ALLELOPATHIC INHIBITION OF NORTHERN RED OAK BY INTERRUPTED FERN AND GOLDENROD[1]

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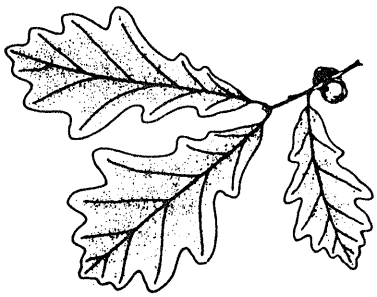

ABSTRACT. -- A reduced incidence of oak regeneration in the presence of fern understory has been observed. This study examined the allelopathic effects of leachates from interrupted fern fronds, goldenrod shoots, and northern red oak leaves on the survival and growth of northern red oak seedlings. The oak seedlings were grown in a glasshouse under full sunlight and shaded (25% of full sunlight) conditions. Leachates were applied to the sandy loam soil 15 times over a 120 day period to simulate a rainfall induced transfer of allelopathic chemicals from aerial plant parts to the soil. Survival and root growth of oak seedlings were significantly reduced by fern and goldenrod leachates. Oak leaf leachate had no significant effects on survival or growth. Shaded conditions reduced plant growth. The results suggest that allelopathy may account for the field observation of reduced oak regeneration in the presence of a fern understory.

Oak regeneration in the driftless area of the upper Mississippi River valley is poor on mesic sites particularly on northern and eastern slopes (Johnson 1982). Ferns, such as interrupted fern (Osmunda claytoniana L.), often form dense layers of vegetation on these mesic sites. Scholz (1955) reported that sensitive fern (Onoclea sensibilis L.) reduced survival of northern red oak (Quercus rubra L.) seedlings to a greater extent than similar layers of woody shrubs and sod. Ferns and goldenrods have also been identified as a source of allelopathic agents (Fisher et al. 1978; Gliessman and Muller 1978; Hollis et al. 1982; Horsley 1977a; Larson and Schwarz 1980; Norby and Kozlowski 1980). Phenolic acids have been implicated as the chemicals responsible for the allelopathic effects of ferns and many other plants (Fisher 1980; Glass 1976).

Since interrupted fern produces a variety of phenolic acids (Bohm and Tyron 1967), we hypothesized that it may inhibit the establishment and subsequent growth of northern red oak seedlings through allelopathy. Other understory species such as goldenrod (Solidago altissima L.) have been shown to have allelopathic effects on oak seedlings (Larson 1984). Previous studies have not always evaluated the relationship between allelopathic agents and environmental variables such as soil fertility, pH or light conditions. Therefore, our study was designed to determine if interrupted fern frond, oak leaf, and goldenrod shoot leachates have a potential allelopathic effect on the establishment and growth of northern red oak seedlings when grown under two levels of light.

MATERIALS AND METHODS

Plant Materials and Culture

Acorns were pre-germinated in moist vermiculite and sown in rootrainers (Spencer-Lemaire, Edmonton, Alberta, Canada) containing approximately 350 cm^3 of a loamy sand soil of the Menaga-Marquette association (Arneman 1963). All seedlings were planted 4 per rootrainer, and grown in a glasshouse for 120 days. The initial glasshouse environment included a 15 hr photoperiod with 34 to 24/24 to 21°C day/night temperatures, but by the end of the experiment photoperiod and day/night temperatures were reduced to 9.5 hr and 29 to 23/24 to 21°C, respectively. Plants were watered with deionized water or leachate as needed to maintain soil

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moisture near field capacity. A split plot factorial experiment was implemented with 2 levels of light as whole plots, and 4 types of leachate treatments (3 plant leachates and a control) randomized within each whole plot. Twelve seedlings were planted for each of the 8 treatment combinations.

The two light regimes were full glasshouse photosynthetic photon flux density (PPFD), 950 to 1050 $\mu E\ m^{-2}\ s^{-1}$, and approximately 25% of full glasshouse PPFD, 200 to 300 $\mu E\ m^{-2}\ s^{-1}$. Shade conditions were implemented with a double layer of neutral density shade cloth suspended 50 cm above and around the seedlings. Ambient temperature differences between the two light regimes did not differ significantly (± 2°C).

Leachate Solutions

Northern red oak leaves (Q. rubra L.), goldenrod shoots (Solidago canadensis L.), and interrupted fern fronds (Osmunda claytoniana L.) were collected near Lanesborough, Minnesota, in midsummer, and stored until needed in polyethylene bags in the dark at 3°C. Plant material was collected in midsummer because Larson (1984) and Glass and Bohm (1969) reported that the allelopathic agents were more prevalent during this time. Leachates, made up 2 to 3 days prior to each irrigation, were obtained by combining 200 g of the respective plant material with 4 liters of deionized water in a flask (Horsley 1977a). The plant material and deionized water were shaken on a reciprocating shaker for two hours and allowed to leach for 24 hr at 3°C. After the extraction period, the leachate mixtures were filtered through a double layer of cheesecloth and stored at 3°C in a sealed container. A subsample of each patch of leachate was collected for analysis of element content and pH.

Leachates and control solutions were allowed to equilibrate to glasshouse temperatures before application to plants. Forty ml of the oak leaf, goldenrod shoots, or fern frond leachates or a control of deionized water was added to each plant once a week throughout the experiment. A total of 15 leachate applications were made to each plant.

Plant and Soil Measurements

Oak seedling survival, dry weights, leaf area, number of leaves, and number of lateral roots were determined after 120 days. Component dry weights of each seedling were measured after drying at 70°C for 24 hr. Number of lateral roots were considered the total number of first order laterals on the tap root that were greater than 1 cm in length. Nonsurviving plants were defined as those whose leaves abscised and whose cambium was brown prior to harvest.

Phosphorus, potassium, calcium, magnesium, aluminum, and iron contents of leachates and soils were measured using inductively coupled plasma atomic emission spectroscopy (ICP) as discussed by Munter et al. (1984). Elements were extracted from soil samples with 2N HCl for ICP analysis. A 0.01 molar $CaCl_2$ solution was used for soil pH measurements (Page et al. 1982).

RESULTS

Fern frond and goldenrod shoot leachates significantly reduced oak seedling survival (Figure 1). Leachate applications had no effect on seedling shoot variables (Table 1), but weight of lateral and tap roots was reduced by goldenrod and fern leachates (Table 2). Fern frond leachate showed a trend towards increasing the number of lateral roots per seedling, but it was not significant at the 0.05 level (Table 2). Oak leaf leachates did not produce responses different from the deionized water control for any variable.

Shade reduced the number of leaves, leaf area, root dry weight, and shoot dry weight (compare treatment means between light regimes Tables 1 and 2). Even though the light regimes had no significant effect on seedling survival, the greatest mortality occurred under full light for fern leachates and under shaded conditions for goldenrod leachates (Figure 1). Under partial sunlight conditions fern and goldenrod leachates reduced lateral and tap root biomass accumulation. However, under full sun the same treatments showed no difference in root biomass when compared to the control treatments (Table 2).

Element concentration of the different batches of plant leachates increased during the experiment, but analysis of final soil element concentration revealed no differences in soil fertility between treatments (data not shown). The pH of the different batches of plant leachates increased throughout the experiment as the plant material in storage decomposed (Table 3). The deionized water had the lowest pH, and the fern frond leachate the highest (Table 3). Even though the leachates had significantly different pH values, the final soil pH of the different treatments were approximately the same ranging from 6.3 to 6.8 (Figure 2).

DISCUSSION

Fuerst and Putnam (1983) outlined criteria necessary to establish proof of an allelopathic response and suggest that the first step is to identify a symptom of interference independent of environmental and competitive effects. Our study, conducted under defined environmental conditions and in the absence of competition, meets this criterion. Moreover, consistent soil pH and element concentrations across treatments exclude these as casual factors and suggests that an agent may exist in the fern frond leachate that is inhibitory to northern red oak seedlings.

Fern frond leachate reduced seedling survival and inhibited lateral and tap root growth, but did not affect the accumulation of shoot biomass. Since the acorn is a major source of carbon for the developing seedling (Richardson 1956), allelopathic

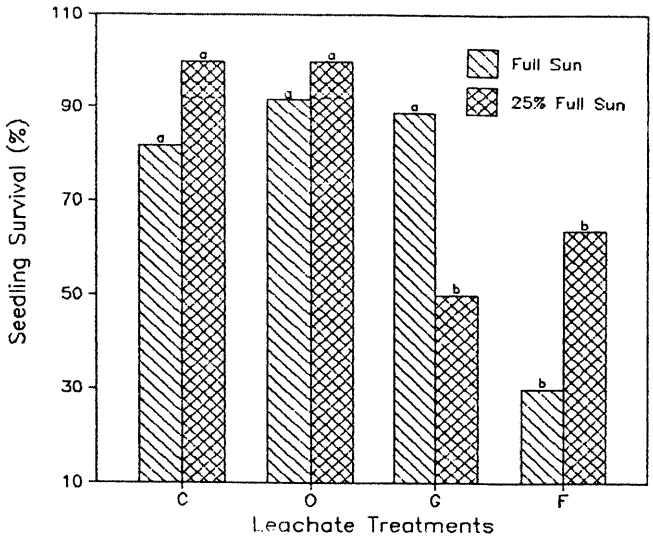

FIGURE 1.--Survival of seedlings receiving deionized water (C), oak leaf (O), goldenrod shoot (G), and fern frond (F) leachates. Bars topped by the same letter are not significantly different at the 0.05 level using Duncan's multiple range test.

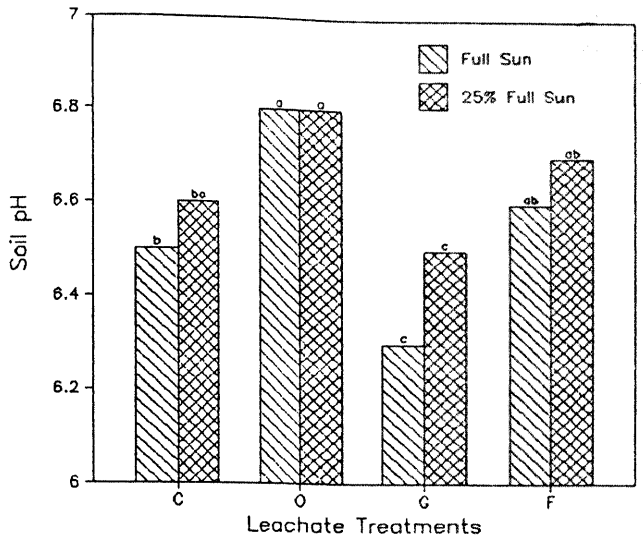

FIGURE 2.--Soil pH of seedlings which received deionized water (C), oak leaf (O), goldenrod shoot (G), and fern frond (F) leachates. Bars topped by the same letter are not significantly different at the 0.05 level using Duncan's multiple range test.

TABLE 1.--Shoot growth of northern red oak seedlings exposed to two light regimes and four leachate treatments for 120 days in a glasshouse.

	Shoot Variables (Means)				
Treatments	Leaves (#)	Leaf Area (cm2)	Leaf Weight (mg)	Stem Weight (mg)	Height (cm)
Full Sunlight					
Control	5.9	104.2	482	189	7.8
Oak Leaf	5.6	109.0	455	168	7.8
Goldenrod	6.0	109.4	476	180	7.5
Fern Frond	6.6	117.3	566	202	9.4
Partial Sunlight					
Control	5.0	103.8	391	192	9.7
Oak Leaf	4.6	89.4	360	115	6.7
Goldenrod	4.7	81.6	303	100	8.0
Fern Frond	5.6	95.8	354	107	8.4
Main Effects					
Light	Y[1]	Y	Y	Y	N
Leachates	N	N	N	N	N
Interactions					
Light x Leachate	N	N	N	N	N

[1]Y= significance at the 0.05 level of confidence, N=not significant at the same level.

TABLE 2.--Root growth of northern red oak seedlings exposed to two light regimes and four leachate treatments for 120 days in a glasshouse.

Treatments	Root Variables (Means) Laterals (#)	Lateral Weight (mg)	Taproot Weight (mg)
Full Sunlight			
Control	64	359 a[1]	455 a
Oak Leaf	63	395 a	758 a
Goldenrod	46	226 a	787 a
Fern Frond	153	251 a	520 a
Partial Sunlight			
Control	63	242 a	436 a
Oak Leaf	39	212 a	455 a
Goldenrod	60	110 b	182 b
Fern Frond	113	132 b	177 b
Main Effects			
Light	N[2]	Y	Y
Leachates	N	Y	Y
Interactions			
Light x Leachate	N	N	N

[1]For each variable, means within each column followed by the same letter are not significantly different at the 0.05 level using Duncan's multiple range test.

[2]Y= Significance at the 0.05 level of confidence, N= Not significant at the same level.

TABLE 3.--Deionized water (control), oak leaf, goldenrod shoot, and fern frond leachate pH during the course of the 120 day experiment.

Leachates Measured[1]	Control Water	Plant Leachates Oak Leaf	Goldenrod Shoot	Fern Frond
Early Leachates (#s 1 to 3)	4.6 d[2]	6.1 c	6.0 c	6.1 c
Middle Leachates (#s 7 to 9)	5.0 d	5.6 c	6.6 b	6.8 b
Late Leachates (#s 13 to 15)	4.9 d	6.9 b	6.9 b	7.5 a

[1]Leachate pH represents the mean of the designated batches.

[2]Means followed by the same letter are not significantly different at the 0.05 level using Duncan's multiple range test.

effects during early development may be modified. Thus, insignificant differences in shoot growth between leachate treatments could be expected. However, since fern and goldenrod leachates induced leaf abscission and seedling mortality after 10 weeks of growth, it is obvious that the shoot was susceptible to the fern and goldenrod leachates. Horsley (1977a) observed that growth reductions of black cherry (Prunus serotina Ehrh.) due to grass, fern, aster, or goldenrod foliage leachates occurred only after the seedling had exhausted cotyledonary reserves. Our observations indicate that acorn reserves would have been depleted or cotyledons detached from the seedlings after 10 weeks of growth.

A reduction in oak seedling root growth due to allelopathic agents has been reported previously (Larson 1984). Fisher (1980) suggested that root function may be disrupted by allelopathic agents, and this could be the cause of mortality and growth reduction seen in this study. Allelopathic chemicals are known to retard growth by disrupting cell division, interfering with respiration, and inhibiting nutrient absorption and translocation (Horsley 1977b).

Our observation that shade conditions reduce root and shoot dry matter accumulation agrees with previous work with northern red oak seedlings (McGee 1968; Musselman and Gatherum 1969; Phares 1971). Our additional observation that fern and goldenrod leachates only reduced root biomass under shaded conditions might suggest that a reduced supply of carbohydrates from the shoot predisposes the seedlings to allelopathic damage. Seedling survival was not significantly affected by light regime; however, the lowest survival among fern frond and goldenrod shoot treatments occurred under contrasting light conditions. It is not clear why this was the case. The physiological relationship between seedling illumination and response to allelopathic agents deserves further investigation.

The agent or agents responsible for the potential allelopathic effects in this study are not known. Gliessman and Muller (1978) reported that allelopathic phenolic acids are present in fern fronds. Bohm and Tyron (1967) report that interrupted fern produces p-coumaric, ferulic, p-hydroxybenzoic, and vanillic acids. Glass (1976) implicated these acids with bracken fern (Pteridium aquilinum L.) allelopathy. These reports suggest that allelopathic effects on northern red oak observed in this study are most likely due to phenolic compounds.

Our analysis showed that the batches of leachate made later in the experiment contained higher element concentrations and had higher pH. Decomposition of the stored plant materials would account for this observation. Fisher et al. (1978) reported that putrified fern litter released greater amounts of allelopathic chemicals than fresh fern litter, and this may have also occurred in some of our batches of leachates.

Evaluation of how leachate applications in the laboratory compare to the presence and activity of allelopathic agents in natural field situations is difficult to achieve. Horsley (1977b) discussed the interactions and modifications that might occur between allelopathic agents and the environment, and his data showed that a considerable accumulation of agents occurred over the years. Patrick (1971) and Rietveld (1983) reviewed past studies and concluded that the effect of allelopathic agents is amplified in waterlogged or poorly drained soils. Since our soils were allowed to drain freely between irrigations, it is unlikely that the fern and goldenrod leachate effects are a result of excessive moisture. Borner (1959) states that allelopathic agents may be unstable and subject to metabolism by microorganisms -- effectively negating any effects the agents may have. Because field observations have documented reduced oak regeneration in the presence of a dense fern understory (Scholz 1955), it would seem likely that the allelopathic agents from the ferns do accumulate in natural stands. Thus, we hypothesize that our leachate treatments represent a reasonable exposure to allelopathic agents when compared to field conditions.

Ferns exhibit a strong dominance over associated plants in a variety of ecosystems (Gliesmann and Muller 1978). Thus, it is likely that ferns are influencing succession in the oak-hickory forests of the driftless region (Scholz 1955). Tree seedlings growing on wet or mesic sites tend to be most susceptible to allelopathy (De Bell 1971). Curtis (1959) observed that removal of the fire cycle increased the incidence of ferns in the oak-hickory forests of Minnesota and Wisconsin. According to Fisher (1977) fire will destroy or inactivate allelopathic substances permitting oak regeneration to occur. The presence of allelopathic substances in soils tends to magnify competitive influences of other vegetation. Allelopathic influences on oak regeneration may be minor in comparison to competition for light, soil moisture, or soil nutrients. However, oak silviculturalists should consider the role of allelopathy when selecting site preparation and weed control methods during the regeneration process.

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