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Allelopathy of Crop Residues Influences Corn Seed Germination and Early Growth

V. L. Martin, E. L. McCoy,* and W. A. Dick

ABSTRACT

Crop residues produce alleochemicals that may inhibit corn [*Zea mays* (L.)] seed germination and early growth. Studies were conducted in which residues of corn, soybean [*Glycine max* (L.) Merr.], oat [*Avena sativa* (L.)], and mixed grass hay were extracted under N_2 gas or air. Organic debris was removed and half of each extract was filter sterilized. Corn seeds were incubated in the extracts for 96 h at 25 °C. Percent germination, and lengths of coleoptile, radicle, and secondary roots were measured. Residues extracted under N_2 gas or air did not differ significantly in their toxicity. Nonsterile residue extracts decreased germination to 74% for soybean and oat straw and 27% for corn and hay residues. Sterile extracts did not affect germination. Nonsterile soybean and oat extracts did not reduce coleoptile lengths but did reduce radicle and secondary root lengths by 34% compared to the water treatment. Sterilized extracts reduced radicle and secondary root lengths by 63%. Nonsterile corn and hay extracts reduced coleoptile lengths by 42% and radicle and secondary root lengths by 81%. A second extraction was performed by incubating the residues without aeration at 25 and 0.5 °C. Seed germination for treatments with nonsterile extracts obtained at 25 °C were similar to those for nonsterile extracts of Exp. 1. Extraction at 0.5 °C and filter sterilization also improved germination. Soybean and oat extracts did not strongly inhibit coleoptile lengths; however, a 61% reduction occurred in radicle and secondary root lengths for the sterilized, 0.5 °C extract. Corn and hay residues were generally more inhibitory to coleoptile, radicle and secondary root lengths; however, no consistent effects were observed from temperature and sterilization treatments.

A GOAL of conservation tillage is the maintenance of surface residues that reduce soil and water loss (Triplett and Van Doren, 1977). Decomposing surface residues may release allelopathic compounds that are phytotoxic and reduce seedling vigor (Putnam and Duke, 1978; Rice, 1984; Shilling et al., 1985). These compounds are released directly through the leaching action of rainfall or indirectly as products and by-products of microbial activity during residue decomposition (Tukey, 1969; Putnam and Duke, 1978; Rice, 1984).

Early work on environmental conditions favoring the formation of allelopathic compounds (McCalla and Duley, 1948) determined that in vitro extractions of alfalfa [*Medicago sativa* (L.)] and sweet clover [*Melilotus alba* (Desr.)] residues were detrimental to germination and growth of corn seedlings. In a greenhouse experiment (McCalla and Duley, 1949) mulched, supersaturated soils decreased corn germination by 50% compared with unmulched, supersaturated soils. Mulched soils wetted to optimal moistures did not inhibit germination. The allelopathic response of corn was attributed to either anaerobic production of microbial by-products using crop residues as a C source and/or the direct release of organic compounds from the residue.

Recent research has sought to more precisely identify the conditions favorable for the production of phytotoxins that are active on corn. Aging of residues in the field for various periods decreased the phytotoxic potential of oat and wheat [*Triticum aestivum* (L.)] straw, while corn residues were still strongly phytotoxic after 22 wk of field decomposition (Guenzi et al., 1967). An in vitro experiment by Yakle and Cruse (1983) found that fresh corn residues were markedly more inhibitory to root and shoot growth than older, more decomposed residues. However, in a greenhouse study, no combination of residue age or placement decreased corn seed germination.

Microbial phytotoxin production is greater at higher extraction temperatures (20–25 °C) as compared to lower temperatures (8–10 °C) (Wallace and Elliot, 1979; Chou et al., 1981; Jessop and Stewart, 1983). Lower pH also favors phytotoxin production, but once the toxins are present they remain active over a broad range of pH values (Patrick and Koch, 1958). The H_2 ion concentration does not affect germination or growth (Yakle and Cruse, 1984).

The most commonly identified phytotoxins are acetogenins, including simple organic acids, straight chain alcohols, and ketones (Shilling et al., 1986). These compounds are produced under anaerobic conditions and accumulate as the result of microbial activity during residue decomposition (Wallace and Elliot, 1979; Harper and Lynch, 1982).

With the increased importance of crop residues in conservation tillage and multiple cropping systems, this study was conducted to investigate possible mechanisms of allelopathic responses of corn to crop residues. The study employed crop residue into which

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corn planting would potentially occur either during subsequent or the same growing season. This study examined: (i) the effects of common crop residue extracts on corn seed germination and growth and, (ii) the effects of temperature, aeration, and microbial activity on phytotoxicity of crop residue.

MATERIALS AND METHODS

Soybean straw, oat straw, mixed-grass hay, and corn stover were collected postharvest during the 1984 growing season and allowed to air dry. Corn stover was collected from hand harvested rows in mid-October, soybean straw immediately after harvest. Oat straw was collected from bales produced on site from the 1984 harvest. Hay was from the first cutting and consisted of various grasses with little alfalfa or clover. The residues were ground in a Wiley mill to pass a 2-mm mesh. The corn cultivar selected for bioassay was Landmark C-733X.

Residue Extraction

Ground residues were extracted by combining 30 g residue with 300 g double deionized water. The 1:10 ratio has been used by other researchers in this area (Nielsen et al., 1960; Yakle and Cruse, 1984) and preliminary experimentation demonstrated that this ratio insures elucidation of phytotoxic effects. In Exp. 1, extraction was conducted in the dark for 24 h at 25 °C with aerated and N_2 gas treatments. The treatments were established by either bubbling air or N_2 through the solution at 0.5 L min^{-1}. The method of Bartholomew and Broadbent (1949) was used to insure equal gas flow rate in each flask. In Exp. 2, extraction was conducted in the dark for 24 h at either 25 or 0.5 °C with flasks stoppered and stationary to reduce aeration of the extract.

Extracts were separated from the residues by pouring through cheese cloth followed by filtering through no. 1 and then no. 2 filter paper. Filtering of extracts obtained at 0.5 °C was conducted in an ice bath. Aseptic extracts were prepared by passing through a 0.45-μm filter. All solutions were stored at 0.5 °C.

A double deionized water control was prepared in the same manner as residue extracts. When appropriate, the water control was steam sterilized. The nutrient solution control was full strength Hoagland solution (Hoagland and Arnon, 1939). The nutrient solution was prepared similarly to the water control except each of the four compounds in the solution were steam sterilized separately and then mixed aseptically. All solutions were prepared no more than 48 h in advance and were stored at 0.5 °C until needed. Prior to use in the bioassay, the extracts were equilibrated at room temperature for 1 h.

The pH and electrical conductivity was determined for each extract in both experiments. Total N was determined for Exp. 2 with a modified Micro-Kjeldahl technique (Bremner and Mulvaney, 1982). Phosphorus, K, Ca, Ms, B and Al were measured using emission spectrophotometry for Exp. 2.

Bioassay Procedure

The bioassay procedure used was similar to that of Guenzi and McCalla (1962); Steinsiek et al. (1982); Leather (1983); and Rose et al. (1984). All corn seeds were surface sterilized for 5 min in a 5% sodium hypochlorite solution and rinsed three times in sterile, deionized water. Ten corn seeds were placed germ side up on no. 1 filter paper in a sterile petri dish (100 by 15 mm). A second piece of no. 1 filter paper was placed over the corn seeds and 10 mL of the appropriate extract was applied.

When sterilized extracts were used, aseptic techniques were employed in all steps of the bioassay. To verify sterility of the extracts, the extracts were plated on a sterilized medium containing 5.0 g L^{-1} peptone, 3.0 g L^{-1} beef extract, 1.0 g L^{-1} yeast extract, and 15.0 g L^{-1} Difco agar (Wollum, 1982). These plates were inoculated with 0.5 mL extract and incubated in the dark for 24 h 25 °C. All filter-sterilized extracts contained <2 cfu mL^{-1} except for the corn residue extract from Exp. 2 which averaged 14 cfu mL^{-1} for the 0.5 °C extraction, and 60 cfu mL^{-1} for the 25 °C extraction.

Each petri dish represented an experimental unit. Petri dishes were placed in a loosely sealed plastic bag located in the dark for 96 h at 25 °C. Visual observation of petri dishes containing nonsterilized extracts showed fungal growth under aerated conditions and bacterial growth under nonaerated conditions. Little visual evidence of microbial growth was observed for sterilized extracts. After incubation, percent germination, coleoptile length, radicle length, number of secondary roots, and total length of secondary roots were measured. A seed was considered germinated if both the radicle and coleoptile length were ≥ 2 mm. Coleoptile length, radicle length, number of secondary roots, and total length of secondary roots were calculated for each experimental unit as the mean value for those seeds that had germinated. All measurements were to the nearest mm. The experimental design was a completely randomized block with residue, extraction condition, and sterility comprising three factors. Analysis of variance indicated that the highest order interaction (residue $\times$ extraction procedure $\times$ sterility) was significant for both experiments. As such, $LSD_{(0.05)}$ values were calculated from the highest order interaction to facilitate a conservative comparison between each factor for each experiment.

Experiment 1

The treatments for Exp. 1 were as follows: (i) residues extracted under aerated conditions, nonsterilized; (ii) residues extracted under aerated conditions, sterilized; (iii) residues extracted under N_2 conditions, nonsterilized; and (iv) residues extracted under N_2 conditions, sterilized. Extracts including a water control were prepared for corn, soybean, hay, and oat residues. Five replications were conducted using one sample of the ground residues and a second set of five replications were conducted using a second sample of the ground residues. No significant differences were observed between the residue samples and the data sets were combined to yield 10 replications.

Experiment 2

The treatments for Exp. 2 were as follows: (i) residues extracted at 25 °C, nonsterilized; (ii) residues extracted at 25 °C, sterilized; (iii) residues extracted at 0.5 °C, nonsterilized; and, (iv) residues extracted at 0.5 °C, sterilized. In addition to the residues and control used in Exp. 1, a Hoagland solution control was added. Ten replications were conducted using one sample of the ground residues and a second set of five replications were conducted using a second sample of the ground residues. No significant differences were observed between the residue samples and the data sets were combined to yield 15 replications.

RESULTS

Experiment 1

This experiment was conducted to assess (i) influence of aeration during extraction and (ii) sterilization of the extracts on the response of corn seed germination and early growth. The water control yielded

germination rates of 96 to 100% (Table 1). Nonsterile soybean and oat residue extracts reduced corn seed germination to between 60 and 83%. Nonsterile hay and corn extracts lowered germination to between 17 and 43%. Extraction under N_2 decreased germination in the corn extract, increased germination in the soybean extract while having no effect in the oat and hay extracts. However, residue treatment effects were largely ameliorated by filter sterilization, and germination rates improved to between 67 and 95% across all residue and aeration treatments.

Nonsterile corn and hay extracts reduced coleoptile lengths from 28 to 55% as compared to the water controls (Fig. 1). Neither aeration status nor sterility consistently affected coleoptile inhibition by corn and hay residues. Soybean and oat extracts did not significantly ($P \leq 0.05$) reduce coleoptile lengths relative to the controls, except for the sterilized, aerated soybean extract which slightly reduced coleoptile length.

Nonsterile corn and hay extracts reduced radicle lengths to between 51 and 90% (Fig. 1). The inhibition of radicle length by corn and hay extracts was not consistently influenced by aeration or filter sterilization treatments. Nonsterile oat extracts reduced radicle length 24 to 29%. Filter sterilization strongly increased the inhibitory effects of oat residue extracts on radicle length. Soybean straw extracted under N_2 was unaffected by sterilization, however, filter sterilization greatly increased the inhibitory affects when extracted with aeration. The nonsterilized, aerated soybean extract was the only extract that did not significantly reduce radicle length. The numbers and total length of secondary roots were influenced by the residues and treatments in a similar fashion as compared to the radicle lengths.

Extract pH ranged from 5.2 to 7.1 and no relationship was observed between pH and germination or growth response. Only the pH of the soybean and oat residue extracts were affected by aeration status. Both had higher pH when extracted under aerated conditions, however, this did not translate into any difference in the levels of inhibition except for the soybean where growth was significantly better at the higher pH. There was little pH difference with aeration status among the corn and hay extracts. These findings agree with Patrick and Koch (1958), and Yakle and Cruse (1984) who found that pH did not appear to directly affect corn seed germination and growth.

Electrical conductivities of the residue extracts ranged from 156.0 to 498.0 dS m^{-1}. There was no apparent relationship, however, between electrical con-

Table 1. Germination of corn seeds in residue extracts obtained under aerated and N_2 gas conditions.

	Aerated extraction		N_2 extraction	
	NFS†	FS‡	NFS	FS
	%		%	
Water	100	99	96	99
Soybean straw	60	95	82	91
Oat straw	83	84	72	86
Corn stover	43	67	17	79
Hay	21	81	25	83
$LSD_{(0.05)}$§	11.5%			

† Not filter sterilized.
‡ Filter sterilized.
§ For comparison between any two values.

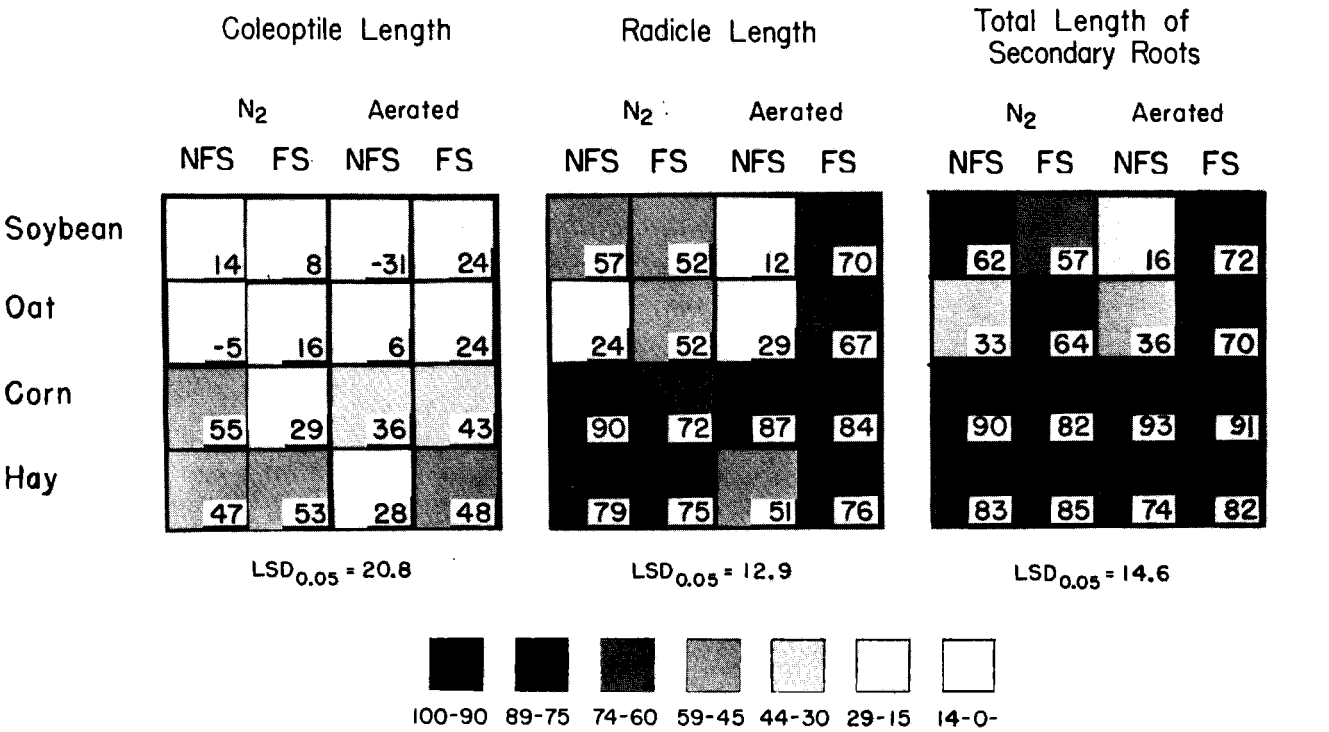

Fig. 1. Coleoptile lengths, radicle lengths, and total length of secondary roots of 96 h corn seedlings grown in residue extracts obtained under aerated and N_2 gas conditions. Data from Exp. 1 expressed as percent inhibition as compared to the water control. LSD(0.05) values for comparison between any two values.

ductivity and germination or growth response. This agrees with the work of Guenzi and McCalla (1962) and Yakle and Cruse (1984) who found that the electrical conductivity did not account for the observed inhibition of growth.

Experiment 2

This experiment was conducted to assess (i) influence of temperature during residue extraction and (ii) sterilization of the extracts on the response of corn seed germination and growth. The water and Hoagland solutions yielded germination rates of between 84 and 99% (Table 2). Germination was significantly inhibited by extraction of the organic residues at 25 °C relative to 0.5 °C. The exception occurred in the nonsterile hay extract where the germination rate was 29% for the 0.5 °C extraction. Nonsterile corn and hay extracted at 25 °C reduced germination rates to 7 and 30%, respectively; and nonsterile soybean and oat residue extracted at 25 °C reduced germination rates to 68 and 56%, respectively. These extracts became markedly less inhibitory with filter sterilization. Germination in the filter sterilized extracts obtained at 0.5 °C were not different from the controls.

Table 2. Germination of corn seeds in residue extracts obtained at 0.5 and 25 °C.

	0.5 °C Extraction		25 °C Extraction	
	NFS†	FS‡	NFS	FS
	%		%	
Water	99	99	92	97
Hoagland	95	98	84	97
Soybean straw	89	92	68	81
Oat straw	89	95	56	77
Corn stover	69	93	7	43
Hay	29	91	30	70
LSD (0.05)§	11.0%			

† Not filter sterilized.
‡ Filter sterilized.
§ For comparison between any two values.

Coleoptile lengths after 96 h incubation were significantly greater in the Hoagland solution than in the water control (Fig. 2). This was, however, the only occurrence where the Hoagland solution improved growth relative to the water control. Soybean residue extracts did not significantly inhibit coleoptile growth compared to the water control for all treatment combinations. Oat residue extracts slightly depressed coleoptile growth with significant length reductions of 18 and 36% in the 25 °C nonsterile and the 0.5 °C filter sterilized extracts, respectively. All treatment combinations of the corn and hay extracts, however, significantly reduced coleoptile lengths by 20 to 78%. Neither filter sterilization or extraction temperature exhibited consistent trends.

The nonsterile soybean and oat extracts obtained at 25 °C did not significantly depress corn radicle lengths after 96-h exposure. All other extract and treatment combinations significantly decreased corn radicle lengths. At 25 °C extraction, soybean and oat reductions were between 7 and 31%; while corn and hay reductions were between 59 and 93%. At 0.5 °C extraction, the distinction between residues was less clear with filter sterilized oat more closely related to filter

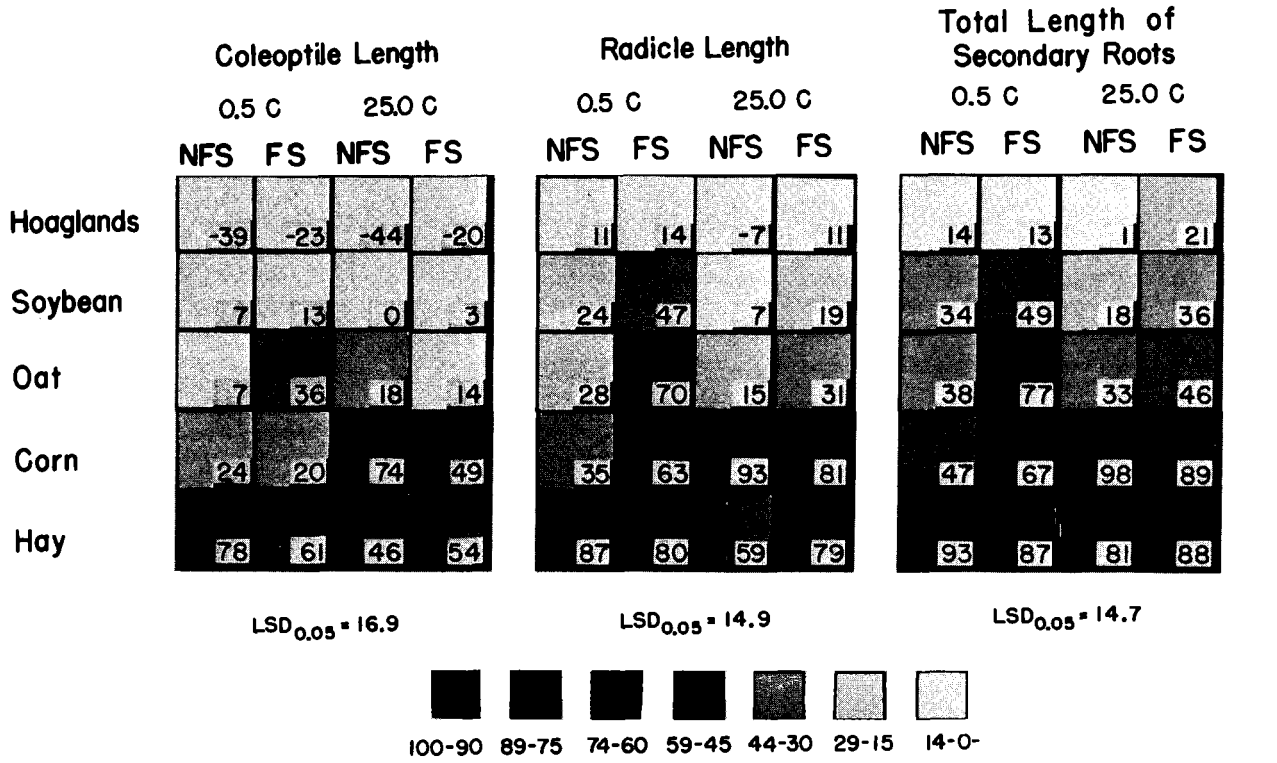

Fig. 2. Coleoptile lengths, radicle lengths, and total length of secondary roots of 96 h corn seedlings grown in residue extracts obtained at 0.5 and 25 °C. Data from Exp. 2 expressed as percent inhibition as compared to the water control. LSD(0.05) values for comparison between any two values.

sterilized corn and hay, having reductions of between 63 and 80%, and nonsterile corn more closely related to nonsterile soybean and oat, having reductions of between 35 and 24%. For the soybean and oat residue extracts, filter sterilization created an additional decrease in radicle lengths over that of the nonsterile extracts. On the other hand, filter sterilization yielded variable results for the corn and hay residue extracts. The numbers and total length of secondary roots exhibited a similar trend to the residues and treatments effects on radicle length.

Chemical analysis indicated that B and Al were well below levels toxic to plant growth for all residues and treatments. The pH of the residue extracts ranged from 5.0 to 7.0, however, there was no relationship between pH and germination or growth response. With the exception of the double deionized water treatments, the electrical conductivities ranged between 140.0 to 500.0 dS m^{-1}, however, there was no apparent relationship between electrical conductivity and germination or growth response.

DISCUSSION

The organic residues fell into two general levels of inhibition. Corn and hay extracts were normally at least twice as inhibitory as oat and soybean extracts, regardless of extract treatment. This is partially due to differences in the composition of the residues. The soybean and oat straw were older tissue left in the field until dry; hay was collected while actively photosynthesizing; and corn stover while still moist. Another important consideration is the level of N found in the extracts. Averaged across all treatments, N content of the soybean, oat, corn, and hay extracts (Exp. 2) were 162.0, 136.0, 283.0, and 612.0 mg L^{-1}, respectively. Corn and hay extracts contained 1.9 and 4.1 times more N, respectively, than the average N content of soybean and oat extracts. McCalla and Duley (1949) found that the addition of an organic N source to decomposing wheat straw stimulated microbial activity and resulted in a corresponding increase in the inhibition of corn seed germination and growth.

Extraction under N_2 gas conditions had little effect on the relative level of toxicity. The exception occurred with the nonsterile soybean straw where aerated conditions significantly decreased germination and significantly increased coleoptile, radicle, and secondary root lengths. This contradicts, at least in part, the previous work of McCalla and Duley (1949), Wallace and Elliot (1979), and Harper and Lynch (1982) where much greater production of toxins was observed under anaerobic conditions, primarily in the form of acetogenins resulting from anaerobic microbial metabolism. The soybean residue was composed primarily of stem tissue with few leaves and may have been more resistant to microbial decomposition. Therefore, it may have been necessary for a very active microbial population to be present for sufficient decomposition and toxin production. This is supported by results of Exp. 2 which, except for coleoptile length, showed that lowering the extraction temperature or minimizing the microbial community eliminated any significant inhibition associated with the nonsterilized soybean extract obtained at 25 °C.

Germination inhibition was greatest when extracts were obtained at 25 °C, where conditions favored microbial growth, and least at 0.5 °C. These findings agree with other work that found residue extractions at temperatures up to 25 °C increased inhibition (Chou et al., 1981; Wallace and Elliot, 1979). Wallace and Elliot (1979) found the major toxins produced to be acetogenins. This suggests that as microbial activity is increased, there is a corresponding increase in toxin production and these toxins are metabolic by-products. The phytotoxic substances that inhibit germination are, however, relatively short-lived since removing the microbes prior to the seed germination test greatly increased germination particularly in extracts from corn and hay residues that were on average 2 to 5 times more toxic than soybean and oat residue extracts. Patrick et al. (1964) provided evidence that phytotoxins produced were rapidly inactivated, but the inactivation was balanced by new toxin production by an active microbial population.

The results obtained for the nonsterile extracts obtained at 25 °C agree with the work of McCalla and Duley (1984) and Guenzi et al. (1967), but in part disagree with the work of Yakle and Cruse (1983, 1984) particularly concerning the effect of corn residue extract on corn seed germination. Yakle and Cruse (1984) found no decrease in germination regardless of age of residue or treatment of extract. In this study, corn extracts (excluding sterile obtained at 0.5 °C) reduced germination by 20 to 92% of control. Overall, corn and hay extracts were 2 to 10 times more detrimental to corn germination and growth than soybean and oat straw which had little inhibitory activity. This agrees with the observations of Guenzi and McCalla (1962).

Residues decomposing in saturated soils, and presumably anaerobic conditions, are shown to produce higher levels of inhibition than in soils at field capacity or lower moisture contents (Patrick and Koch, 1958; McCalla and Duley, 1949). Under these O_2 limiting conditions, the dominant microbial population would consist primarily of facultative and obligate anaerobic bacteria (Alexander, 1977) whose metabolic by-products would consist primarily of acetogenins inhibitory towards seedling germination and growth (Tang and Waiss, 1978; Chou and Patrick, 1976; Harper and Lynch, 1982). However, fungi which are active in residue decomposition under aerobic conditions, are also known to produce phytotoxins (Norstadt and McCalla, 1963; McCalla and Haskins, 1964; Norstadt and McCalla, 1968). In this study, petri dishes containing nonsterilized extracts of hay and corn residue obtained under aerated conditions, supported profuse fungal growth. Nonsterilized extracts of corn and hay obtained under N_2 gas contained little if any visible fungal hyphae, but all plates were covered with bacterial growth. These two different populations, therefore, appear to have similar inhibitory influences as evidenced by the small impact of aeration status in vitro.

Soybean and oat extracts showed little toxicity towards coleoptile growth regardless of extract treatment. Corn and hay residue extracts exhibited greater coleoptile inhibition, however, these levels were similar regardless of extraction procedure. Evidently the

coleoptile toxins in corn and hay were fairly stable and may have been released directly from the residue. This agrees with Guenzi et al. (1967) and Guenzi and McCalla (1966) who showed compounds, primarily phenolic derivatives, released directly from crop residues were detrimental to shoot growth.

Radicle length, number of secondary roots, and secondary root length were significantly inhibited by most organic extracts. Except for the soybean extract obtained under N_2, sterilization reduced root growth approximately 50% with soybean and oat straw extracts. This suggests that a microbial population present during corn seedling growth promotes root development irrespective of toxins from the soybean and oat straw. Filter sterilizing the water controls supports this as root growth tended to be lower in the sterilized controls. For corn and hay extracts, sterilization had a variable effect.

CONCLUSION

Overall, soybean and oat residue extracts were only mildly inhibitory while corn and hay residue extracts were extremely detrimental to seed germination and seedling growth. The degree of inhibition appears to be linked to the age of the residue and its N composition. Comparison of the responses between germination and growth indicated fundamental differences with regard to the extraction conditions and the presence of microorganisms during seed incubation. Corn germination was generally improved with the 0.5 °C extraction and by reducing the microbial population in the incubation. The largest improvement in germination was observed where the greatest germination inhibition occurred. On the other hand, the mildly phytotoxic response for coleoptile and root lengths observed with the soybean or oat extracts could be ameliorated by the 25 °C extraction and the presence of microbes in the incubation. This response was not consistently observed for the corn and hay extracts where the greatest reductions of coleoptile and root lengths occurred.

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