STABILITY OF MICROBIAL-PRODUCED AUXINS DERIVED FROM L-TRYPTOPHAN ADDED TO SOIL

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Soil microorganisms are capable of producing secondary metabolites such as auxins upon the addition of tryptophan (L-TRP) that may significantly influence plant growth and development. This study was conducted to determine the stability and availability of indole-3-acetic acid (IAA) and proposed intermediates in the production of auxins from the addition of L-TRP to soil. L-TRP metabolism was not observed with the addition of L-TRP to a steam-sterilized soil when incubated for up to 7 days, indicating a biotic mechanism in the production of soil auxins. Incubation of 3'-14C-L-TRP in non-sterile soil resulted in the conversion of the L-TRP label into indole-3-acetamide, indole-3-lactic acid, indole-3-acetic acid, indole-3-ethanol, and indole-3-aldehyde by the soil microbiota. The production of indole derivatives was dependent on the amount of L-TRP added to the soil. Adsorption-desorption isotherms showed a low affinity of auxin derivatives (5-hydroxy-indole-3-acetic acid, indole-3-acetamide, indole-3-lactic acid, indole-3-acetic acid, indole-3-ethanol, and indole-3-aldehyde) for the soil colloids. The persistence of L-TRP in five soils, measured in half-life (t½), ranged from 22.8 to 28.7 h. The t½ measured for the intermediates of auxin production indicated that several auxin derivatives were stable in soil and may have a greater effect on plant growth and yield when compared with auxins of lower soil stability.

Soils are known to contain compounds that exhibit strong auxin-like activity (Sheldrake 1971; Whitehead 1969). Indole-3-acetic acid (IAA) is considered to be one of the major auxin-like products of the soil microflora. Previous studies have revealed that soil fertility status and organic matter content may regulate the microbial formation of IAA (Chandramohan and Mahadevan 1968; Hamence 1946; Stewart and Anderson 1942). Also, higher auxin production has been reported in nutrient-rich rhizosphere soils compared with root-free soils (Narayanaswami and Veerraju 1969). Production of microbial auxin-like compounds in soil is often linked directly to substrate availability (Arshad and Frankenberger 1990; Lynch 1985). L-Tryptophan (L-TRP) has been reported to serve as an active physiological precursor for the microbial formation of IAA in soil (Purushothaman et al. 1973, 1974; Frankenberger and Brunner 1983; Frankenberger and Poth 1987a and b). The importance of understanding the conversion of L-TRP in soil has been demonstrated by Frankenberger and his co-workers who have reported that the addition of L-TRP as a soil drench to developing plant seedlings may result in increased plant yield (Frankenberger et al. 1990; Frankenberger and Arshad 1991a and b).

The pathway of IAA formation in soils has not been conclusively demonstrated. Previous work has suggested the presence of several pathways of IAA formation in soil and pure cultures. Frankenberger and Poth (1988) isolated a rhizosphere bacterium from Festuca octoflora that produced an aminotransferase that converted L-TRP into indole-3-pyruvic acid (IPyA). IPyA is further oxidized into indole-3-acetaldehyde (IAAID) and then converted into IAA. A second identified pathway involves the transformation of L-TRP into indole-3-acetamide (IAM) by a monooxygenase reaction and then conversion to IAAID by a hydrolyase with subsequent oxidation into IAA (Frankenberger and Brunner 1983). This pathway is the route of IAA formation by the phytopathogenic bacteria, Agrobacterium tumefaciens and Pseudomonas syringae pv. savastanoi, which are responsible for crown gall disease in plants (Magie et al. 1963). In addition to soil microorganisms, Chalvignac and Mayaudon (1971) extracted an extracellular enzyme complex from soil that converted L-TRP into IAM and IAA.

A third pathway utilized by soil microorganisms involves the conversion of L-TRP to tryptamine (TAM) by a TRP decarboxylase which is then converted to IAAID by a monoamine oxidase reaction (Hartmann et al. 1983). Al-

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though TAM is commonly found in plant tissues, its importance as a microbial intermediate of IAA formation is not known. It is likely that in some soils, different pathways may be utilized in the conversion of L-TRP to IAA. Frankenberg and Bruner (1983) found evidence supporting the first two previously described pathways of L-TRP conversion to IAA occurring in a Tollhouse soil. Martens and Frankenberg (1991) also reported that a soil-derived *Pseudomonas* sp. produced IAA, IAM, and IPyA when incubated in an L-TRP-enriched medium.

Although L-TRP is believed to be the primary precursor of IAA in plants and microorganisms, the stability of applied L-TRP and the derived intermediates of auxin transformations in soil are not well understood. Since the production of auxins is regulated by the availability of L-TRP, factors such as adsorption of L-TRP or the auxin intermediates with soil constituents will significantly influence the supply of exogenous sources of auxins available for plant uptake (Müller et al. 1989).

The objectives of this study were to identify auxin intermediates produced during L-TRP metabolism in various California soils and to determine their stability based upon calculated half-life (t½) and soil adsorption (Kd values) data which would influence the availability of these auxins for plant assimilation and use.

**MATERIALS AND METHODS**

**Reagents**

The auxins were obtained from Sigma Chemical Co. (St. Louis, MO) except for 3-indoleacetyl-aspartic acid and 3-indoleacetyl-glycine which were obtained from Research Organics (Cleveland, OH). Labeled TRP [L-(3′-14C)tryptophan] was obtained from Amersham Corporation (Arlington Heights, IL).

**Procedure**

Surface samples of five California soils (0–25 cm) were selected to obtain a diverse range in chemical and physical properties (Table 1) and maintained in a moist condition (~33 kPa). The soil characterization methods are described by Martens and Frankenberg (1991). The production of soil auxins upon addition of L-TRP or auxin intermediates to sterile and non-sterile soils was monitored as follows: L-TRP or an auxin derivative (560 μg) in 1 ml H2O was added to 2.5 g of soil in a 50-ml Erlenmeyer flask and incubated at 30°C for various times. Stock solutions of the auxin derivatives were made by dissolving the compound in 45% methanol, and an aliquot (110 μl) was added to 0.89 μl of H2O and then applied to the soil sample. Because of the insolubility of IPyA in water, this compound was added directly to the soil, and the soil moisture was adjusted with 1 ml of water; or 110 μl of IPyA (560 μg) in 100% methanol was added to 0.89 μl of water and then added to the soil. The L-TRP remaining after incubation and the auxin derivatives were extracted with 4 ml 0.1 M KH2PO4 (pH 7.0) and shaken on a rotary shaker (200 rev min⁻¹; 4°C; 10 min), and an aliquot was filtered through a 0.22 μm Millipore GS filter (Bedford, MA).

In place of liquid-liquid partitioning of the soil auxins with ethyl acetate, an on-line HPLC solid phase extraction system was employed as described by Martens and Frankenberg (1991). Briefly this involves adding a calibrated aliquot (5–40 μl) of the filtered soil extract to 0.4 ml of water and injection onto a 5-μm O.D.S. guard column (30 × 4.6 mm). Rinse with water and mobile phase removed ionic interferences, and the auxins were eluted with the mobile phase onto a separator column (R-Sil C18) for subsequent UV detection (280 nm). The auxins

<table>
<thead>
<tr>
<th>Soil</th>
<th>pH</th>
<th>Organic C</th>
<th>Total N</th>
<th>Clay</th>
<th>Sand</th>
<th>CEC a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheephead</td>
<td>6.87</td>
<td>7.9</td>
<td>2.0</td>
<td>260</td>
<td>560</td>
<td>13.9</td>
</tr>
<tr>
<td>Altamont</td>
<td>6.45</td>
<td>12.3</td>
<td>2.6</td>
<td>460</td>
<td>210</td>
<td>26.8</td>
</tr>
<tr>
<td>Domino</td>
<td>8.55</td>
<td>7.4</td>
<td>1.1</td>
<td>290</td>
<td>430</td>
<td>16.8</td>
</tr>
<tr>
<td>Redding</td>
<td>6.56</td>
<td>2.0</td>
<td>1.2</td>
<td>640</td>
<td>250</td>
<td>25.4</td>
</tr>
<tr>
<td>Hesperia</td>
<td>7.22</td>
<td>8.6</td>
<td>2.9</td>
<td>180</td>
<td>740</td>
<td>6.6</td>
</tr>
</tbody>
</table>

* CEC, cation exchange capacity (cm+ kg⁻¹ soil).
were identified by co-chromatography and UV spectral confirmation with authentic standards. Under sterile conditions, the soils were steam sterilized (121°C; 0.104 MPa, 2 h), and the L-TRP solutions were filter-sterilized (0.22 μm filter).

The conversion of [3-14C]-L-TRP (specific activity 53.5 mCi mM⁻¹) into soil auxins was determined by treating 2.5 g of soil with 500 μg L-TRP plus 1.85 kBq of [3-14C]-L-TRP. The treated soil sample was incubated for 48 h at 30°C. Labeled auxins were separated by HPLC as described above, and 0.25-ml fractions were collected with an ISCO Retriever II fraction collector (Lincoln, NE) in 4.5-ml scintillation cocktail (Complete Counting Cocktail, Research Products, Mt. Prospect, IL). Radioactivity in each of the fractions was determined on a Beckman Model 5000 TD liquid scintillation counter (Beckman Instruments, Inc., Fullerton, CA).

Adsorption or partition isotherms of auxins were constructed for five soils. The auxins were applied in 1 ml of water at 5, 15, 25, 45, and 60 μg g⁻¹ soil in 50 ml Erlenmeyer flasks, allowed to equilibrate for 10 min, and then equilibrated with the addition of 4 ml of phosphate extraction solution (0.1 M KH₂PO₄, pH 7.0). The flask was shaken on a rotary shaker as previously described (10 min). Longer equilibration times were not used to limit microbial degradation of the auxins in soil. An aliquot was filtered through a 0.22-μm Millipore GS filter, and the auxins remaining in the soil solution were analyzed by the IS-HPLC method described. The quantities sorbed by the soil were determined by an indirect sorption method with the difference between the amounts added and that in soil solution assumed to be the amount sorbed.

Soil respiration (carbon dioxide evolution) upon addition of L-TRP or auxin derivatives (0 or 2500 μg) was monitored by incubating 10-g soil samples with 1 ml H₂O for 0, 1, 2, or 5 days at 30°C in a 125-ml Erlenmeyer screw-cap flask equipped with a Mininert gas-sampling valve (Dynatech, Baton Route, LA). A 1-ml headspace sample was separated on a Porapak Q column (Alltech Assoc., Inc., Deerfield, IL). The constituent peaks were detected by thermal conductivity on a gas chromatograph (Varian Associates, Inc., Model 3700) with a He flow rate of 30 ml min⁻¹, a column temperature of 70°C, an injector temperature of 70°C, and a detector temperature of 110°C. Constituent peaks (CO₂) were confirmed through use of authentic external standards.

Correlation coefficients were determined in accordance with the SAS procedure (SAS Institute, Inc. 1985).

RESULTS AND DISCUSSION

The necessity for liquid-liquid partitioning with ethyl acetate to extract and purify the auxins produced in soil and the complications involved with this extraction procedure have limited research investigating the pathways and soil factors influencing microbial formation of IAA from L-TRP. To eliminate the need for liquid-liquid partitioning, Martens and Frankenberger (1991) developed an on-line, solid phase partitioning IS-HPLC method for the determination of the substrate (L-TRP), acidic, neutral, and basic auxins, and auxin conjugates in soil extracts and bacteria broths. The potential of this on-line extraction methodology for purification of standard auxin derivatives and the substrate, L-TRP, is shown in Fig. 1.

Soil bacteria have been isolated that produce IAA in L-TRP amended minimal media (Martens and Frankenberger 1991; Müller et al. 1989; Frankenberger and Poth 1987b; Ernst et al. 1987; Priekyl et al. 1985; Hartmann et al. 1983). In addition, a soil enzyme complex has been extracted from soil which converts L-TRP to IAA (Chalvignac and Mayandon 1971). To determine if this transformation is a biotic reaction, a steam-sterilized soil (Hesperia soil) was monitored for auxin formation. Although IAA was not detected, low levels of 5-hydroxyindole-3-acetic acid (5-OH-IAA) and 5-hydroxytryptophan (5-OH-TRP) were found upon the amendment of L-TRP, suggesting a nonbiological hydroxylation reaction of L-TRP occurring in soil (Fig. 2).

The chemical and physical properties of the five soils used in this study are shown in Table 1. The low molar phosphate extraction solution (0.1 M) utilized in this investigation accounts only for auxin products released into the soil environment by the soil microbiota and not for the intracellular intermediates of L-TRP metabolism. When L-TRP was added to soils at a rate of 80, 160, 320, 640, and 1280 μg L-TRP g⁻¹ soil, the two lowest rates resulted in rapid metabolism of the applied L-TRP and very low levels of IAA production (<3 μg IAA g⁻¹ soil) (Table 2). Higher levels of L-TRP addition resulted in
a greater rate of IAA production in as little as 1 day of incubation (Table 2). The formation of IAA in soil is highly dependent on the availability of L-TRP for the soil microbiota (Arshad and Frankenberger 1990; Lynch 1985). Factors such as adsorption (partitioning of L-TRP) and competing metabolic pathways for L-TRP will limit the availability of this substrate for IAA production. The formation of IAA from L-TRP (average of five soils) followed first order kinetics ($R^2 = 0.99$).

The pathway of IAA formation and the importance of auxin intermediates in soil has not been conclusively established. To establish which auxin intermediates are present in soils, $3^{'-14}$C-L-TRP ($1.85 \text{ kBq}$) was incubated with $200 \mu\text{g L-TRP}$ g$^{-1}$ soil. The extracts were separated by HPLC, fractionated and the disintegrations per minute (dpm) in the collected fractions were compared with resulting UV chromatograms. The peaks of activity aligned with the retention times for 5-OH-IAA, 5-OH-TRP, 5-OH-TAM, IAM, ILA, TOL, IAId and IAA. Ernst et al. (1987) reported that pure cultures of *Rhizobium phaseoli* synthesized labeled IAA, TOL, and indole-3-methanol when $^3$H-, $^{14}$C- and $^3$H-labeled L-TRP was used as a substrate. The detection of elevated levels of 5-OH indole compounds indicates the presence of a tryptophan-5-hydroxylase in soil (Joseph 1989). This pathway is important for the synthesis of the biogenic amine, serotonin (5-OH-TAM) in mammals, but its importance in the metabolism of L-TRP in soil is not known.

The influence of auxins on plant growth and development may be affected by the availability of these applied auxins in soil. The adsorption of nonionic organic compounds by soil from aqueous systems is controlled mainly by the organic matter content of the soil (Chiu 1989). In previous work, we have noted that the application of L-TRP to a sterilized standard U.C. mix (33% sand; 33% peat; 33% soil) did not result in increased plant growth or yield promotion. The high percentage of peat in this mixture may have partitioned much of the L-TRP or auxin derivatives out of the soil solution, making it unavailable for plant uptake. The extent of auxin partitioning from the soil solution was measured by use of adsorption-desorption isotherms of five soils for six auxin com-
STABILITY OF MICROBIAL AUXINS IN SOIL

TABLE 2
IAA production in soil upon L-TRP addition

<table>
<thead>
<tr>
<th>L-TRP addition</th>
<th>Soil</th>
<th>µg IAA g⁻¹ soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>µg g⁻¹ soil</td>
<td>Sheephead</td>
<td>Altamont</td>
</tr>
<tr>
<td>0</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>80</td>
<td>ND</td>
<td>1.8</td>
</tr>
<tr>
<td>160</td>
<td>2.9</td>
<td>5.6</td>
</tr>
<tr>
<td>320</td>
<td>12.2</td>
<td>6.2</td>
</tr>
<tr>
<td>640</td>
<td>21.0</td>
<td>24.3</td>
</tr>
<tr>
<td>1280</td>
<td>72.0</td>
<td>100.8</td>
</tr>
</tbody>
</table>

*Soil samples (2.5 g) were treated with the specified level of L-TRP and incubated at 30°C for 5 days.
ND: not detected.

pounds. The adsorption-desorption of many organic compounds applied at low concentrations is frequently represented by a linear adsorption isotherm. The results showed a linear relationship \( R^2 = 0.98 \) between the equilibrium concentrations of the indole derivatives applied and the amounts not recovered. The \( K_d \) values were calculated from a modified Freundlich equation of \( S = K_d C \), where \( S = \text{amount sorbed} \ (\mu g \ g^{-1} \ \text{soil}) \) and \( C = \text{equilibrium concentration} \ (\mu g \ mL^{-1}) \). \( K_w \) values were calculated as the ratio of the calculated \( K_d \) values to the organic C content. The resulting slopes or \( K_d \) and the \( K_w \) values for partitioning of the auxin derivatives are given in Table 3. The measured \( K_d \) values suggest limited soil adsorption and are comparable to \( K_d \) values reported for ionic carboxylic herbicides such as chloramben and picloram, with little to no adsorption to soil colloids (Hamaker and Tompson 1972). The measured partitioning or \( K_d \) values of the auxins, 5-OH-IAA, IAM, IAA, IIA, TOL, and IAID were not significantly correlated with the organic C content of the soils used in this study. This may be due in part to the short equilibration times used in establishing the adsorption isotherms which may not have allowed all of the soils to approach the same level of equilibrium with the auxins. However, longer equilibration times would have introduced errors due to auxin transformations by the soil microbiota. Also, the lack of significant correlation with the organic C content of these soils may be due to a limited range of organic C content in the soils used or due to the ionic nature of the auxin derivatives at the measured soil pH values (Table 1) limiting partition uptake with the soil organic C. The low partitioning coefficients suggest that the auxin derivatives are not adsorbed to a great extent by soil organic matter.

Carbon dioxide evolution studies indicated that most (avg. 80%) of the applied L-TRP-C

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TABLE 3
The distribution coefficient, \( K_d \), and sorption coefficient, \( K_{OC} \), of five California soils treated with auxin derivatives

<table>
<thead>
<tr>
<th>Auxin</th>
<th>Sheephead</th>
<th>Altamont</th>
<th>Redding</th>
<th>Hesperia</th>
</tr>
</thead>
<tbody>
<tr>
<td>5-OH-indole-3-acetic acid</td>
<td>0.20</td>
<td>0.40</td>
<td>0.35</td>
<td>0.35</td>
</tr>
<tr>
<td>Indole-3-acetamide</td>
<td>0.14</td>
<td>0.25</td>
<td>0.50</td>
<td>0.50</td>
</tr>
<tr>
<td>Indole-3-lactic acid</td>
<td>0.20</td>
<td>0.33</td>
<td>0.50</td>
<td>0.50</td>
</tr>
<tr>
<td>Indole-3-acetic acid</td>
<td>0.28</td>
<td>0.36</td>
<td>0.48</td>
<td>0.48</td>
</tr>
<tr>
<td>Indole-3-ethanol</td>
<td>0.27</td>
<td>0.34</td>
<td>0.30</td>
<td>0.30</td>
</tr>
<tr>
<td>Indole-3-aldehyde</td>
<td>0.35</td>
<td>0.60</td>
<td>0.63</td>
<td>0.63</td>
</tr>
</tbody>
</table>

* 2.5 g of field-moist soil were treated with 1 ml water containing 5-60 µg of auxin derivative g⁻¹ soil, allowed to react for 10 min and then equilibrated with 4 ml 0.1 M KH₂PO₄ (pH 7.0) for 10 min, filtered and analyzed by IS-HPLC.
was mineralized into CO$_2$-C after 5 days of incubation (Table 4). Mineralization of the auxin derivatives in soil resulted in a more rapid breakdown in the Altamount soil when compared with the other four soils. Considerably less CO$_2$-C was evolved upon mineralization of TOL (avg. 29%), IAA (avg. 40%), IPyA (avg. 45%), and IAM (avg. 43%) after 5 days of incubation (Table 4). IS-HPLC analysis indicated that the L-TRP and auxin derivatives not recovered in soils were accounted for by CO$_2$-C analyzed in the flask headspace.

The persistence of auxins produced in soil upon L-TRP applications will no doubt influence the extent to which auxin derivatives could possibly affect plant growth and development. Auxins and L-TRP recovery studies were conducted from 0 to 7 days. Decomposition of L-TRP and auxin derivatives in soil followed first-order kinetics. The measured half-lives ranged from an average of 26 h for L-TRP to over 127 h for IAM with the five soils tested (Table 5). IPyA and IAAID were also evaluated for their persistence, but neither was extracted from soils. IPyA and IAAID have been reported to be very unstable indole compounds (Frankenberger and Poth 1987b). Frankenberger et al. (1990) reported that IPyA was less effective than IAA, IAM, and ILA additions in stimulating the growth of Raphanus sativus (radish). The diminished growth promotion effectiveness of IPyA may be related to the instability of this compound. IAM addition was found to be the most effective among the auxin derivatives tested in growth promotion of radish, and the effectiveness of IAM may be related to its stability in soil.

The production of IAA from the auxin intermediates, ILA and TOL, resulted in an average (five soils) of 1% and <1% conversion to IAA, respectively, after 5 days of incubation at 30°C compared with a 5% rate for L-TRP (Figs. 3a and b and 4a). Figure 3b also shows the detection of L-TRP upon addition of ILA to soil suggesting a reversible reaction of the IPyA pathway. However, the addition of the proposed direct precursor, IAAID, resulted in little or no IAA formation in the five soils tested (Fig. 4b). The addition of IAM or TAM resulted in larger percentages of conversion to IAA (20 and 18%, respectively) (Figs. 4c and 5). The longer stability and relatively high percentage of substrate conversion into IAA suggests that IAM and TAM may hold promise as a soil additive in affecting plant growth and yield.

In summary, the formation of IAA from L-TRP was a biological transformation and dependent on the level of substrate available for microbial conversion. L-TRP and the interme-

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**TABLE 4**

Recovery of CO$_2$-C from five soils after treatment with 225 µg of L-TRP or auxin derivative g$^{-1}$ soil after 5 days of incubation

<table>
<thead>
<tr>
<th>Soil</th>
<th>L-TRP</th>
<th>TOL</th>
<th>IAA</th>
<th>IPyA</th>
<th>IAM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheephead</td>
<td>80</td>
<td>33</td>
<td>51</td>
<td>73</td>
<td>40</td>
</tr>
<tr>
<td>Altamount</td>
<td>86</td>
<td>83</td>
<td>84</td>
<td>85</td>
<td>86</td>
</tr>
<tr>
<td>Domino</td>
<td>86</td>
<td>&lt;1</td>
<td>10</td>
<td>13</td>
<td>18</td>
</tr>
<tr>
<td>Redding</td>
<td>78</td>
<td>8</td>
<td>21</td>
<td>18</td>
<td>26</td>
</tr>
<tr>
<td>Hesperia</td>
<td>72</td>
<td>20</td>
<td>35</td>
<td>37</td>
<td>43</td>
</tr>
<tr>
<td>Average</td>
<td>80</td>
<td>29</td>
<td>40</td>
<td>45</td>
<td>43</td>
</tr>
</tbody>
</table>

* Values are corrected for CO$_2$-C evolved from the control soil (no compound added).

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**TABLE 5**

Half-life ($t_{1/2}$) of L-TRP, IAA, and intermediates of IAA formation in soil

<table>
<thead>
<tr>
<th>Compound</th>
<th>Soil</th>
<th>Altamount</th>
<th>Domino</th>
<th>Redding</th>
<th>Sheephead</th>
<th>Hesperia</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tryptophan</td>
<td>23.7</td>
<td>24.9</td>
<td>28.7</td>
<td>22.8</td>
<td>24.8</td>
<td>25.0</td>
<td></td>
</tr>
<tr>
<td>Indole-3-acetic acid</td>
<td>34.4</td>
<td>58.7</td>
<td>45.6</td>
<td>30.7</td>
<td>19.5</td>
<td>37.8</td>
<td></td>
</tr>
<tr>
<td>Indole-3-acetamide</td>
<td>47.7</td>
<td>292.4</td>
<td>121.8</td>
<td>114.6</td>
<td>60.9</td>
<td>127.5</td>
<td></td>
</tr>
<tr>
<td>Indole-3-ethanol</td>
<td>51.6</td>
<td>147.6</td>
<td>135.8</td>
<td>53.6</td>
<td>39.2</td>
<td>85.6</td>
<td></td>
</tr>
<tr>
<td>Indole-3-lactic acid</td>
<td>50.9</td>
<td>59.0</td>
<td>65.7</td>
<td>54.0</td>
<td>36.1</td>
<td>53.1</td>
<td></td>
</tr>
<tr>
<td>Tryptamine</td>
<td>40.8</td>
<td>230.6</td>
<td>110.4</td>
<td>105.7</td>
<td>57.3</td>
<td>109.0</td>
<td></td>
</tr>
</tbody>
</table>

* Soil samples (2.5 g) were treated with 225 µg compound g$^{-1}$ soil and incubated at 30°C for 0, 1, 3, 5 and 7 days.
FIG. 3. IS-HPLC chromatogram of an extract of a) an Hesperia soil incubated for 2 days after treatment with L-TRP and b) a Domino soil incubated for 5 days after treatment with ILA. 1 = 5-OH-IAA; 4 = 5-OH-TRP; 5 = IAM; 6 = ILA; 7 = 5-OH-TAM; 8 = IAA; 13 = IPA (internal standard); 15 = TRP.

FIG. 4. IS-HPLC chromatogram of an extract of a) an Altamont soil incubated for 5 days after treatment with TOL, b) an Hesperia soil incubated for 5 days after treatment with IAAID; and c) a Domino soil incubated for 5 days after treatment with IAM. 1 = 5-OH-IAA; 4 = 5-OH-TRP; 5 = IAM; 6 = ILA; 7 = 5-OH-TAM; 8 = IAA; 10 = TOL; 11 = IAAID; 13 = IPA (internal standard).

FIG. 5. IS-HPLC chromatogram of an extract of a Redding soil incubated for 5 days after addition of TAM. 2 = IAA-Asp; 3 = IAA-Gln; 5 = IAM; 6 = ILA; 8 = IAA; 9 = IAAID; 13 = IPA (internal standard); 19 = TAM.
diates of L-TRP metabolism to IAA were not readily adsorbed to the soil organic matter. IAM and TAM show promise as stable auxin compounds for promotion of plant growth and yield.

**ABBREVIATIONS USED**

- **IAA**: indole-3-acetic acid
- **IS-HPLC**: ion suppression reverse phase high performance liquid chromatography
- **TAM**: tryptamine
- **IAAID**: indole-3-acetaldehyde
- **IAM**: indole-3-acetamide
- **IAN**: indole-3-acetonitrile
- **IAcry**: 3-β-indoleacyclic acid
- **IAID**: indole-3-aldehyde
- **IBA**: indole-3-butyric acid
- **TOL**: indole-3-ethanol
- **ILP**: indole-3-lactic acid
- **IM**: indole-3-methanol
- **IPA**: indole-3-propionic acid
- **IPyA**: indole-3-pyrolic acid
- **IAA-Asp**: 3-indoleacetyl-aspartic acid
- **IAA-Gln**: 3-indoleacetyl-glutamine
- **5-OH-IAA**: 5-hydroxyindole-3-acetic acid
- **5-OH-TAM**: 5-hydroxytryptamine
- **5-OH-TRP**: 5-hydroxtryptophan
- **TRP**: tryptophan

**REFERENCES**


