JUGLONE REDUCES GROWTH, NITROGENASE ACTIVITY, AND ROOT RESPIRATION OF ACTINORHIZAL BLACK ALDER SEEDLINGS

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Abstract—European black alder trees [Alnus glutinosa (L.) Gaertn.] fix nitrogen with nodular symbionts and are interplanted with valuable black walnut trees (Juglans nigra L.) to increase soil nitrogen fertility. However, on some soils interplanted alder can be killed by black walnut’s allelochemical juglone. In order to better understand the effects of juglone directly on the growth, nitrogen fixation, and root respiration of black alder, we grew nodulated alders hydroponically in a nitrogen-free nutrient solution at juglone levels of $2 \times 10^{-6}$, $2 \times 10^{-5}$, and 0 molar (M). Results indicate that nitrogenase activity (acetylene reduction) of alders growing in $2 \times 10^{-5}$ M juglone was reduced relative to alders without added juglone after one day, and in $2 \times 10^{-6}$ M juglone after five days. Root respiration (CO$_2$ evolution) and the relative increase of plant fresh weight were reduced in the $2 \times 10^{-5}$ M juglone treatment. In a related experiment, black alder germinants were grown in Flanagan silt loam soil dosed with $10^{-3}$, $10^{-4}$, and 0 M juglone. The inhibitory effects of $10^{-3}$ M juglone on radicle elongation ceased 22–37 days after juglone treatments were started, suggesting that this soil can readily detoxify juglone.

Key Words—Acetylene reduction, allelopathy, Alnus glutinosa, black walnut, Frankia, Juglans nigra, juglone, nitrogen fixation, root respiration.

INTRODUCTION

Black walnut (Juglans nigra L.) is able to inhibit the growth of many plant species (Cook, 1921; Strong, 1944; Gabriel, 1975) through its allelochemical juglone (5-hydroxy-1,4-naphthoquinone). In living tissue this compound is in
a reduced, nontoxic form called hydrojuglone (Gries, 1943; Lee and Campbell, 1969), but when plant tissue is incorporated into the soil, hydrojuglone is oxidized and toxic juglone is released (Rietveld, 1983).

Plant species show varying responses to the presence of juglone (Funk et al., 1979; Rietveld, 1983). The effect of juglone on black alder trees \textit{[Alnus glutinosa L. (Gaertn.)]} is of particular interest because of its use as a nitrogen-fixing intercrop with commercially valuable black walnut. Of 16 herbaceous and woody species tested for juglone sensitivity, black alder was one of five most inhibited in seedling shoot elongation and dry weight accumulation, showing depressed growth at a concentration as low as $10^{-6}$ M juglone (Rietveld, 1983). Rietveld et al. (1983) also reported the sudden decline and death of black alder as a result of juglone toxicity in four mixed plantings with black walnut 8–13 years after planting.

Juglone also affects the nitrogen-fixing endophyte of black alder. A concentration of $10^{-4}$ M juglone inhibited in vitro growth of the symbiotic actinomycete \textit{Frankia} (Dawson et al., 1981; Dawson and Seymour, 1983; Vogel and Dawson, 1985, 1986). Nodulation of black alder by \textit{Frankia} was also significantly depressed by the addition of $10^{-4}$ M juglone to soil (Vogel and Dawson, 1985).

One mechanism by which juglone is thought to affect plant growth is through a reduction in respiration. Perry (1967) reported the inhibition of oxygen uptake by leaf disks of tomato \textit{(Lycopersicon esculentum Mill.)} and bean \textit{(Phaseolus vulgaris L.)} at juglone concentrations greater than $10^{-5}$ M. Similarly, juglone concentrations as low as $5 \times 10^{-5}$ M reduced O$_2$ uptake in excised corn roots (Köeppe, 1972).

Edaphic conditions may influence the toxicity of juglone. On well-drained soils, red and white pine \textit{(Pinus resinosa Ait. and P. strobus L.)} did not exhibit any adverse allelopathic effects when interplanted with walnut, but on imperfectly and poorly drained soils, pines growing with walnut showed poorer survival and growth than pines without adjacent walnut (Fisher, 1978). In the same study, a bioassay of “wet” and “dry” soils dosed with juglone showed that inhibition of radicle extension in red pine and detection of juglone (using thin-layer chromatography) occurred for a substantially longer period of time in the “wet” soil. Fisher considered this evidence that microbial degradation of juglone is determined by the moisture regime and, hence, aeration of the soil. He thought it less likely that differences in soil moisture had affected the sorption of juglone by the soil. Microorganisms that break down aromatic and phenolic substances similar to juglone are aerobic heterotrophs (M. Alexander, 1977). Schmidt (1988) isolated a bacterium \textit{(Pseudomonas J1)} from soil beneath black walnut trees that could grow rapidly using juglone as its sole source of carbon and energy.

As well as possibly limiting microbial degradation of juglone, a wet soil will reduce the O$_2$ available for root respiration. What effect the presence of