THE IMPORTANCE OF BELOW GROUND INTERACTIONS FOR HARDWOOD GROWTH [1]

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Abstract--Interfering plants can seriously impede regeneration efforts under some site and forest conditions. Nutrient release, nutrient accumulation, and microbial activity may, however, be enhanced depending on the plants, their associated underground activity, and the microorganisms involved. Most of the mechanisms by which the microbiota affects higher plants are yet to be established.

INTRODUCTION

Studies of competition between trees and unwanted vegetation and among trees themselves usually involve above ground factors such as light, space, and carbon dioxide and below ground factors such as water, nutrient elements, and oxygen. Interactions between microorganisms, their substrate, mineral sources, and plant-produced chemicals are rarely considered.

Soil character, including "available" soil fertility, results from interactions between plant constituents and soil microbiota. The nature and results of these interactions are influenced primarily by the availability of nutrient elements to plants and of energy to microorganisms. The supply of these resources, in turn, influences plant productivity.

Most of the important below ground activity takes place on and around the root system (rhizosphere activity). The rhizosphere is not a uniform, well-defined region but a zone with a microbial gradient extending from the root surface to soil a centimeter or two surrounding the root. Many compounds are both taken up and released in this region.

The purpose of this paper is to review information on competition associated with nutrient element availability and allelopathy, in soils beneath hardwoods and to suggest areas where more research is needed. Data and discussion in this review center on soil activity within the tree-root influence but are not limited to the rhizosphere.

Nutrient Availability

The growth benefits afforded non-nitrogen-fixing plants when grown in mixture with nitrogen-fixing plants are well documented (Ashby and Baker 1968, Funk *et al*. 1979, Haines and DeBell 1979). Growth enhancement is attributed to reduced grassy competition and cooler temperatures (Dawson and Funk 1981, Funk *et al*. 1979), but mostly to biologically fixed nitrogen and the increase of nitrate nitrogen (NO_3-N) in the soil (Ike and Stone 1958, Finn 1953, DeBell and Radwan 1979). In a 10-year-old mixed planting of black walnut (*Juglan nigra* L.) and autumn olive (*Elaeagnus umbellata* Thumb.), only NO_3-N of all measured soil nutrient elements increased (Ponder *et al*. 1980).

Nitrogen nutrition explains only part of the better growth of walnut planted in mixtures. In a study of plots that included European alder (*Alnus glutinosa* (L.) Gaertn.) mixed with walnut in addition to plots of autumn olive/walnut and walnut alone, soil samples were analyzed for available potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), zinc (Zn), and sodium (Na). The amount of Cu and Na did not differ between treatments, but the mean K and Ca concentrations did. Potassium was highest in soils from autumn olive/walnut plots and lowest in walnut alone plots. At the 60 cm soil depth 0.9 m from the walnut trees, autumn olive/walnut plots contained nearly twice as much K as European alder/walnut plots. Calcium was highest in autumn olive/walnut plots; it did not differ between European alder/walnut and walnut alone plots. Both Mg and Zn were highest in European alder/walnut plots. The mean concentration of Mg in autumn olive/walnut plots was intermediate between plots of European alder/walnut and walnut alone. Zinc concentrations were similar in autumn olive/walnut and walnut alone plots.

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Changes in nutrient concentrations within the soil of the various treatments cannot be readily explained but are believed to be associated with microorganisms in the rhizosphere and on the roots themselves. Particularly important are the mycorrhizae. For example, where ammonium nitrogen (NH_4^+-N) is the primary source of N, the mycorrhizae increase the competitive uptake by higher plants for NH_4^+-N (Raven et al. 1978). Mycorrhizae do this by converting NH_4^+-N to glutamine, which moves from the mycorrhizal fungi to the plant for uptake. The hydrogen ion (H+) produced by the assimilation of the NH_4^+-N is excreted by the fungus to obtain more NH_4^+-N in competition with other microorganisms. The excreted H+ may produce pH changes that may further affect nutrient availability.

Thus it may be concluded that part of the explanation for the modified growth of black walnut or other trees in mixtures compared with pure stands is to be found in the interactions between roots, other organic substrates, invertebrates, and microorganisms in the soil and litter. This in no way diminishes the importance of symbiotically fixed nitrogen in mixed culture.

The roots of some plants have adaptive mechanisms for taking up nutrients in short supply (Atwill 1986). Mulette et al. (1974) showed that eucalyptus (Eucalyptus gummifera (Gaertn.), Hochr.) seedlings, regardless of their mycorrhizal condition, could get phosphorus from highly insoluble iron and aluminum phosphates. Gardner et al. (1983) showed that roots of a lupin secrete acid citrate, which solubilizes iron phosphate. Yet to be defined are the mechanisms by which some trees can extract and accumulate large amounts of specific nutrient elements such as calcium in the oaks (Weaver and Jones 1987).

Nitrifying Bacteria

Many hardwoods produce phytotoxins (Kuiters and Sarink 1986). Most notorious among allelopathic chemicals is juglone, which is produced by black walnut and members of the walnut family. Juglone and most of the other phytotoxins of concern in regeneration are phenolic compounds. In cases where phytotoxins occur, nitrification may be inhibited (Atwill 1986). Rice (1964, 1965) found that many of the plants in old-field succession contained phenolic substances that were very inhibitory to nitrogen-fixing and nitrifying bacteria. Therefore, such substances may reduce nitrifying bacteria populations in walnut plantings.

Two kinds of bacteria of concern are Nitrosomonas and Nitrobacter. Soil samples were collected from the 0-8 cm soil layer 0.9 m from walnut trees. Data showed mean mid-November juglone level in a mixed planting to be highest in European alder/walnut and walnut alone plots and lowest in autumn olive/walnut plots (Ponder and Tadros 1985). With this information on juglone concentrations as a background, the most-probable-number technique was used to determine nitrifying bacteria counts. Counts were highest in European alder/walnut plots, followed by autumn olive/walnut, and walnut alone plots. Nitrate nitrogen was found to be highest in European alder/walnut plots, followed by autumn olive/walnut, and walnut alone plots. Because NO_3^--N levels, which are never static and may not represent mineralization of nitrogen, and juglone concentration were both highest in European alder plots, juglone was not inhibiting nitrification. But, why the higher counts of nitrifying bacteria in both types of mixed plots?

The dominant vegetation in walnut plots without alder or autumn olive was broomsedge (Andropogon virginicus L.). European alder/walnut plots were undergoing vegetational change due to the decline and death of European alder; autumn olive/walnut plots were developing a forest-like understory. Lodhi (1978) reported that the number of Nitrosomonas and Nitrobacter showed a direct relationship with amounts of nitrate nitrogen. Nitrosomonas and Nitrobacter increased by 18 and 34 times, respectively, after a forest clearcut in Connecticut (Smith et al. 1968). It appears that the differences in the amount of available substrate that can be utilized by the bacteria account for the differences in the number of bacteria between treatments. The vegetational change is probably responsible for the overall higher nitrifying bacteria counts in European alder/walnut plots.

Specific inhibition of nitrification in the field is not always observed. For example, Chandler (1985) found no inhibition of nitrification by phenolic or by leaf litter extracts in Malaysian forest soils. Robertson and Vitousek (1981) found no evidence in favor of the hypothesis that increasing levels of allelochemicals inhibit nitrification during either a primary or a secondary succession in the North Central and Northeastern United States.

The use of nitrification inhibitors that block the nitrification pathway is a way of affecting nitrifying bacteria. The chemical inhibitor suppresses the activity of the nitrifying bacteria, preventing the conversion of NH_4^+-N to NO_3^--N. Because NH_4^+-N is slowly leached and relatively immobile in the soil compared to NO_3^--N, preventing the conversion should increase the overall nitrogen utilization. However, because proportionately more NH_4^+-N than NO_3^--N may be available for uptake, plant growth response will likely depend on the plant's nitrogen preference.

The survival and growth of white ash (Fraxinus americana L.), white oak (Quercus alba L.), and black walnut seedlings were investigated using the nitrification inhibitor, N-serve, (2-chloro-6[trichloromethyl]pyridine) in an old field planting. Before planting, a fescue (Festuca arundinaceae Schreb.) sod had been

rototilled the previous fall and again in the spring. Plots were designated to receive or not to receive N-serve. N-serve was applied at a rate of 1.5 Kg/ha and raked into the upper 4-cm soil layer before 1-year-old seedlings were planted. N-serve was reapplied the following spring and mixed into the upper soil layer with a garden tiller. Weeds were controlled by hoeing the first year and by a combination of hoeing and one application of Roundup the second year.

Seedlings treated with N-serve survived much better than untreated seedlings for all three species, with improvements of 28, 15, and 10 percent, respectively, for ash, oak, and walnut. After 3 years of growth, however, only the white oak had greater height and diameter growth in N-serve treated plots. Nitrate nitrogen levels were lower in N-serve plots than in control plots, indicating that the inhibitor did affect the conversion of NH_4^+-N to NO_3^--N. Both ash and walnut grew better without N-serve. Although the preliminary results suggest that young oaks may grow better with NH_4^+-N rather than NO_3^--N (Auchmoody 1982), further research is needed before making conclusions on N preference for oak.

Allelopathy

Competition due to allelopathy has been demonstrated in several greenhouse studies (Gilmore 1980, Larson and Schwarz 1980, Patrick 1971). Allelopathy in forest stands has been much harder to prove because of the fewer controls over environmental conditions such as moisture, temperature, and competition (Rietveld *at al*. 1983, Rink and Van Sambeek 1985). The allelopathic effects of plants can sometimes be detected by their influence on the mineral uptake of their associates (Balke 1985). This was demonstrated in a study investigating the effects of three weeds commonly found in walnut plantings (Ponder 1986). Foliage litter of tall fescue, broomsedge, or blackberry (*Rubus allegheniensis* T. Porter) was either incorporated or not in plots with seeded black walnut. Of the three weed species tested, unincorporated and incorporated broomsedge litter significantly reduced total dry weight below that of the control seedlings. The total dry weight of seedlings with incorporated fescue was greatly reduced considerably whereas phosphorus content was not.

The mean absorption of N but not P by seedlings in soil with incorporated broomsedge litter was reduced considerably. Nitrogen, phosphorus, and potassium were also reduced in seedlings grown with incorporated fescue. In another experiment using the extracts of these weeds, both N and P absorption were reduced in seedlings grown with fescue extract, but only N was reduced in seedlings grown with broomsedge extract. We can, therefore, assume that these plant materials act in some way in the soil to reduce either the availability or the uptake of nutrient elements by the plant. Horsley (1986) was able to significantly increase the growth of black cherry (*Prunus serotina* Ehrh.) seedlings in an orchard soil previously dominated by grasses and forbs only when NO_3^--N, P, and Ca were applied repeatedly. From this he concluded that an inhibitory molecule may compete with a soil colloid to render nutrient elements unavailable for uptake.

Kolesnichenko and Aleikena (1976) reported that absorption of minerals from soil was lower in oak roots (*Quercus robur* L.) growing close to ash (*Fraxinus excelsior* L.) than in oak roots growing near other oak roots. In the laboratory, the uptake of minerals by oak roots was inhibited by chemical compounds from ash.

The inhibitory constituents of plant materials might be bound by the soil and used as carbon sources by soil microorganisms. We know in the case of some herbaceous weeds that removing the weeds significantly reduces the inhibitory effect. In a 10-year-old plantation in southern Illinois, elimination of a fescue sod understory by annual cultivation for 5 years produced trees that were 69 percent larger in diameter at age 15 than those in untreated areas. In a 17-year-old planting, Schlesinger and Van Sambeek (1986) found that eliminating fescue sod or establishing hairy vetch (*Vicia villosa* Roth.) among the walnut trees resulted in a 250-percent increase in diameter 3 years later. The response to cultivation seems to be more than just a response to nutrient element availability and organic matter added to the soil by incorporating fescue and broomsedge because such a response would not continue for 5 years. At least part of the response to eliminating the fescue sod seems to be a function of eliminating allelopathic plants.

In some instances allelochemicals appear to accumulate in the soil over a period of years so that even when the inhibitory plants are removed, seedlings on the site continued to grow poorly (Gabriel 1965). This is believed to be the condition in some orchard stands in the Northeastern United States (Horsley 1986). In well-aerated soils organic chemical residues are normally metabolized by indigenous soil microorganisms. Conditions such as imperfect soil drainage, high soil acidity, low soil organic matter content, and residual plant parts in the soil increase the time needed for the inhibitory effects to disappear (Rietveld *et al*. 1983).

Much less is known about possible allelopathic interference from herbaceous vegetation on the development of mycorrhizal fungi that colonize the roots of forest trees (Rice 1979). The number of mycorrhizal-infected root segments of black walnut seedlings grown in mixture with unincorporated litters of fescue, blackberry, or broomsedge was more than twice the number of infected root segments of seedlings grown with incorporated litter. Poor mycorrhizal colonization was reported for *Populus* spp. cuttings

planted on an old-field site in Iowa (Walker et al. 1982). The effects of plants within tree stands on mycorrhizal development have not been studied.

Root Competition

The extent of a tree's roots determines the region in which it may influence the roots of its neighbors. A root system may be restricted by such factors as shallow soils, fragipans, and moisture, in addition to competition from its neighbors. Very little has been done to substantiate and explain competition in forest stands in the soil root interface. Much of what we know has been adapted from various grasses and legumes either separate or in mixtures (Vallis 1978, Wit et al. 1965, Werner 1979).

Root restriction often causes more intensive permeation of the soil by the roots and consequently more complete utilization of the available soil. Tree species that are genetically capable of producing more root tips or more fibrous roots than other species have a site adaptative advantage, especially on shallow soils, over species that lack these characteristics. On deep soils, both shallow- and deep-rooting species may coexist whereby the deep-rooted species would be forced to use nutrients from deeper soil layers; this would not be the case in monoculture (Berendse 1982). Two species may have different competitive abilities in different parts of the soil, which may mean exposure to different microhabitats, nitrogen compounds, and element concentrations. Much more needs to be learned about the seasonality of root growth, competition-induced changes of the shoot-to-root ratio, and phenotypic responses of root activity.

CONCLUSION

To improve tree growth, we need to better understand the mechanisms that enable roots of some plants to compete better than others for growth substances. This information will provide a scientific basis for predicting changes in composition, growth, position of dominance, and response to silvicultural practice as trees mature. To obtain such information far more attention must be devoted to the biological, chemical, and physical processes that go on below ground, especially in the rooting zone.

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