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Allelochemic Interference by Quaking Aspen Leaf Litter on Selected Herbaceous Species

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Abstract. Freshly fallen quaking aspen leaf litter incorporated in red clay soil to achieve 2 percent and 4 percent organic carbon resulted in substantial decrease of growth of *Festuca elatior*, *F. rubra*, and *Poa pratensis* compared to growth in unamended and peat amended soils. *Lotus corniculatus* had limited response differences to these soil additives. The allelochemic response apparently was restricted to early seedling growth as germination of these four species and two other species (*Bromus inermis* and *Lolium perenne*) was not affected by leaf litter extracts. The results are consistent with earlier reports of reduced understory growth in aspen stands. The allelochemic potential demonstrated may result in a need to develop new aspen forest management plans including crop rotation. Forest Sci. 26:429–434.

Additional key words. *Populus tremuloides*, understory species, seedling growth, nutrients, germination.

The quality and productivity of aspen (quaking aspen, *Populus tremuloides* Michx.) forests are a function of soil conditions including texture, drainage, and nutrient status (Fralish and Loucks 1967, Johnston and Bartos 1977, Bartos and Johnston 1978), fire response (Perala 1974), clonal genetics (Barnes 1966 and 1975), diseases (Anderson and Anderson 1968), and postharvest response (DeByle 1976). Also, since associated species may interfere with the growth and development of each other through competition or allelopathy or both (Knight and Loucks 1969, Tubbs 1973 and 1976, Rice 1974 and 1979), knowledge of community structure and function is important in evaluating potential growth and management practices.

Vegetation of the Nemadji River watershed in the red clay region of the western Lake Superior Basin is typified by various stages of succession from aspen forest with 185 trees·ha^{-1} at maturity to northern hardwood forests dominated by maple and basswood with 450 trees·ha^{-1} (Kapustka and others 1978). Densities of herb and shrub layers were low under the more open canopy of aspen. An inverse relationship between understory aerial phytomass and the Importance Percentage of aspen in this region suggested the possibility of allelochemic interference on the part of aspen. Here we present evidence to support this hypothesis and discuss the possible implications on aspen forest ecology.

Methods

Freshly fallen aspen leaf litter was collected in a 10- to 15-year-old aspen stand in the red clay zone of the Nemadji River watershed of northwestern Wisconsin.

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The litter was air dried, ground, and sifted through a 2-mm sieve. A portion of the processed litter was boiled in deionized water (1.0 percent w/v) for 5 min. The resulting extract was filtered and aqueous serial dilutions of 1, 0.1, 0.01, and 0.001 percent were made.

Germination of smooth brome (*Bromus inermis* Leyss), creeping red fescue (*Festuca rubra* L.), tall fescue (*F. elatior* L.), birdsfoot trefoil (*Lotus corniculatus* L.), perennial rye (*Lolium perenne* L.), and Kentucky bluegrass (*Poa pratensis* L.) was tested against the various concentrations of aspen leaf litter extracts.[1] Five 50-seed replicates of each species were placed on filter paper moistened with either 8 ml of extract for each concentration or deionized water (control). Seeds with emergent radicles were tallied as germinated seeds and removed daily for 15 days. The Germination Index Value (Czabator 1962) was calculated.

Soil for early-growth studies was collected from the C horizon in the red clay region of the Nemadji River watershed of northwestern Wisconsin from an unvegetated, exposed hillside. This soil from the Nemadji-Newson Association is a montmorillinite clay with small quantities (<5 percent) of unsorted sand with a pH of 7.8 and 0.2 percent organic carbon. Soils (upper 15 cm) from adjacent, noneroding forested areas have 1.3 to 3.9 percent organic carbon (Kapustka and others 1978). The ground aspen leaf litter was incorporated into the clay soil to obtain 2 percent and 4 percent additions by dry weight. Similarly, soil mixtures of 2 percent and 4 percent peat moss were made. A control soil without additional organic carbon was included.

Six replicate pots of creeping red fescue, tall fescue, birdsfoot trefoil, and Kentucky bluegrass for each soil treatment were planted. Hoagland nutrient solution approximating 50 kg $N \cdot ha^{-1}$ was applied to three of the replicates. A siphon watering system maintained the potted soil at ~80 percent field capacity. After the first week the emergent seedlings were thinned and maintained at 20 plants per replicate. Height of the tallest plant in each replicate was measured weekly beginning 1 week after planting. After 5 weeks of growth, the aerial phytomass was harvested and fresh and ovendry weights were recorded. Calculations of 1-way ANOVA and significance of means were performed (Bruning and Kintz 1977).

Results

Each of the species tested germinated rapidly and obtained good cumulative percentages of germination. For the controls the speed of germination as reflected in the Germination Value (Czabator 1962) and the cumulative percentage germination for the six species were *Bromus inermis,* 22, 41; *Festuca elatior,* 46, 86; *F. rubra,* 65, 85; *Lolium perenne,* 96, 90; *Lotus corniculatus,* 71, 73; and *Poa pratensis,* 44, 74. No differences in either the speed of germination or the cumulative percentage occurred with any of the extracts for any of the species tested.

The addition of aspen leaf litter to the clay soil resulted in a pronounced reduction in growth compared to control plants as early as the first week (Fig. 1). Growth, measured as the height of the shoots essentially ceased after the second week in the aspen amended treatments. Significantly less growth in height was measured at 5 weeks in the 2 percent aspen amended soils ($P < 0.05$) and the 4 percent aspen amended soils ($P < 0.01$). The addition of peat often stimulated

[1] All seeds were obtained from Trico Services, Duluth, MN. These species are used extensively for erosion control roadside plantings and are found as naturalized species in the red clay area.

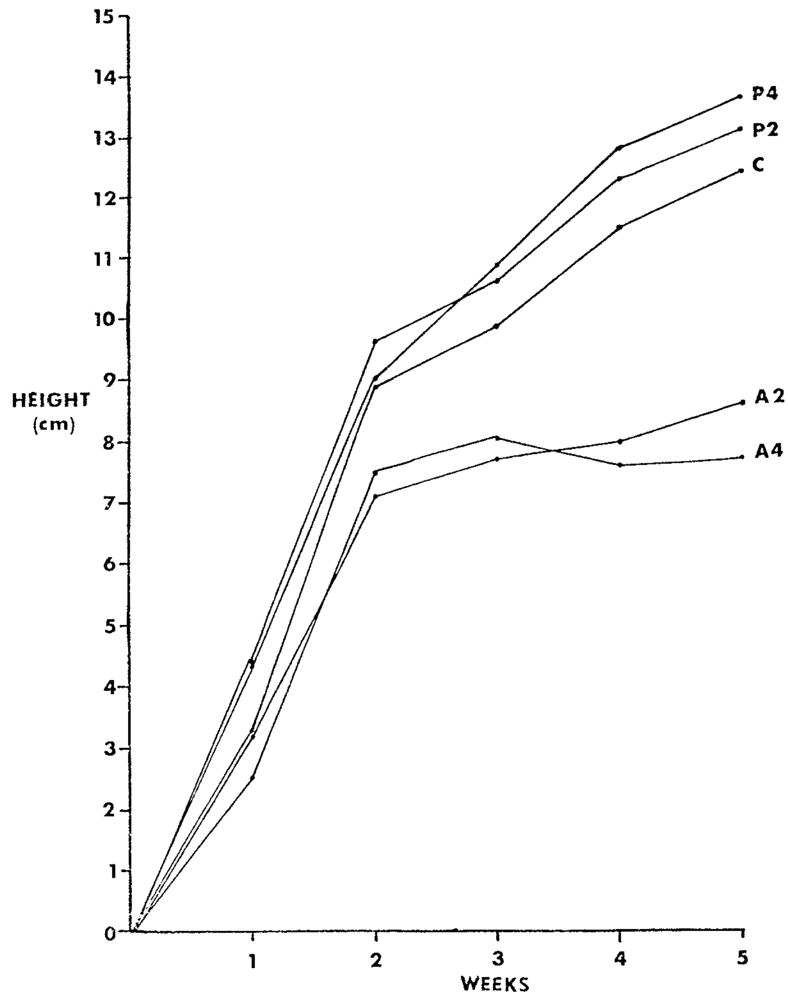

FIGURE 1. Cumulative height growth of tall fescue on control and amended soils, nutrients added.

the growth of the test plants although the differences among controls and peat amended soils generally were not significant even at the 0.1 level.

Tall fescue achieved significantly less growth when aspen leaf litter and nutrients were added to the soil when compared to treatments without nutrients (Table 1). This reduction in growth tended to be greater with the higher amounts of aspen litter. The decreases in aerial phytomass (dry weight) compared to the control was 48 percent for 2 percent aspen plus nutrients and 67 percent for 4 percent aspen plus nutrients treatments. Creeping red fescue and perennial rye responded similarly to the various treatments (Table 1).

Nutrients stimulated the growth in control and peat amended soils, whereas the nutrients tended to enhance the inhibition in the 4 percent aspen amended soil. Also, the extent of stimulation in the 2 percent aspen amended soil was generally less than for the controls of peat amended soils. Only birdsfoot trefoil did not exhibit this response to nutrients.

In all tests height, fresh weight, and dry weight followed similar patterns.

TABLE 1. Aerial phytomass (g dry wt) of 5-week-old test plants expressed as means ± standard error of the three replicates with levels of significance.[1]

Species, with and without nutrients	Amended soils[2]				
	A4	A2	C	P2	P4
Festuca elatior					
w/o nutrients	0.1009 ± 0.0103	0.0916 ± 0.0057	0.1030 ± 0.0023	0.1113 ± 0.0088	0.0969 ± 0.0066
w/nutrients	0.0719 ± 0.0036[ad]	0.1093 ± 0.0014[ad]	0.2115 ± 0.0234	0.1615 ± 0.0013[c]	0.1879 ± 0.0048
Stimulation percent[3]	−28.7	19.3	105.0	45.1	93.9
F. rubra					
w/o nutrients	0.0814 ± 0.0090	0.0565 ± 0.0055	0.0846 ± 0.0030	0.0670 ± 0.0075	0.0685 ± 0.0025
w/nutrients	0.0555 ± 0.0060[be]	0.0628 ± 0.0024[b]	0.1150 ± 0.0137	0.0925 ± 0.0143	0.1029 ± 0.0048
Stimulation percent	−31.8	11.2	35.9	38.1	50.2
Poa pratensis					
w/o nutrients	0.0172 ± 0.0042	0.0110 ± 0.0025	0.0121 ± 0.0003	0.0170 ± 0.0018	0.0125 ± 0.0023
w/nutrients	0.0106 ± 0.0009[ce]	0.0235 ± 0.0042	0.0242 ± 0.0030	0.0292 ± 0.0042	0.0297 ± 0.0030
Stimulation percent	−38.4	113.6	100.0	71.8	137.6
Lotus corniculatus					
w/o nutrients	0.0647 ± 0.0031[d]	0.0651 ± 0.0011	0.0786 ± 0.0068	0.0910 ± 0.0103	0.1057 ± 0.0051[b]
w/nutrients	0.0803 ± 0.0027	0.0829 ± 0.0063	0.1161 ± 0.0146	0.1229 ± 0.0189	0.1161 ± 0.0032
Stimulation percent	24.1	27.3	47.7	35.1	9.8

[1] [a]—mean different than control mean, $P < 0.01$; [b]—mean different than control mean, $P < 0.05$; [c]—mean different than control mean, $P < 0.10$; [d]—mean different than P4 mean, $P < 0.01$; [e]—mean different than P4 mean, $P < 0.05$.

[2] A4—4 percent aspen amended soils, A2—2 percent aspen amended soils, C—control, P2—2 percent peat amended soils, P4—4 percent peat amended soils.

[3] Percentage stimulation by nutrients (wt w/nutrients − wt w/o nutrients) ÷ (wt w/o nutrients) × 100.

Discussion

The aspen forest represents the largest forest type of the Great Lakes region. In the next few decades the importance of aspen should increase as a result of conversion of aspen forest to pasture or cropland, succession toward northern hardwood forests, and increased demands for pulpwood. Brinkman and Roe (1975) project adequate supplies for the next two decades for the Lake States region, though in Wisconsin removal of aspen was 136 percent of the annual desirable cut. In addition to the expanding economic interest, aspen forests provide prime habitat and food resources for wildlife. In response to the developing need to improve stand conditions and inventory, and maintain wildlife habitat, multiple use management of aspen is being encouraged (Leuschner 1972, Patten and Jones 1977, Perala 1977).

Ellison and Houston (1958) reported reduced growth of herbaceous plants under aspen stands but were unable to distinguish between moisture/nutrient competition or allelopathy as the causative factor. Subsequently, Mathes (1963) reported inhibition of various microorganisms by *in vitro* cultured aspen cambial tissue. Pyrocatechol isolated from aspen bark has been shown to inhibit *Hypoxylon pruinatum* (Hubbes 1962). Dormaar (1970) reported concentrations of polyphenol and *o*-dihydroxyphenol of up to 140 mg/g and 13 mg/g respectively in leaves of *Populus* × 'Northwest' (Hort.). Olsen and others (1971) identified benzoic acid and catechol in leaves of *P. tremula* as inhibitors of several mycorrhizal fungi. They reported concentrations of benzoic acid of 1.3 mM in green leaves and 0.04 mM in yellow leaves while catechol concentrations were 2.3 mM in green leaves and 0.6 mM in yellow leaves. Even the lower concentrations of catechol in the yellow leaves inhibited growth of *Boletus* spp.

Similar phenolic constituents have been shown to inhibit a broad spectrum of angiosperms. Further, these compounds have been shown to accumulate in the soil to concentrations which interfere with several plant and microbial processes including nitrogen fixation, resistance to pathogens, reproductive potential, and net primary production (Rice 1974 and 1979).

The aspen forests of the Lake States sometimes are associated with alder, a major contributor of symbiotic N_2-fixation (Torrey 1978). Cyanobacteria in association with lichens and as free-living colonies may also be significant in the N economy of these forests. The possibility of interference by phenolics from aspen on any of the N_2-fixing organisms should be considered.

In the aspen forests in the red clay region in northern Wisconsin, soil loss by surface and slump erosion proceeds at a rate of several millions of tons of soil annually.[2] Kapustka and others (1978) determined that aspen, because of its relatively weak roots, tendency to reduce soil moisture below the plastic limits of the clay, and poorly developed understory layers, offered relatively little protection against erosion compared to vegetation of later successional stages.

The species used in this study constitute only a small portion of the typical herbaceous layer of the forests of the region. However, the allelochemic effect may operate on a wider array of species and ecological processes. An accumulation of toxic substances in the soil also may be related to lower stand density, stand decadence, and reduced potential for regeneration of older clones. Agriculturalists have realized the benefits of crop rotation, which we now recognize in some instances is related to the accumulation of toxins. Additional studies may reveal a need to incorporate similar considerations into forest management practices in order to achieve goals of increasing aspen production.

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[2] Sydor, M. 1976. Red clay turbidity in western Lake Superior. University of Minnesota–Duluth, Final Report. EPA Grant #R005175, 150 p.

Literature Cited

Anderson, G. W., and R. L. Anderson. 1968. Relationship between density of quaking aspen and the incidence of *Hypoxylon* canker. Forest Sci 14:107–112.

Barnes, B. V. 1966. The clonal growth habit of American aspens. Ecology 47:439–447.

Barnes, B. V. 1975. Phenotypic variation of trembling aspen in western North America. Forest Sci 21:319–328.

Bartos, D. L., and R. S. Johnston. 1978. Biomass and nutrient content of quaking aspen at two sites in the western United States. Forest Sci 24:273–280.

Brinkman, K. A., and E. I. Roe. 1975. Quaking aspen: silvics and management in the Lake States. US Dep Agric, Agric Handbk 486, 52 p.

Bruning, J. L., and B. L. Kintz. 1977. Computational handbook of statistics. 2d ed. Scott, Foresman and Co., Glenview, Ill. 308 p.

Czabator, F. J. 1962. Germination value; an index combining speed and completeness of pine seed germination. Forest Sci 8:386–396.

DeByle, N. V. 1976. The aspen forest after harvest. *In* Utilization and marketing as tools for aspen management in the Rocky Mountains: proceedings of the symposium, Ft. Collins, Colo, 8–9 September 1976, p 35–40. USDA Forest Serv Gen Tech Rep RM-29, 138 p. Rocky Mt Forest and Range Exp Stn, Fort Collins, Colo.

Dormaar, J. F. 1970. Seasonal pattern of water soluble leaf constituents from leaves of *Populus* × 'Northwest' (Hort.). J Soil Sci 21:105–110.

Ellison, L., and W. R. Houston. 1958. Production of herbaceous vegetation in openings and under canopies of western aspen. Ecology 39:337–345.

Fralish, J. S., and O. L. Loucks. 1967. Prediction of aspen site index for correlation with site factors in Wisconsin. Univ Wis For Res Note 132, 6 p.

Hubbes, M. H. 1962. Inhibition of *Hypoxylon pruinatum* by pyrocatechol isolated from bark of aspen. Science 136(3511):156.

Johnston, R. S., and D. L. Bartos. 1977. Summary of nutrient and biomass data from two aspen sites in western United States. USDA Forest Serv Res Note INT-227. 15 p. Intermt Forest and Range Exp Stn, Ogden, Utah.

Kapustka, L. A., D. W. Davidson, and R. G. Koch. 1978. The significance of vegetation in moderating red clay erosion. *In* Voluntary and regulatory approaches for nonpoint source pollution control (R. G. Christensen and C. D. Wilson, eds), p 79–96. USEPA, Great Lakes Natl Program Off, Chicago. 224 p.

Knight, D. H., and O. L. Loucks. 1969. A quantitative analysis of Wisconsin forest vegetation on the basis of plant function and gross morphology. Ecology 50:219–234.

Leuschner, W. A. 1972. Projecting the aspen resources in the Lake States. USDA Forest Serv Res Pap NC-81, 32 p. North Cent Forest Exp Stn, St. Paul, Minn.

Mathes, M. C. 1963. Antimicrobial substances from aspen tissue growth *in vitro*. Science 140(3571):1101.

Olsen, R. A., G. Odham, and G. Lindberg. 1971. Aromatic substances in leaves of *Populus tremula* as inhibitors of mycorrhizal fungi. Physiol Plant 25:122–125.

Patten, D. R., and J. R. Jones. 1977. Managing aspen for wildlife in the southwest. USDA Forest Serv Gen Tech Rep RM-37, 7 p. Rocky Mt Forest and Range Exp Stn, Fort Collins, Colo.

Perala, D. A. 1974. Prescribed burning in an aspen-mixed hardwood forest. Can J Forest Res 4:222–228.

Perala, D. A. 1977. Managers handbook for aspen in the northcentral states. USDA Forest Serv Gen Tech Rep NC-36, 30 p. North Cent Forest Exp Stn, St. Paul, Minn.

Rice, E. L. 1974. Allelopathy. Academic Press, New York. 353 p.

Rice, E. L. 1979. Allelopathy: an update. Bot Rev 45:15–109.

Torrey, J. G. 1978. Nitrogen fixation by actinomycete-nodulated angiosperms. Bioscience 28:586–592.

Tubbs, C. H. 1973. Allelopathic relationship between yellow birch and sugar maple seedlings. Forest Sci 19:139–145.

Tubbs, C. H. 1976. Effect of sugar maple root exudate on seedlings of northern conifer species. USDA Forest Serv Res Note NC-213, 2 p. North Cent Forest Exp Stn, St. Paul, Minn.