PHYSIOLOGICAL AND GENOTYPIC RESPONSES OF CENTRAL HARDWOOD SPECIES TO ALLELOCHEMICALS, OTHER STRESSES, AND THEIR INTERACTIONS

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In response to increasing carbon dioxide levels, most general circulation models (GCMs) predict increasing temperatures and decreasing precipitation for the central hardwood region of the United States. Plants in this region will need to adapt to these changes as well as to other stress agents if they are to germinate, grow, and reproduce. For the last five years, our research program under the global change initiative has been designed to increase our understanding of the physiological and genetic mechanisms used by plants to respond and adapt to multiple stresses in forest ecosystems. To achieve this objective, we have conducted a series of field, greenhouse, and laboratory studies aimed at understanding how plants respond to allelochemicals, drought, and competition.

Rangewide provenance trials provide us with information about the amount of the genetic variation that exists within a species as well as information on the effects of moving local populations to new environments. Recently, we remeasured several rangewide provenance tests for black walnut (*Juglans nigra* L.) and white ash (*Fraxinus americana* L.) that had been established in the 1960s to mid 1970s. These studies continue to provide new information about the genetic variation that exists within these species as they enter their mature growth phase. In addition, we can continually test previous recommendations about the effects of moving seed to new environments. The up-to-date information will help us predict how local populations might respond to altered climatic conditions.

Bresnan and others (1994) recently confirmed our previous recommendations that collecting black walnut seed from 160 to 320 km (100 to 200 miles) south of a planting site results in increased growth of black walnut with acceptable survival for most of the central hardwood region. Similar movement of seed from sources along the edges of the natural range for black walnut, however, resulted in reduced survival or growth. Except in the test plantings along the western edge of the natural range, seed collected east of a planting site tended to show faster tree growth than seed collected west of the planting sites. Southward movement of seed to warmer climates and westward movement of seed to drier sites may simulate the effects of a warmer, drier climate such as that predicted by various GCMs. Few correlations, however, were found between latitude or longitude of the provenance source and subsequent height or diameter growth. These results suggest that sufficient genetic variation exists in black walnut populations throughout most of the central hardwood region to enable them to adapt to changes predicted by the various GCMs.

Recommendations similar to those for black walnut have also been made for white ash. With white ash, the movement of seed or seedlings up to 320 km (200 miles) northward also results in growth increases over local plant material for the central hardwood region. Recently, Roberds and others (1991) found that white ash seed from the southern part of the natural range of white ash tended to be more broadly adapted and had acceptable growth considerably north of their origin. On the other hand, moving seed from the northern parts of the natural range led to

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reduced tree growth. Rink and Kung (1991) confirmed earlier findings by using response surface regression modeling of new data to estimate genotypic responses of white ash to different environments. Latitudinal (north - south) movement of seed had a significant effect on tree growth at 10 of 12 test sites, while longitudinal (east - west) movement of white ash seed had a significant effect at only 4 of the 12 plantings. These results suggest that white ash adaptation to temperature gradients predicted by current GCMs will be more sensitive than its adaptation to decreased precipitation in the central hardwood region.

Greenhouse studies using a modified stair-step approach have also been done to evaluate the genetic and physiological response of black walnut, white ash, and white oak (*Quercus alba* L.) to drought and other stresses. In these studies, progenies of four to six local trees (half sib families) of each species were evaluated for their response to moisture stress, altered nutrient regimes, and leachates produced by a tall fescue sod (*Festuca arundinaceae* Schreb.). Interference by tall fescue on growth of hardwood trees is thought to involve reduced nitrogen cycling and the production of allelochemicals (Van Sambeek 1989, Van Sambeek and others 1989). In our greenhouse studies, 36 to 40 seedlings of each species were grown in 170 L, 60 cm deep wooden boxes filled with a mixture of 1:1 sand:silt-loam topsoil. A vacuum system was used to control available soil moisture at either 0.01 MPa (field capacity) or between 0.04 and 0.05 MPa (McBride and Rink 1986). Half the boxes were watered as needed with leachates collected from under a tall fescue sod. The remaining boxes were watered as needed with distilled water or water collected from under a sand bed. Depending on the species tested, nutrient regimes were altered by the addition of 6N-24P-24K fertilizer or growth of bluegrass (*Poa pratensis* L.) between the rows of seedlings.

Significant differences existed among the half-sib families of white ash, black walnut, and white oak in response to drought and/or allelochemicals produced by tall fescue sod. Leachates from tall fescue had a greater effect on height growth of black walnut seedlings when soils were near field capacity than when available soil moisture was limiting (Rink and Van Sambeek 1985). These observations confirm results from a field planting in which irrigated walnut trees with a tall fescue ground cover had slower growth than the non-irrigated walnut trees (Van Sambeek and McBride 1993). Conversely, tall fescue leachates reduced white ash seedling growth more when the seedlings were under moisture stress than when they were under adequate soil moisture (Rink and Van Sambeek 1987). In two separate trials, height growth of white oak seedlings was unaffected by reduced available soil moisture, tall fescue leachates, or altered soil nutrient levels (Van Sambeek and Rink 1990). Several demonstration plots at our Hardwood Research Demonstration Area confirm that black walnut and white ash trees are more responsive to cultural treatments for controlling tall fescue than are white oak trees (Van Sambeek and Walters 1989).

A subsequent study using dittany (*Cunila origanoides* (L.) Britton) confirmed how difficult it is even under controlled conditions in a greenhouse to separate the factors controlling interference by one plant on neighboring plants (Kobe and others 1992). Although the stair-step method was used, height growth of dittany may have differed in response to either rapid uptake of added nutrients in the recycled leachate or the production of allelochemicals by seedlings of either white oak, sugar maple (*Acer saccharum* Marsh.), flowering dogwood (*Cornus florida* L.), pawpaw (*Asimina triloba* (L.)Dunal), or black walnut. Although dittany is more commonly found in white oak stands than in sugar maple stands, leachates from white oak seedlings reduced dittany growth more than leachates from sugar maple. As with many other field and greenhouse studies on allelopathy, genotypic growth differences among the dittany plants apparently masked any response to allelochemicals.

Recent developments in hardwood micropropagation have made it possible to efficiently vegetatively propagate white ash (Navarrete and others 1989). In addition, the system used for in vitro culture provided a highly controlled environment for testing response of hardwood plantlets to allelochemicals and other stresses. The main advantage of the in vitro studies over greenhouse or field studies is the use of chemically defined growth medium eliminating possible growth inhibition from phytotoxic chemicals naturally occurring in soil that may mask effects of allelochemicals.

Preece and others (1991) recently described and tested the suitability of using cloned white ash plantlets as part of an in vitro bioassay to test for allelochemicals. They found significant differences in root growth among three ash clones grown on Murashige and Skoog (MS) medium, a high salt medium containing all essential macronutients and micronutrients, organics, sucrose, and a gelling agent. No differences in root growth were found within clones when roots were allowed to elongate on one-quarter to three-quarter strength MS medium. Thus, small aliquots of plant extracts or soil leachates could be added to one-quarter strength MS medium without creating osmotic potentials that would inhibit root growth of the ash microplants. Navarrete (1993) used the bioassay to confirm that leaf extracts from tall fescue contain one or more phytotoxic compounds at low concentrations, which can inhibit root growth of cloned ash microplants. By altering the macroenvironment, this bioassay could also be used to test for effects of increased temperature or elevated carbon dioxide on microplant growth along with their potential interaction with other stress factors including moisture stress, allelochemicals, pesticides, and air pollutants.

In conclusion, the high-value tree species in the central hardwood region have the ability to respond and to adapt to multiple stresses and their interactions. Our research program will continue to evaluate the physiological and genetic mechanisms used by trees to adapt to changes in their environments as well as options for adaptation or mitigation management.

LITERATURE CITED

Bresnan, D. F., G. Rink, K. E. Diebel, and W. A. Geyer. 1994. Black walnut provenance performance in seven 22-year-old plantations. Silvae Genet. 43:246-252.

Kobe, J. M., J. S. Fralish, and J. W. Van Sambeek. 1992. The effect of allelochemicals produced by sugar maple, white oak, flowering dogwood and pawpaw on growth of dittany, (*Cunila origanoides*) (L.) Britton. Assoc. of Southeast. Biol. Bull. 39:93.

McBride, F. D. and G. Rink. 1986. A soil moisture control system for greenhouse plant stress studies. Tree Planters' Notes 37:27-32.

Navarrete, N. E. 1993. Estudio del effecto alelopático del pasto (*Festuca eliatior var. arundinaceae* Schreb.) Wimm. en plantas micropropagadas de cenizo blanco (*Fraxinus americana* L.). In: M. A. Orellana Nuñez and J. A. Nuila de Mejía (eds.), Primer Congreso Nacional de Cultivo in vitro de Tejidos Vegetales, Universidad de El Salvador, pp. 25-31.

Navarrete, N. E., J. W. Van Sambeek, J. E. Preece, and G. R. Gaffney. 1989. Improved micropropagation of white ash (*Fraxinus americana* L.). In: G. Rink and C. A. Budelsky (eds.), Proceedings of the Seventh Central Hardwood Conference, USDA Forest Service Gen. Tech. Rep. NC-132, pp. 146-149.

Preece, J. E., N. Navarrete, J. W. Van Sambeek, and G. R. Gaffney. 1991. An in vitro microplant bioassay using clonal white ash to test for tall fescue allelopathy. Plant Cell. Tissue and Organ Culture 27:203-210.

Rink, G. and F. H. Kung. 1991. Height and diameter variation in twelve white ash provenance/progeny tests in eastern United States. In: L. H. McCormick and K. W. Gottschalk (eds.), Proceedings 8th Central Hardwood Forest Conference, USDA Forest Service Gen.Tech. Rep. NE-148, pp. 179-187.

Rink, G. and J. W. Van Sambeek. 1985. Variation among black walnut seedling families in resistance to competition and allelopathy. Plant and Soil 88:3-10.

Rink, G. and J. W. Van Sambeek. 1987. Variation among four white ash families in response to competition and allelopathy. For. Ecol. Manage. 18:127-134.

Roberds, J. H., J. O. Hyun, G. Namkoong, and G. Rink. 1991. Analysis of height growth response function for white ash provenances. Silvae Genet. 39: 121-129.

Van Sambeek, J. W. 1989. Vegetation management in established stands. In: J. E. Phelps (ed.), The Continuing Quest for Quality, Walnut Council, pp. 114-129.

Van Sambeek, J. W. and F. D. McBride. 1993. Grass control improves early growth of black walnut more than either deep ripping or irrigation. No. Nut Growers Assoc. Ann. Rep. 84:9-19.

Van Sambeek, J. W. and G. Rink. 1990. Competitive and allelopathic components of grass sod interference on white oak seedling growth. In: J. W. Van Sambeek and M. M. Larson (eds.), Fourth workshop on seedling physiology and growth problems in oak plantings. USDA Forest Service Gen. Tech. Rep. NC-139, p. 8.

Van Sambeek, J. W. and N. R. Walters. 1989. Hardwood research demonstration area walking trail guide. USDA Forest Service, North Central Forest Experiment Station Misc. Publ., 16 p.

Van Sambeek, J. W., R. C. Schlesinger, P. L. Roth, and I. Bocoum. 1989. Revitalizing slow-growth black walnut plantings. In: G. Rink and C.A. Budelsky (eds.), Proceedings of the Seventh Central Hardwood Conference, USDA Forest Service Gen. Tech. Rep. NC-132, pp. 108-114.