
Letter to the Editor

BACTERIAL DEGRADATION OF JUGLONE Evidence Against Allelopathy?

Recently, Schmidt (1988) isolated from the soil under *Juglans nigra* L. a bacterium capable of degrading juglone, the allelotoxin reputed to inhibit neighboring vegetation (Davis, 1928; Rietveld, 1983; Rietveld et al., 1983). Schmidt's report is noteworthy because it supports the previously hypothesized degradation of juglone by microorganisms (Fisher, 1978; Rietveld, 1983; Rietveld et al., 1983). However, Schmidt's (1988, p. 1561) conclusion that "Rapid degradation of juglone and other suspected allelochemicals by soil bacteria make it unlikely that these compounds are important mediators of plant-plant interactions under natural conditions" appears to us to be premature. In fact, the author might have argued equally convincingly that such specialized strains of soil bacteria confirm the frequent, if not continuous, presence of putative phytotoxins in the soil, and therein lend support to the allelopathic hypothesis. Neither contention is free of ambiguity.

The phytotoxicity of allelochemicals in soil solution will depend on input and output rates as well as the effective concentration (Winter, 1961; Blum and Shafer, 1988). Schmidt's *Pseudomonas* J1 provides one output sink for juglone. Juglone may be removed from the soil in numerous other ways, including, as Schmidt notes, soil physical and chemical processes. However, just as plants compete with microorganisms for nutrients (Pastor et al., 1984), the roots of plants inhibited by phytotoxins are potential competitors with microorganisms for the available phytotoxins (Winter, 1961; Hoffman and Lavy, 1978; Weidenhamer et al., 1987, 1989). The outcome of this competition may determine whether or not allelopathic effects are manifested. Therefore, bacterial affinities for juglone must be evaluated relative to target plant affinities and soil abiotic processes.

Output rates themselves must be weighed against input rates of juglone into the soil solution (Winter, 1961). Influx may be a function of the amount of plant biomass (Rietveld et al., 1983), root exudation, litter decay, and precipitation throughfall, although in the case of juglone little is known in this regard.

The actual available concentration of juglone will reflect the various input

and output rates. Toxicity is likely to be a function of both concentration and flux, where the former measures static availability and the latter measures dynamic or potential availability. Static availability is the existing concentration in soil solution, while dynamic availability is the renewal rate (input or production measured under controlled output). In order to determine the dynamic availability of compounds in relation to processes affecting them (Vitousek et al., 1982), chemical ecologists may resort to controlled incubation techniques, analogous to those employed to estimate available soil nutrients (Keeney, 1980; Powers, 1980). Until such studies are carried out, it would be premature to disavow the involvement of juglone in allelopathic interactions.

In fact, evidence already exists contrary to Schmidt's conclusion that juglone concentrations in soil are maintained below phytotoxic levels by *Pseudomonas* J1 and other bacteria. Ponder and Tadros (1985) found concentrations of juglone under black walnuts to be 3.6–4.0 $\mu\text{g/g}$ in surface soils—potentially sufficient to produce a soil solution of 10^{-4} M, a level known to cause toxic effects in the laboratory (Funk et al., 1979; Rietveld, 1983) and well above those mineralized by *Pseudomonas* J1. In addition, recent experiments with tomatoes grown in unsterilized black walnut soil demonstrated density-dependent effects on growth, characteristic of the presence of toxic substances in soil (Weidenhamer et al., 1989). If microbes are "literally waiting to consume compounds such as juglone" (Schmidt, p. 1569), they appear not to be as effective at scavenging juglone in the field soils as Schmidt's lab data would suggest. Furthermore, Schmidt isolated *Pseudomonas* J1 from only three of five soil samples. These microorganisms may be distributed patchily or respond facultatively to juglone enrichment only under certain conditions. For example, ferulic acid, when applied experimentally to soils, was readily degraded by microorganisms under nutrient-rich conditions but accumulated temporarily under nutrient limitation (Blum and Shafer, 1989).

Finally, we note that microorganisms can toxify as well as detoxify secondary compounds. In soil, transformation of allelochemicals seems to be common, but the outcome is not necessarily detoxification (Einhellig, 1986; Liebl and Worsham, 1983; Kaminsky 1981).

Much remains to be learned about the fate of plant allelochemicals in the environment. We heartily endorse Schmidt's call for tests of allelochemical effects in unsterilized soils under natural field conditions, especially combined with the more traditional studies in sterile soil or artificial media, and his admonition to question allelopathic claims based only on the latter. However, let us not discard the allelopathic hypothesis as perfunctorily as it may have been accepted (Harper, 1975, 1977; Williamson, 1990).

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G. Bruce Williamson
Department of Botany
Louisiana State University
Baton Rouge, Louisiana 70803

Jeffrey D. Weidenhamer
Department of Chemistry
Ashland University
Ashland, Ohio 44805

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