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Effect of Glyphosate on Indole-3-acetic Acid Metabolism in Tolerant and Susceptible Plants

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Abstract. A comparison study was conducted on the effect of glyphosate (*N*-[phosphonomethyl]glycine) on indole-3-[2-^{14}C]acetic acid (IAA) metabolism, ethylene production, and growth of 7-day-old seedlings of different plants. The plants tested were American germander (*Teucrium canadense* L.), soybean (*Glycine max* L. Merr.), pea (*Pisum sativum* L. cv. Alaska and Little marvel), mungbean (*Vigna radiata* L.), and buckwheat (*Fagopyrum esculentum* Moench). A spray with 2 mM glyphosate affected IAA metabolism to a varied degree. The induced increase of IAA metabolism was greater in buckwheat, Alaska pea, and mungbean than soybean, Little marvel pea, and American germander. The increased IAA metabolism was correlated with the inhibition of growth and with the decrease of ethylene production.

The natural rate of IAA metabolism was markedly different among the plant species and cultivars tested and appeared to be related to the sensitivity of the plants to glyphosate. American germander and Little marvel pea with high rates of IAA metabolism were more tolerant to glyphosate than buckwheat and Alaska pea, which had low rates of IAA metabolism. Plants with a high natural rate of IAA metabolism were probably less dependent on IAA and thus less susceptible to glyphosate.

Glyphosate (*N*-[phosphonomethyl]glycine) is a relatively new, broad-spectrum herbicide and a sugarcane ripener (Nickell 1982). In recent years, a considerable amount of work has been reported on its mode of action (Amrhein et al. 1980, 1983, Cole et al. 1979, Comai et al. 1983, Duke and Hoagland 1978, Holländer and Amrhein 1980, Jaworski 1972, Rogers et al. 1983, Roisch and Lingens 1980). Using radiolabeled indole-3-acetic acid (IAA), it was shown

that a glyphosate treatment markedly increased IAA metabolism and lowered the free IAA level in tobacco callus compared to that of the untreated control (Lee 1982ab). A pretreatment with glyphosate also decreased the IAA-induced ethylene production in tobacco callus (Lee and Dumas 1983). With the same tissue, the extent of inhibition of fresh weight growth by glyphosate and structurally related compounds was correlated with the increased rate of IAA metabolism (Lee et al. 1983). The glyphosate inhibition of growth of tobacco and soybean callus was partially reversible by high concentrations of IAA (Lee 1980b). These results all indicate an involvement of IAA metabolism in glyphosate action in plant tissues cultured *in vitro*.

To investigate further whether the promotion of IAA metabolism by glyphosate occurs also in intact plants, the study was extended to seedlings of five plant species with different degrees of susceptibility to glyphosate. In this report we compare the rates of IAA metabolism, ethylene production, and growth of the seedlings with and without glyphosate treatment.

Materials and Methods

Plant Material

The plant species tested were American germander (*Teucrium canadense* L.), soybean (*Glycine max* L. Merr. cv. Evans), mungbean (*Vigna radiata* L.), pea (*Pisum sativum* L. cv. Alaska and Little marvel), and buckwheat (*Fagopyrum esculentum* Moench). Seeds and rhizomes (American germander) were planted in soil in clay pots in the greenhouse. After germination, the plants were grown in a growth chamber at 28°C under 12-h light and 12-h dark cycles. The light with 270 $\mu E.m^{-2}s^{-1}$ was provided by a mixture of incandescent and fluorescent lamps. Seven-day-old seedlings were used for the experiments.

Glyphosate Treatment

The seedlings were sprayed once with an aqueous solution of glyphosate (2 mM) to wet the upper surface of all leaves. The commercial formulation Roundup and the analytical grade glyphosate were used with similar results.

Experiment on [2-^{14}C]IAA Metabolism

Labeled IAA ([2-^{14}C]IAA) was used for the study of IAA metabolism in the treated and control plants. Five days after glyphosate treatment, the stems were washed with sterile water and 1-cm sections were cut from the internodes. Five grams of the sections from each treatment was incubated with 3.2 nmole [2-^{14}C]IAA (42.2 μCi/μmole, New England Nuclear, Boston, Mass., USA) and 0.6 mmole sterile maleate buffer (pH 5.5) in a total volume of 10 ml. After incubation at 25°C in a shaking water bath for 4 h, the sections were thoroughly washed with water, boiled for 2 min in 80% methanol containing 0.02% sodium diethyldithiocarbamate, and homogenized. The extract was filtered and the

residue was washed with fresh extracting medium. Methanol was removed *in vacuo*, and the remaining aqueous phase was successively extracted with freshly purified diethyl ether at pH 3.5 and 8.0, and then with 1-butanol at pH 2.5. The acidic ether fraction was used for further isolation of free [2-^{14}C]IAA. The 80% methanol-insoluble residue, which contained macromolecular constituents of cells, was extracted with 1 N NaOH at 37°C for 16 h. The insoluble residue was further treated with NCS tissue solubilizer (Amersham). Radioactivity recovered from the fractions other than free [2-^{14}]IAA was used to assess the relative activities of conjugation and oxidation of IAA in these plants. Radioactivity was measured by liquid scintillation counting in a Beckman LS9000 system.

Measurement of Free [2-^{14}C]IAA

The acidic ether fraction was freeze-dried and taken up in 0.1 ml HPLC-grade methanol. A portion was injected into a programmed HPLC (Waters) equipped with a reverse phase μBondapak-C_{18} column and a fluorescence detector (excitation at 280 nm, emission at 338 nm). The mobile phase was 69% water, 30% methanol, and 1% acetic acid. Authentic IAA was used as the standard. The [2-^{14}C]IAA isolated was confirmed by using an anion exchange column, Partisil-10-SAX (Whatman) with 1% acetic acid as the mobile phase. The loss of IAA in the procedure was estimated by including a control with a known amount of [2-^{14}C]IAA at the beginning of extraction and by counting the radioactivity of [2-^{14}C]IAA at the end of isolation. The recovery was from 65.2% to 72.0%. The experiment was repeated three times.

Measurement of Ethylene

Five days after the glyphosate treatment, the internodes of the treated and the control plants were cut into 1-cm sections. The time interval between the end of cutting and the beginning of ethylene collection was 10 min for all treatments. One to two grams of the stem sections were weighed, sealed in an all-glass flask fitted with a 6-mm i.d. sampling port and a silicone seal, and kept in the dark to avoid a possible interference by CO_2 (Bassi and Spencer 1982). After 5 h, a 1-ml sample was analyzed for ethylene by a gas chromatograph equipped with a nickel column and a flame ionization detector. The experiment was repeated 12 times.

To study the interaction of glyphosate and IAA on ethylene production, exogenous IAA was introduced into the control and the glyphosate-treated plants by cutting the stems above the soil surface and dipping the cut ends in an aqueous solution of IAA (0.1 mM) for 24 h. Thereafter the stems were excised and ethylene was analyzed. The experiment was repeated 12 times.

Measurement of Growth

For measurement of the effect of glyphosate on growth, 7-day-old seedlings were sprayed with a series of concentrations of glyphosate (0.05–2.0 mM).

Table 1. Effect of glyphosate on uptake and metabolism of [2-^{14}]IAA in the stems of different plant species.

Plant	Total uptake dpm(gFW)$^{-1}10^{-2}$		Free [2-^{14}C]IAA in tissue dpm(gFW)$^{-1}10^{-2}$		% Metabolized	
	Control	Treated	Control	Treated	Control	Treated
American germander	216 ± 11	189 ± 21	27 ± 15	16 ± 6	87.5	91.5
Pea (Little marvel)	170 ± 70	191 ± 95	28 ± 9	22 ± 1	83.5	88.5
Soybean	177 ± 36	160 ± 38	21 ± 4	13 ± 4	88.0	91.9
Mungbean	216 ± 14	216 ± 22	84 ± 2	41 ± 9	61.1	81.0**
Pea (Alaska)	130 ± 17	126 ± 18	69 ± 8	25 ± 2	46.9	80.2**
Buckwheat	195 ± 42	175 ± 25	132 ± 23	76 ± 6	32.3	56.6**

The incubation with [2-^{14}C]IAA was done 5 days after the spray with 2 mM glyphosate and the duration of the incubation was 4 h. Means with ** were significantly different from the corresponding controls at the 1% level.

The height of the plant was measured from the base to the terminal bud 8 days after the glyphosate treatment. Each experiment had 20 plants per species, and the experiment was repeated three times.

Results

Effect on [2-^{14}C]IAA Metabolism

A pretreatment with glyphosate increased the rate of IAA metabolism by 75% in buckwheat, 71% in Alaska pea, and 33% in mungbean compared to the untreated controls (Table 1). However, the change was small, if any, in soybean, Little marvel pea, and American germander.

From Table 1 it is also evident that the rate of IAA metabolism in the control seedlings without the glyphosate pretreatment differed markedly among the plant species. In American germander and soybean, 88% of [2-^{14}C]IAA were metabolized in the 4-h period whereas in buckwheat only 32% were metabolized, a difference of 170%. As a result, the amount of free [2-^{14}C]IAA remaining in the tissue differed greatly between these plants. Also there was a considerable difference in the rate of IAA metabolism between the two pea cultivars; the rate was 75% higher in the dwarf (Little marvel) than the normal pea (Alaska).

The promotion of IAA metabolism by glyphosate in buckwheat, Alaska pea, and mungbean seedlings was also indicated by the increase of radioactivity in the butanol fraction (Table 2) which contained metabolites of IAA, particularly conjugated IAA (Lee 1980a). The increase was 73% in buckwheat, 54% in mungbean, and 44% in Alaska pea over that of the controls. By contrast, there was no increase of radioactivity in this fraction by glyphosate in American

Table 2. Effect of glyphosate on incorporation of radioactivity of [2-^{14}C]IAA into the butanol-fraction extracted from the stems of different plant species.

Plant	Radioactivity % of total [2-^{14}C]IAA uptake		% Change over control
	Control	Treated	
American germander	66.1 ± 3.3	60.4 ± 2.0	−8.6
Pea (Little marvel)	56.7 ± 13.7	52.8 ± 1.5	−6.9
Soybean	66.6 ± 1.0	67.6 ± 2.4	+1.5
Mungbean	37.2 ± 0.2	57.1 ± 2.0**	+53.5
Pea (Alaska)	28.5 ± 0.7	41.0 ± 0.7**	+43.8
Buckwheat	28.5 ± 8.6	49.4 ± 8.4**	+73.3

The incubation with [2-^{14}C]IAA was done 5 days after the spray with 2 mM glyphosate and the duration of the incubation was 4 h. Means with ** were significantly different from the corresponding controls at the 1% level.

Table 3. Effect of glyphosate on incorporation of radioactivity of [2-^{14}C]IAA into the methanol-insoluble fraction of the stems of different plant species.

Plant	Radioactivity % of total [2-^{14}C]IAA uptake		% Change over control
	Control	Treated	
American germander	7.8 ± 0.4	10.6 ± 0.9	+36
Pea (Little marvel)	9.0 ± 1.4	15.1 ± 5.0	+68
Soybean	5.9 ± 1.7	11.9 ± 5.1	+102
Mungbean	4.4 ± 0.8	7.5 ± 1.2	+70
Pea (Alaska)	13.2 ± 3.8	19.3 ± 5.6	+46
Buckwheat	4.0 ± 0.8	3.3 ± 0.9	−18

The incubation with [2-^{14}C]IAA was done 5 days after the spray with 2 mM glyphosate, and the duration of the incubation was 4 h.

germander, Little marvel pea, and soybean under the same conditions. Clearly, this fraction showed significant differences in the response to glyphosate between the two groups of plants. This fraction, which contained up to 66% of the total radioactivity from [2-^{14}C]IAA after a 4-h incubation, was a major metabolite fraction of IAA.

The radioactivity found in the methanol-insoluble fraction was relatively small compared to that in the butanol fraction. Despite a greater variability, a pretreatment with glyphosate also increased the incorporation of radioactivity from [2-^{14}C]IAA into the methanol-insoluble residue of most plants (Table 3). However, the relative effect of glyphosate on this fraction appeared to be different from that on the butanol fraction (Table 2). The glyphosate treatment increased radioactivity in the methanol-insoluble fraction more in soybean, mungbean, and Little marvel pea than in other plants. In this fraction, the radioactivity was solubilized by 1 N NaOH as no or very little radioactivity was found in the residue after hydrolysis. From the results obtained with to-

Table 4. Effect of glyphosate on ethylene production in the stems of different plant species.

Plant	Ethylene production $ng(gFW)^{-1}h^{-1}$		% Change over control
	Control	Treated	
American germander	1.9 ± 0.3	2.1 ± 0.4	+10.5
Pea (Little marvel)	1.8 ± 0.2	2.6 ± 0.9**	+44.4
Soybean	2.1 ± 0.4	1.5 ± 0.3**	−28.6
Mungbean	2.2 ± 0.1	1.2 ± 0.3**	−45.4
Pea (Alaska)	3.6 ± 0.4	1.7 ± 0.2**	−52.8
Buckwheat	1.8 ± 0.4	0.7 ± 0.2**	−61.1

The samples for ethylene measurement were taken 5 days after the spray with 2 mM glyphosate. Means with ** were significantly different from the corresponding controls at the 1% level.

bacco callus, less than 10% of the radioactivity in the methanol-insoluble residue after hydrolysis was identified as [2-^{14}C]IAA. Thus, the radioactivity in this fraction probably was largely derived from oxidation products of [2-^{14}C]IAA. The alkaline diethyl ether fraction, which contained basic and neutral metabolites of IAA, was found to contain only 0.8–2.6% of the total radioactivity from [2-^{14}C]IAA after a 4-h incubation. Although the glyphosate treatment increased the radioactivity of this fraction in all plant species tested, the fraction was small and negligible.

Effect on Ethylene Production

The stem sections of the seedlings tested all produced ethylene, and a pretreatment with glyphosate decreased or increased it depending on the plant species and cultivars (Table 4). The glyphosate-induced decrease of ethylene production was 61% in buckwheat, 53% in Alaska pea, 45% in mungbean, and 28% in soybean. In Little marvel pea and probably American germander, however, ethylene production was increased by glyphosate. Both increase and decrease in ethylene production resulting from a glyphosate treatment have been observed previously in tobacco callus culture, and the difference has been found to be related to IAA levels (Lee and Dumas 1983).

The interaction of glyphosate and IAA on ethylene production was tested by feeding the glyphosate-treated and the control seedlings with 0.1 mM IAA for 24 h before the stem sections were excised for ethylene measurement. The IAA treatment increased ethylene production by 778% in Alaska pea, 327% in mungbean, 243% in soybean, 222% in Little marvel pea, 63% in American germander, and 61% in buckwheat (compare Tables 4 and 5). A pretreatment with glyphosate decreased ethylene production in most IAA-treated plants; Alaska pea, buckwheat, soybean, and mungbean were more sensitive than Little marvel pea and American germander. The response of the plants to glyphosate was in general agreement with that without exogenously supplied IAA. A correlation between free IAA level and ethylene production has been observed previously in tobacco callus (Lee and Dumas 1983). Thus, the effect

Table 5. Effect of glyphosate on ethylene production in the stems of different plant species fed with a high concentration of IAA.

Plant	Ethylene production $ng(gFW)^{-1}h^{-1}$		% Change over control
	Control	Treated	
American germander	3.1 ± 0.5	3.3 ± 0.7	+6.4
Pea (Little marvel)	5.8 ± 0.8	4.8 ± 0.2**	−17.2
Soybean	7.2 ± 1.3	3.4 ± 0.8**	−52.8
Mungbean	9.4 ± 1.0	5.0 ± 1.4**	−46.8
Pea (Alaska)	31.6 ± 2.9	5.9 ± 0.7**	−81.3
Buckwheat	2.9 ± 0.5	1.3 ± 0.1**	−55.6

The samples for ethylene measurement were taken 5 days after the spray with 2 mM glyphosate and 1 day after the treatment with 0.1 mM IAA. Means with ** were significantly different from the corresponding controls at the 1% level.

of glyphosate on ethylene production in susceptible plants (Table 4) probably was due to decreased levels of free IAA as a result of increased IAA metabolism.

Effect on Growth

The effect of glyphosate on growth of the 7-day-old seedlings of different plant species is sumarized in Fig. 1. Under the experimental condition, glyphosate inhibited the growth of the seedlings to a varied degree. In order of decreasing susceptibility, the plants were buckwheat, Alaska pea, mungbean, soybean, Little marvel pea, and American germander. A comparison of growth of the most susceptible and the most tolerant plants tested is shown in Fig. 2.

Discussion

The effect of glyphosate on IAA metabolism and growth of the seedlings differed greatly among the plant species and cultivars tested. A comparison of the results (Table 1 and Fig. 1) indicates a correlation between the glyphosate-promoted IAA metabolism and the inhibition of growth. Glyphosate promoted IAA metabolism more in buckwheat, Alaska pea, and mungbean than in other plants; the inhibition of growth by glyphosate was also greater in these than in other plants. A similar relationship between fresh weight growth and IAA metabolism in tobacco callus as affected by glyphosate and related compounds has been reported (Lee et al. 1983). The glyphosate inhibition of fresh weight growth in tobacco and soybean callus cultures supplemented with low levels of IAA was partially reversible by high levels of IAA or low levels of 2,4-dichlorophenoxyacetic acid (Lee 1980b and unpublished data). These results suggest that the induced increase of IAA metabolism was related to the inhibition of growth.

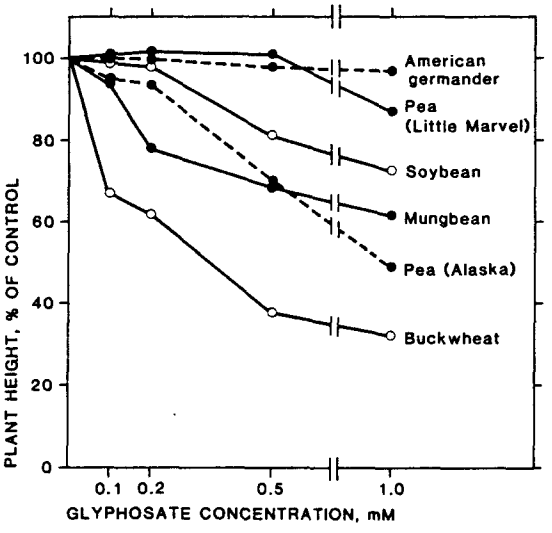

Fig. 1. Inhibition of growth by glyphosate in seedlings of tolerant and susceptible plants. Growth measurement was made 8 days after the spray with glyphosate.

A negative correlation between the rate of [2-^{14}C]IAA metabolism and ethylene production as affected by glyphosate (Tables 1 and 4) is indicative of a change in the endogenous free IAA concentration in the susceptible plants. Previously, it has been shown that a decrease of ethylene production by glyphosate in tobacco callus and a promotion of lateral bud growth by glyphosate in pea and soybean seedlings were correlated with a decrease of free IAA concentration (Lee and Dumas 1983, Lee 1984). Results obtained from separate experiments also showed that the free IAA level in glyphosate-treated susceptible plants was decreased by 61% in buckwheat, 52% in mungbean, and 48% in Alaska pea as compared to the untreated controls.

Conjugation is a major route for IAA metabolism in plants. It is also known that IAA can be degraded by oxidation. As conjugation and oxidation of IAA are complex, the data presented in Tables 2 and 3 serve only as indications of change in conjugation and oxidation of IAA affected by glyphosate. From a comparison of these data it appears that glyphosate affected the metabolic routes of IAA differently in these plants. Whether conjugation was affected more in one group of plants, such as buckwheat and Alaska pea, and whether oxidation was affected more in another group of plants, such as soybean and Little marvel pea, remain to be investigated.

From Table 1, it is interesting to note the marked differences among the untreated plants in the rate of IAA metabolism, ranging from 32% in buckwheat to more than 83% in American germander, soybean, or Little marvel pea. A comparison of the natural rate of IAA metabolism and the response of the plants to glyphosate (Tables 1 and 4 and Fig. 1) suggests a relationship between the two. For example, buckwheat had the lowest rate of IAA metabolism among the plants tested, but showed the highest rate of increase in IAA metabolism and the highest degree of growth inhibition after the glyphosate treatment. This contrasts with little change in IAA metabolism and growth by glyphosate in American germander, in which the natural rate of IAA metabolism was 170% higher than that in buckwheat. It appears that the natural rate of IAA metabolism is related to the sensitivity of the plants to glyphosate.

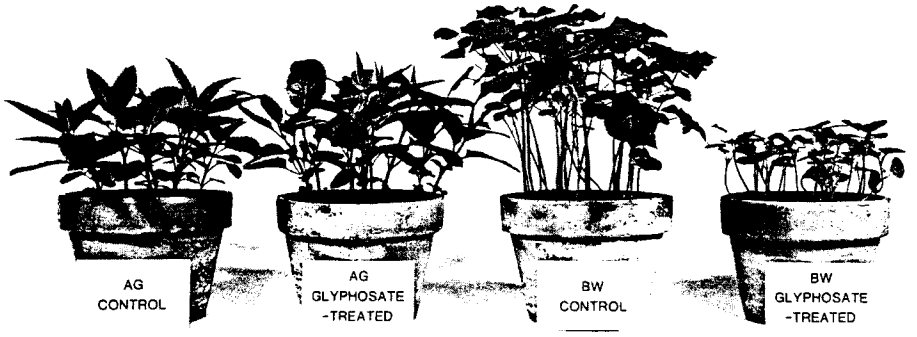

Fig. 2. Comparison of growth response of American germander and buckwheat to glyphosate 7 days after the spray. The concentration of glyphosate was 1 mM for American germander (AG) and 0.5 mM for buckwheat (BW).

Plants with high natural rates of IAA metabolism probably are less dependent on IAA and thus less susceptible to glyphosate.

The site of glyphosate action has been suggested to be the 5-enolpyruvyl-shikimate-3-phosphate (EPSP) synthase (E.C. 2.5.1.19) in the shikimate pathway (Amrhein et al. 1980, 1983, Comai et al. 1983, Rogers et al. 1983). However, little information is available to link the inhibition of this specific enzymic step with the various observed glyphosate-induced changes in plants, such as the stimulated lateral bud growth (Baur et al. 1977, Caseley 1972, Lee 1984), increased chlorophyll degradation (Abu-Irmaileh and Jordan 1978, Lee 1981), increased ripening in sugarcane (Nickell 1982), increased abscission in citrus (Klosterboer 1974), decreased ethylene production (Lee and Dumas 1983), inhibited chlorophyll synthesis (Holländer and Amrhein 1980, Kitchen and Witt 1981, Lee 1981), and inhibited ion uptake (Brecke and Duke 1980, Duke et al. 1983). The shikimate pathway is a chain of reactions from which various primary and secondary aromatic metabolites, including phenolic compounds, are formed. Decreases of soluble phenols by glyphosate have already been reported (Berlin and Witte 1981, Hoagland et al. 1978, Holländer and Amrhein 1980, Lee 1982b). Preliminary experiments with radiolabeled cinnamic acid indicated that glyphosate might directly affect phenolic metabolism in tobacco callus beyond the cinnamic acid step in the shikimate pathway. Based on an earlier observation that feeding phenolic compounds to maize stems affected conjugation and oxidation of IAA (Lee 1980a), it is speculated that the increased IAA metabolism in the glyphosate-treated susceptible plants may be related to changes in phenolic metabolism. Thus, the promotion of IAA metabolism may provide a link between the action(s) of glyphosate in the shikimate pathway and certain IAA-related plant responses, such as the inhibition of growth and the decrease of ethylene production in susceptible plants observed here.

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