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Variation among Four White Ash Families in Response to Competition and Allelopathy

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ABSTRACT

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Analysis of three environmental variables affecting seedling growth of four half-sib white ash families was dominated by a three-way interaction between soil moisture stress, fescue leachate, and family. Of these, soil moisture stress contributed by far the most to the interaction and resulted in an average growth decline of 62%. Although fescue leachate appeared to be phytotoxic to ash seedlings, it had a lesser effect resulting in changes in height rankings among families. Seedling families which grew well under moisture stress also tended to be tallest in the presence of fescue leachate. However, seedling families which were tallest under optimum growing conditions were not necessarily tallest when exposed to moisture stress.

INTRODUCTION

Guidelines for establishment of hardwood plantations dictate that weeds be controlled for up to 5 years after planting. Weeds are usually controlled by herbicides, mechanical cultivation, or both. Neglecting to properly control weeds generally results in either growth reduction or seedling mortality. The expense of proper weed control and the consequences of neglecting control have tended to discourage hardwood plantation establishment.

The ground cover in most hardwood plantations in the central United States goes through a series of vegetational changes culminating in tall fescue. Fescue grass has been shown to produce phytotoxins which inhibit the growth of several species of forbs and hardwoods (Walters and Gilmore, 1976; Peters and Luu, 1984; Rink and Van Sambeek, 1985). This study was established to determine if genetic variation in resistance to interference (i.e., the combined effect of competition and allelopathy) exists among half-sib progeny of several high-value hardwoods and, if it does, which environmental variables contribute to the interference. Results from the black walnut (*Juglans nigra* L.) phase of this study have been reported (Rink and Van Sambeek, 1985). This paper presents results from the white ash (*Fraxinus americana* L.) phase.

METHODS

Germinating white ash seeds of four southern Illinois open-pollinated families were planted in 32 plywood chambers ($61 \times 61 \times 61$ cm) and surviving seedlings were grown for 30 weeks (April through October 1984) in a greenhouse. Each chamber contained 37 germinants (ten germinating seeds of each of three families plus seven of a fourth family which had fewer germinating seeds). Sowing rates were comparable to the recommended nursery sowing rate for this species (Williams and Hanks, 1976). Germinating seeds were sown 2 cm deep, 5.5 cm apart in family rows; families were randomly assigned to rows and family identity was maintained throughout the experiment.

The 'soil' in the chambers was a 1:1 mixture of Hosmer silt loam (Typic Fragiudalf) and coarse river sand. Mixing of sand with the soil was intended to dilute the natural fertility of the silt loam and to improve internal drainage. The silt loam was obtained from the A_1 horizon of an upland oak-hickory forest, after removal of the litter layer. Each chamber was filled with 257 kg (fresh weight) of soil mix. The soil mix averaged 11, 10, and 66 ppm of extractable N, P, and K, respectively. These values are considered low for both N and P and medium for K for woody ornamental plants (McVey, 1977). Nitrate-N and P were determined by colorimetry, and K by atomic absorption. The soil pH averaged 5.4.

The 32 experimental chambers were positioned in groups of four blocks of eight chambers. Within groups (blocks), each chamber was randomly assigned one of eight possible treatments. The eight main plot treatments were all possible combinations of two soil moistures regimes (field capacity and moisture stress), two soil fertility levels (fertilized or unfertilized), and two types of watering media (distilled water or fescue (*Festuca arundinacea* Schreb.) leachate). Each factor will be discussed separately.

Moisture stress regime

Soil moisture was controlled by a vacuum pump that provided either 0.5 or 0.1 atm (0.05 or 0.01 MPa, respectively) of continuous tension through a porous ceramic cup located in the bottom of each chamber. The 0.1-atm tension treatment simulated field capacity for the soil mix and the 0.5-atm treatment simulated moisture stress. To enable moisture relations to equilibrate at desired levels, tensions were imposed on the soil 4 weeks prior to planting germinants and maintained for the remainder of the experiment.

The vacuum system responsible for the soil moisture tension also controlled the watering system. When the soil moisture tension exceeded the preset level, water or fescue leachate was drawn into the soil through another porous ceramic cup located in the soil profile and connected with a water- or leachate-filled bottle. Thus, the moisture gradient in the soil resulted from opposing tensions between a moisture source and an imposed vacuum and evapotranspiration. The system maintained a 4% difference in available soil moisture (on a dry weight basis) between field capacity and moisture stress throughout the 30-week growing period (McBride and Rink, 1986). Experimental chambers were weighed weekly and supplementary water or leachate was provided to return soils to preset soil moisture contents.

Fertility regime

Each chamber intended as a high fertility treatment was fertilized with 6 g of elemental 6:24:24 N:P:K fertilizer spread over the surface and mixed into the upper 15 cm of soil 4 weeks before planting germinants. The fertilization was equivalent to 168 kg/ha, a commonly recommended rate for agronomic crops in southern Illinois.

Watering medium

Fescue leachate was used to water half the treatment chambers and distilled water was used for the other half. Fescue leachate was extracted from fescue sod that had been planted in 16 sand-filled plywood chambers ($61 \times 61 \times 61$ cm). The sod was periodically watered by spraying the foliage and soil with water from a local irrigation pond. The leachate was extracted from the bottom of each sand-filled chamber using the vacuum system described above, and stored at 2–4 °C until needed.

Measurements and analysis

Seedling heights were measured at approximately 2-week intervals for 30 weeks. At the end of the experiment each seedling was labeled with masking tape and all leaves removed. The chambers were turned on their sides and seedlings washed out. Labeled seedlings were oven-dried at 105 °C and weighed by individual tree to determine root, shoot, and total dry weights.

Data were analyzed by analysis of variance on an individual seedling basis. The ANOVA model was a randomized complete block design with a split plot arrangement of treatments. Families and associated interactions were assumed to be random and all other treatments (block, nutrient level, moisture stress,

TABLE 1

Probabilities (*P*) of obtaining greater *F* values in analyses of variance of height on different dates

Variable	Number of weeks after planting									
	8	10	12	14	16	18	21	24	26	30
Blocks (B)	0.10	0.04	0.09	0.48	0.59	0.54	0.18	0.17	0.31	0.21
Fert (N)	0.06	0.22	0.35	0.77	0.92	0.80	0.71	0.56	0.52	0.62
Leachate (L)	0.60	0.38	0.16	0.34	0.37	0.39	0.22	0.16	0.14	0.18
M. Stress (M)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Fert × Leach	0.73	0.47	0.29	0.27	0.21	0.19	0.09	0.15	0.13	0.16
Fert × Stress	0.22	0.10	0.17	0.60	0.91	0.95	0.96	0.81	0.85	0.84
Leach × Stress	0.73	0.40	0.17	0.31	0.38	0.40	0.28	0.21	0.22	0.25
N × L × M	0.08	0.09	0.04	0.18	0.15	0.14	0.05	0.07	0.08	0.08
Fam (F)	<0.01	<0.01	<0.01	<0.01	0.03	0.08	0.02	<0.01	<0.01	<0.01
Fam × Fert	0.30	0.29	0.18	0.58	0.61	0.18	0.10	0.21	0.27	0.20
Fam × Leach	0.02	<0.01	<0.01	0.02	0.06	0.11	0.53	0.58	0.68	0.56
Fam × Stress	<0.01	<0.01	<0.01	<0.01	0.18	0.37	0.42	0.53	0.48	0.41
F × N × L	0.06	<0.01	0.06	0.08	0.20	0.27	0.33	0.44	0.53	0.41
F × M × N	0.11	0.15	0.06	0.06	0.08	0.03	0.02	0.05	0.03	0.05
F × M × L	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02	0.03	0.02	0.03
F × N × L × M	<0.01	<0.01	0.03	0.16	0.26	0.27	0.56	0.56	0.50	0.48

Low probabilities ($P < 0.05$) indicate high F-values and statistical significance.

and water medium) and their interactions were assumed to be fixed. A method of Steel and Torrie (1960, p. 207) was used to partition the sums of squares of the interaction between families, watering medium, and moisture stress. An *F*-test was used for planned comparisons between controls and treatment plots for the final seedling height data. Pearson correlation coefficients were calculated on an individual tree basis.

RESULTS

Mean seedling survival was 86% after 30 weeks. Survival was significantly affected only by moisture stress and by family. Seedlings growing under moisture stress had 81% survival while those growing in soil at field capacity had 95% survival. Among families survival ranged from 77% for family C to 92% for family A.

After 30 weeks, the ash seedlings averaged 12.4 cm in height. The bulk of the height growth (88%) occurred during an 84-day period between the 12th and 24th weeks after planting. This reflected a growth pattern substantially different from black walnut; in that species, 90% of height growth was completed after only 6 weeks (Rink and Van Sambeek, 1985).

Analyses of seedling height were dominated by two three-way interactions (Table 1) which obviate discussion of main effects. The first, an interaction among families, moisture stress, and fescue leachate (F × M × L)was very highly

TABLE 2

Planned comparisons of within-family effects of moisture stress and fescue leachate contributing to 3-way interaction among family, moisture stress, and watering medium for the last height measurement

Family	H_2O stress	Fescue leachate
A	$P<0.001$	$P>0.75$
B	$P<0.001$	$0.01<P<0.025$
C	$P<0.001$	$0.50>P>0.25$
D	$P<0.001$	$0.25>P>0.10$

significant for all ten measurements. The second, an interaction among families, moisture stress, and fertilizer (F×M×N) became significant 18 weeks after planting and remained significant throughout the remainder of the experiment.

Analysis of the family-moisture stress-fescue leachate interaction (F×M×L)for the last height measurement (Table 2) showed that the contribution of moisture stress to this interaction was very highly significant for all four families while the contribution of fescue leachate was significant only for family B. Comparison of mean seedling heights (Table 3) also revealed that, of the three components of this interaction, moisture stress had by far the greatest effect; moisture stress resulted in a 62% mean reduction in mean height at the time of the last measurement. As implied by the interaction, height growth reduction was not equally distributed among families (Table 3). In the absence of leachate, family D was tallest under moist soil conditions but suf-

TABLE 3

Average seedling height on the last measurement date (October 1984) by family and by presence or absence of fescue leachate and moisture stress treatments

Soil moisture regime	Family	Watering regime	
		Water	Fescue leachate
Field capacity (0.01 MPa)	A	14.7	16.1
	B	19.4	13.3
	C	18.6	18.0
	D	21.0	16.5
Moisture stress (0.05 MPa)	A	6.9	5.6
	B	5.9	5.7
	C	9.4	7.4
	D	5.9	7.4

fered a growth reduction of 72% under moisture stress, while seedling growth of family C was reduced by only 50%. This interaction also resulted in a reversal in family rankings; families D and C ranked respectively first and third under unstressed, moist conditions and third and first under moisture stress.

Although fescue leachate reduced height growth only 11% overall, differential family response to leachate also contributed to the three-way interaction (Table 3). Family B was most susceptible to fescue leachate. In the presence of both moisture stress and fescue leachate, there were two size classes of seedlings. Families C and D were in the taller size class, while families A and B were in the shorter category. Seedlings in the larger size class averaged 31% taller than those in the shorter category.

The family $\times$ moisture stress $\times$ fertilizer interaction resulted from inconsistent family response to fertilizer under different moisture regimes. After 30 weeks of growth in moist soil seedlings of family A were 38% taller than unfertilized seedlings, whereas seedlings of other families showed a slight growth reduction in response to fertilization. With fertilizer and under moisture stress, seedlings of family B were slightly taller, whereas seedlings of all other families were shorter, than in unfertilized soil.

In general, seedling root, shoot, and total dry-weight means and analyses of variance closely paralleled those for seedling heights of the last measurement. Families and treatments with the tallest seedlings also had the highest dry weights. Individual tree correlations on a family basis between the last four height measurements and root, shoot, and total weight were highly significant and in every case exceeded 0.8.

DISCUSSION

Interactions dominated analysis of white ash seedling growth; all variables evaluated in this study were involved in one of two (or both) second-order interactions. The most prominent of these was an interaction between moisture stress, fescue leachate, and family, which had by far the greatest effect on height growth. Exposure to moisture stress resulted in an average loss of 62% in height compared to trees grown in soil at field capacity, although survival loss was only 10%; apparently white ash seedlings can withstand protracted periods of soil drought. Black walnut and yellow poplar suffered a similar lack of growth when exposed to soil drought (Pope and Madgwick, 1974; Rink and Van Sambeek, 1985). However, as implied by the interaction, different seedling families have varying tolerances to soil moisture stress. Such changes in family rank for height growth evident in this limited experiment, with representation from open-pollinated seed of only four non-selected, naturally growing mother trees, suggest that substantial improvements in early growth of white ash seedlings can be obtained from rigorous selection for tolerance to drought and allelopathy.

Interaction of fescue leachate with family and moisture stress implies toxicity and differential family tolerance to its presence. For example, seedlings of family D were tallest in the absence of moisture stress and leachate but suffered a 21% growth reduction in the presence of fescue leachate. By contrast, family C had next to the shortest seedlings under optimum conditions but suffered a growth reduction of only 4% when watered with fescue leachate and family A showed a height increase of 9%. This resulted in changes in height rankings. Combining moisture stress with exposure to fescue leachate also resulted in changes in rank, although the mean height of moisture-stressed seedlings was the same as those exposed to the combined treatment. Similar results were obtained in analyses of seedling dry weights.

Such results imply phytotoxicity of fescue leachate to white ash seedlings. Allelopathy has been implicated in fescue-derived interference in black walnut and sweetgum plantings (Walters and Gilmore, 1976; Rink and Van Sambeek, 1985), but no reference has yet been made to such an effect on white ash, although cultivation has been shown to improve juvenile growth in plantations (Clausen, 1980).

Results from this experiment imply that selection for stress resistance may need to be evaluated more intensively. Neglecting to evaluate the tolerance could result in substantial growth loss. Under standard nursery practices tree seedlings are grown under relatively optimum conditions and up to 20% of the smallest seedlings are culled after they are lifted. Under such conditions, some of the more drought-tolerant families may be culled and the retained families distributed for outplanting. Under varying degrees of field stress, the retained families may show the resultant typical slow growth associated with many hardwood plantations. Thus, slow growth may in part reflect nursery selection for growth under optimum conditions seldom encountered in production field plantings.

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