had a significant influence on shoot height, uppermost leaf collar base distance, internodal distance and fresh weight of shoot compared with the control. The highest concentration of L-TRP (25 = mg kg^{-1} soil) had a negative effect on leaf width and dry weight of the shoot. The most pronounced response on the corn growth parameters was observed with the application of IAA at lower concentrations (2.2×10^{-5} to 2.2×10^{-2} mg kg^{-1} soil) specifically improving root growth. The highest concentration (22 mg kg^{-1} soil) of IAA had a significant negative effect on plant height, leaf width, stem diameter, shoot fresh and dry weight. These findings indicate that L-TRP applied at the appropriate concentrations can have positive effects on corn growth comparable to pure auxins (TOL and IAA).

Introduction

Plant hormones play a crucial role in controlling plant growth and development. Among the plant hormones known today, auxin (from the Greek term *auxein*, to increase) was the first phytohormone recognized by Darwin (1880). His work on the phototropic response of grass coleoptiles indicated the transfer of a signal from the tip to lower parts of the plant. Later, Went (1926; 1928) was the first to isolate the active substance from an *Avena* coleoptile tip onto agar and reported that the tropistic response was due to a specific diffusable substance. The isolation of auxin (IAA) from a plant was achieved by Haagen-Smit et al. (1942) and was later confirmed by Berger and Avery (1944). Since then, IAA has been isolated from several other plant sources.

Biosynthesis of auxins is not limited to higher plants. Several microorganisms including fungi (Frankenberger and Poth, 1987; Pokojska and Strzelczyk, 1988), bacteria (Hubbell et al., 1979; Muller et al., 1989), and algae (Florenzano et al., 1978; Moss, 1965) also have been reported to synthesize auxins. Comparatively much data have been collected on auxin metabolism in higher and lower plants, but little emphasis has been placed on the role of microbially-derived auxins on plant growth.

Soils also have been reported to contain compounds exhibiting strong auxin-like activity (Hamence, 1946; Sheldrake, 1971; Stewart and Anderson, 1942; Whitehead, 1963) and differ in their auxin synthesizing capacity depending on the fertility status and organic matter content (Chandramohan and Mahadevan, 1968; Hamence, 1946). The literature contains ample evidence that the soil microbiota are active in auxin synthesis (Arshad and Frankenberger, 1992; Bric et al., 1991).

Generally, the rhizosphere and rhizoplane microbial community is more active in auxin production than those from non-rhizosphere soil (Brown, 1972; Dvornikov et al., 1970; Kampert et al., 1975; Purushothaman et al., 1974; Strzelczyk and Pokojska-Burdzeij, 1984; Strzelczyk et al., 1977). Higher auxin production in the rhizosphere is most likely due to the abundance of substrates and diverse microbial populations (Narayanaswami and Veerraju, 1969). Similarly, Rossi et al. (1984) found a higher amount of auxin-like compounds in corn rhizosphere compared with non-rhizosphere environments, especially during seedling emergence. Arshad and Frankenberger (1991) confirmed these findings by reporting a higher percentage of microorganisms from rhizosphere soil than non-rhizosphere soil capable of producing auxins. However, these microbiota could only affect plant growth if microbially-derived auxins are taken up by plant roots.

L-Tryptophan (L-TRP) is considered as a physiological precursor of auxins in higher plants and microbial production. Purushothaman et al. (1973; 1974) reported synthesis of auxins in TRP-amended soil. Frankenberger and Brunner (1983) confirmed this observation with HPLC-MS and proved that IAA was produced in soil when incubated with L-TRP. Recently, Sarwar et al. (1992) studied auxin biosynthesis in L-TRP-amended soil under the influence of several environmental factors and reported that TRP is a physiological precursor of auxins in soil. Microbially-derived auxins from applied TRP within the rhizosphere can have some major effects on plant growth. Frankenberger and Poth (1987) reported dramatically increased growth of Douglas fir by inoculating with the ectomycorrhizae, *Pisolithus tinctorius*, when soil was amended with L-TRP. Frankenberger et al. (1990) also reported a significantly positive effect of L-TRP comparable with the pure auxins (IAA, indole-3-acetamide, indole-3-lactic acid, etc.) on growth of radish when applied at low concentrations (ng to $\mu g\ kg^{-1}$ soil) at the seedling stage.

Although L-TRP and its various analogs have been tested for their effects on growth of various plants, a thorough investigation dealing with the influence of various levels of TRP and pure auxins (indole-3-acetamide, tryptophol and IAA) when applied to soil on the growth of maize, have not been compared. Thus this study was initiated to compare the effects of microbially-derived auxins from L-TRP and pure auxins with the hypothesis that microbially synthesized auxins in soil amended with L-TRP are subject to plant uptake and evoke a physiological response.

Materials and methods

A glasshouse study was conducted to evaluate the influence of indole-3-acetamide (IAM), tryptophol (TOL), L-tryptophan (L-TRP), and indole-3-acetic acid (IAA) added to soil on the growth of *Zea mays* L. var Early Sunglow. All compounds were obtained from Sigma (St. Louis, MO). The physicochemical properties of the soil used for the experiment were determined as follows: pH, 8.11; inorganic nitrogen as NH_4-N, 20.3 mg kg^{-1} and as NO_3-N, 46.8 mg kg^{-1} soil; orthophosphate-P, 9.1 mg kg^{-1} soil; organic carbon, 2.7%; moisture content, 14.8%; sandy clay loam texture (47.5% sand and 27.5% clay), a heterotrophic microbial population of 136×10^5, 74×10^2 and 112×10^3 cfu g^{-1} soil enriched on nutrient agar, a minimal salt medium (MSM) plus L-TRP as the sole C source and MSM plus L-TRP as the sole N source, respectively. The soil was selected on the basis of a preliminary study indicating a positive response of soil applied L-TRP on the growth of maize. Surface

(0-15 cm) soil was collected, homogenized and passed through a 2-mm sieve before filling the pots.

Growth of seedlings

Seeds of *Zea mays* L. cv. Early Sunglow (Burpee, Warminster, PA) were sown directly in plastic pots containing 4.0 kg of sieved field moist soil at the rate of 6 seeds per pot approximately equidistant from each other. Hoagland's mineral solution (500 mL, full-strength) was applied as a one-time application to each pot 10 d prior to treatment with L-TRP and auxins. The controls consisted of treatment with the nutrient solution, but not L-TRP or the auxins. The soil moisture content was maintained at 15% allowing it to dry out before the nutrient solution was applied. Corn seedlings were thinned out to one uniform plant per pot prior to treatment application (10 d after sowing seeds).

Treatment application

Various concentrations of IAM (22 to 2.2×10^{-5} mg kg^{-1}), TOL (20 to 2.0×10^{-5} mg kg^{-1}), L-TRP (25 to 2.5×10^{-5} mg kg^{-1}) and IAA (22 to 2.2×10^{-5} mg kg^{-1}) in solution form were applied to soil 2 d after thinning as a one-time application. All treatments were applied in four different sets, each in a completely randomized design with 10 replicates having one plant per pot.

Growth measurements

Plant growth was monitored over the entire vegetative growth period and harvested at the appearance of tassels (55 d after sowing). Shoot height was measured up to the top of the uppermost leaf every week throughout the experiment and to the base of the uppermost leaf collar. Stem diameter was measured at the fifth internode with a Vernier caliper and leaf width at the mid-point of the leaf originating from the fifth node. Internodal distance was measured between the fourth and fifth nodes from each plant in each set. After harvesting, shoot and root fresh weights were recorded. Then dry shoot and root weights were measured following drying at 65°C for 48 h.

Statistical analysis

The data obtained were subjected to analysis of variance (ANOVA) and all treatment means were compared with the control according to Dunnett's test (Steel and Torrie, 1980).

Results

This glasshouse experiment was conducted to evaluate the influence of L-TRP in comparison with IAM, TOL and IAA on the growth of *Zea mays* L. Growth parameters measured included shoot height, uppermost leaf collar base distance, leaf width, internodal distance, stem diameter, shoot fresh and dry weight, and root fresh and dry weight.

Shoot height

There was no significant difference in shoot height upon the application of IAM at 2.2×10^{-5} to 22 mg kg^{-1} soil (Table 1). TOL promoted shoot height at 2.0×10^{-2} mg kg^{-1} soil with a 10.2% increase over the control (Table 2). L-TRP applied at 2.5×10^{-3} mg kg^{-1} soil also promoted shoot height by 11.7% while other concentrations were ineffective (Table 3). A dramatic response was observed with the application of IAA, particularly at the highest concentration (22 mg kg^{-1} soil). At this concentration, plant height was reduced by 16.4% over the control 5 weeks after treatment. Shoot height was enhanced (7.5% increase) with a lower concentration of IAA (2.2×10^{-3} mg kg^{-1} soil) applied to the rhizosphere (Table 4).

Uppermost leaf collar base distance

While IAM applied to soil had no significant effect on the uppermost leaf collar base distance, TOL at 2.0×10^{-2} mg kg^{-1} soil and L-TRP at 2.5×10^{-3} mg kg^{-1} soil promoted this growth parameter by 10.5% and 12.6%, respectively. Overall the most effective treatment was IAA with an increase in the uppermost leaf collar base distance ranging from 15.9 to 22.8% over

Table 1. Growth parameters of Early Sunglow corn as influenced by indole-3-acetamide (IAM) applied to soil (average of 10 replicates)

IAM application (mg kg^{-1})	Shoot height (cm) Weeks following application 2	3	4	5	Uppermost leaf collar base distance	Leaf width	Internodal distance	Stem diameter (mm)	Shoot fresh wt	Shoot dry wt	Root fresh wt	Root dry wt
					(cm)				(g)			
Control	68.6	88.2	101.1	103.7	71.0	5.59	7.91	11.5	87.3	28.1	2.06	1.89
22	64.6	89.7	104.4	110.5	77.7	5.33	9.00	11.2	89.0	22.5	1.97	1.66
2.2	68.6	87.4	101.7	105.5	73.2	5.55	8.28	11.1	88.1	26.4	2.21	2.02
2.2×10^{-1}	70.0	87.7	102.0	103.7	69.4	5.54	7.94	11.0	85.7	26.9	2.20	2.02
2.2×10^{-2}	72.4	92.1	105.2	107.2	73.7	5.59	8.29	11.8	92.4	28.4	2.30	1.99
2.2×10^{-3}	72.8	92.9	104.4	106.3	74.6	5.67	8.16	10.6	92.4	29.1	2.46	2.27
2.2×10^{-4}	70.3	88.8	101.2	104.2	66.5	5.54	7.96	11.7	88.2	28.1	2.39	1.86
2.2×10^{-5}	69.8	86.0	101.2	103.5	65.1	5.34	7.88	11.2	86.2	27.8	2.46	2.15

*,** = Treatment means significantly different from control at $p \leq .05$ and 0.01, respectively, according to Dunnett's test.

Table 2. Growth parameters of Early Sunglow corn as influenced by tryptophol (TOL) applied to soil (average of 10 replicates)

TOL application (mg kg^{-1})	Plant height (cm) Weeks following application 2	3	4	5	Uppermost leaf collar base distance	Leaf width	Internodal distance	Stem diameter (mm)	Shoot fresh wt	Shoot dry wt	Root fresh wt	Root dry wt
					(cm)				(g)			
Control	63.6	75.3	82.7	84.1	54.1	4.92	5.34	9.6	44.1	21.0	1.43	0.98
20	57.2	72.3	81.5	83.7	58.3	4.20**	6.27	8.9	40.9	19.8	1.28	0.82
2.0	61.9	75.9	83.9	85.1	54.9	4.74	5.58	9.5	42.7	20.5	1.12	0.83
2.0×10^{-1}	62.9	76.4	85.4	87.2	55.4	4.83	5.96	9.6	45.0	20.5	1.21	0.88
2.0×10^{-2}	64.3	78.6	88.5*	92.7**	59.8*	4.98	6.80**	10.0	52.2**	24.1**	1.64	1.12
2.0×10^{-3}	72.8	76.0	84.3	88.2	59.5	4.65	6.25	9.3	43.9	20.2	1.26	0.80
2.0×10^{-4}	70.3	76.1	84.6	86.9	59.5	4.52*	6.14	9.8	45.4	20.9	1.35	0.77
2.0×10^{-5}	69.8	72.6	82.0	82.0	56.0	4.67	5.21	9.2	42.0	20.2	1.30	0.94

*,** = Treatment means significantly different from control at $p \leq .05$ and 0.01, respectively, according to Dunnett's test.

Table 3. Growth parameters of Early Sunglow corn as influenced by L-tryptophan (L-TRP) applied to soil (average of 10 replicates)

TRP application ($mg\ kg^{-1}$)	Plant height (cm) Weeks following application 2	3	4	5	Uppermost leaf collar base distance	Leaf width	Internodal distance	Stem diameter (mm)	Shoot fresh wt	Shoot dry wt	Root fresh wt	Root dry wt
					(cm)				(g)			
Control	63.0	77.6	85.6	88.9	60.4	5.18	5.25	10.3	57.3	15.6	2.47	1.89
25	61.0	77.4	80.1	81.6	60.4	4.38**	5.72	9.3	46.5	12.5*	1.92	1.39
2.5	63.6	76.8	83.4	84.0	63.6	4.88	6.35	9.5	55.1	14.8	2.58	2.00
2.5×10^{-1}	65.5	77.9	85.3	88.1	64.6	5.20	6.40	10.4	56.1	17.1	2.49	1.74
2.5×10^{-2}	64.3	77.7	83.7	92.2	64.7	5.42	6.95*	10.4	62.8	17.0	2.98	1.91
2.5×10^{-3}	64.4	78.3	87.8	99.3*	68.0*	5.68	7.31**	11.0	70.2*	18.1	3.20	2.30
2.5×10^{-4}	60.4	77.8	85.4	96.0	61.6	5.60	6.84	10.2	58.1	15.4	2.94	2.09
2.5×10^{-5}	62.2	76.8	84.8	90.8	60.9	5.13	6.43	10.3	57.4	15.5	2.85	1.98

*,** = Treatment means significantly different from control at $p \leq .05$ and 0.01, respectively, according to Dunnett's test.

Table 4. Growth parameters of Early Sunglow corn as influenced by indole-3-acetic acid (IAA) applied to soil (average of 10 replicates)

IAA application ($mg\ kg^{-1}$)	Plant height (cm) Weeks following application 2	3	4	5	Uppermost leaf collar base distance	Leaf width	Internodal distance	Stem diameter (mm)	Shoot fresh wt	Shoot dry wt	Root fresh wt	Root dry wt
					(cm)				(g)			
Control	58.6	67.8	72.1	73.6	43.9	4.40	4.70	8.9	26.2	7.1	1.59	1.17
22	39.3**	44.9**	51.1**	61.5**	48.8	2.74**	5.80**	6.2**	13.5**	3.8**	1.12	0.80
2.2	53.4*	64.2	69.3	71.2	48.5	4.22	5.15	8.3	22.9	6.9	1.64	1.22
2.2×10^{-1}	56.9	67.1	72.8	74.1	48.6	4.56	4.96	8.9	27.6	7.0	2.05	1.68
2.2×10^{-2}	58.3	67.5	71.5	74.6	50.9*	4.67	5.11	9.2	28.8	7.3	2.23*	1.95**
2.2×10^{-3}	60.7	71.7	77.8*	79.1*	51.4*	4.77	5.48	9.1	32.3*	7.4	2.81**	2.49**
2.2×10^{-4}	60.0	69.8	75.7	77.8	53.9**	4.54	5.22	9.1	30.1	7.0	2.56**	2.07**
2.2×10^{-5}	61.0	70.7	74.8	76.9	50.2	4.65	5.18	9.1	29.8	6.8	2.44**	2.00**

*,** = Treatment means significantly different form control at $p \leq .05$ and 0.01, respectively, according to Dunnett's test.

the control with a concentration of 2.2×10^{-2} to 2.2×10^{-4} mg kg^{-1} soil (Table 4).

Leaf width

There was no significant difference in leaf width upon the application of IAM compared with the control. However, upon the addition of TOL (20 mg kg^{-1} soil), the leaf width decreased by 14.6%, 15.4% with L-TRP (25 mg kg^{-1} soil), and 37.7% with IAA (22 mg kg^{-1} soil). All other concentrations of L-TRP and auxins applied had no significant effect on leaf width.

Internodal distance

The application of IAM had no significant effect on the internodal distance of maize when applied at 2.2×10^{-5} to 22 mg kg^{-1} soil. However, the internodal distance was promoted by 27.3% upon the application of TOL at 2.0×10^{-2} mg kg^{-1} soil (Table 2). L-TRP also increased the internodal distance from 32.3 to 39.2% when treated with a concentration range of 2.5×10^{-2} to 2.5×10^{-3} mg kg^{-1} soil (Table 3). The internodal distance of maize was enhanced upon the application of IAA by 23.4% when applied at 22 mg kg^{-1} soil (Table 4).

Stem diameter

The addition of IAM, TOL and L-TRP had no significant effect on the stem diameter of maize. However, the application of IAA at 22 mg kg^{-1} soil decreased the stem diameter by 30.3% (Table 4). All other concentrations of IAA tested had no significant effect on stem diameter.

Shoot fresh weight

The addition of IAM had no significant effect on the shoot fresh weight of maize, while TOL at 2.0×10^{-2} significantly enhanced this growth parameter by 18.4% (Table 2). L-TRP at 2.5×10^{-3} mg kg^{-1} soil promoted the shoot fresh weight by 22.5% (Table 3). IAA showed both inhibitory and stimulatory effects, depending on the concentration applied. At the higher concentration of 22 mg IAA kg^{-1} soil, shoot fresh weight decreased by 48.5%, while at 2.2×10^{-3} mg kg^{-1} this growth parameter was enhanced by 23.3% (Table 4).

Shoot dry weight

The application of IAM had no significant effect on the shoot dry weight of maize. However, TOL had a positive influence at 2.0×10^{-2} mg kg^{-1} soil with a 14.8% enhancement (Table 2). The addition of L-TRP and IAA decreased the shoot dry weight at the highest concentrations applied (25 and 22 mg kg^{-1}, respectively) by 19.9% (L-TRP) and 46.5% (IAA) (Tables 3 and 4).

Root fresh weight

The application of IAM, TOL and L-TRP had no significant effect on the root fresh weight, however IAA stimulated the root weight at concentrations ranging from 2.2×10^{-5} to 2.2×10^{-2} mg kg^{-1} soil with a 40.3 to 76.7% increase (Table 4).

Root dry weight

The addition of IAM, TOL and L-TRP had no significant effect on the root dry weight of maize, however IAA stimulated this growth parameter by 66.6 to 112.8% with concentrations ranging from 2.2×10^{-5} to 2.2×10^{-2} mg kg^{-1} soil (Table 4).

Discussion

Previous studies have shown that auxins produced by microorganisms in the vicinity of the root tip can have a significant effect on plant growth (Pilet, 1977). Attempts were made to prevent nutrient and water stress, hence the response to the treatments of L-TRP and auxins (TOL and IAA) were most likely a hormonal response.

The increase in plant height in response to a dilute concentration of L-TRP, TOL and IAA represents a typical growth response produced by auxins which are inhibitory at high concentrations and stimulatory at lower levels. Similar results have been demonstrated by Robertson et al. (1976) who reported that high concentrations of IAA strongly inhibited seed germination of lettuce. Likewise, reduced seedling growth of oats by high auxin concentrations was observed by Hwang and Perse (1940). Frankenberger et al. (1990) reported a positive effect of L-TRP on the growth parameter of radish (*Raphanus sativus*) when applied at low concentrations at the seedling stage and was comparable with the effect of auxins (IAM and indole-3-lactic acid).

Many parameters of plant growth such as uppermost leaf collar base distance, internodal length, and shoot fresh weight were all significantly improved by lower concentrations of L-TRP and the auxins (TOL and IAA) applied. Our study also showed a strong root growth stimulation by IAA at the lower levels. IAA was found to be strongly inhibitory to many of the growth parameters such as shoot height, leaf width, internodal distance, stem diameter and shoot and root fresh weights, when applied at the highest concentration (22 mg kg^{-1} soil). Similar findings were reported by Opatrna et al. (1988) who demonstrated root growth inhibition of *Chenopodium rubrum* by IAA at a rate of 1 m*M*, while lower concentrations stimulated the root growth of pea seedlings (Zelena et al., 1988). In this study, L-TRP also inhibited leaf width and shoot dry weight at the highest concentration (25 mg kg^{-1} soil). The inhibitory effects of L-TRP may be a result of a slow and continuous release of IAA in soil due to microbial action.

The growth parameters of maize were not influenced by IAM. Even at the highest application (22 mg kg^{-1}) there was no inhibitory effect. Since IAM is not found in plant tissues (Kosuge et al., 1983), the enzymes necessary to metabolize this auxin may be lacking, thus there was no hormonal response (Leopold, 1980).

This work indicates that L-TRP and auxins (TOL and IAA) can have an ecological effect in modifying plant growth and development. The mechanism of action of L-TRP and auxins on plant growth may be attributed to the direct uptake of these compounds by plant roots, a change in the balance of rhizosphere microflora discouraging root pathogens or by microbial conversion into metabolites resulting in a beneficial rhizosphere for plant growth.

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