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EFFECTS OF BENZOIC AND CINNAMIC ACIDS ON GROWTH, MINERAL COMPOSITION, AND CHLOROPHYLL CONTENT OF SOYBEAN[1]

R. BAZIRAMAKENGA,[2] R.R. SIMARD[3,*] and G.D. LEROUX[2]

[2]*Laval University, Department of Phytology*
Ste-Foy, Québec, Canada, G1K 7P4

[3]*Agriculture and Agri-Food Canada*
Soils and Crops Research Center
2560 Hochelaga Boulevard
Ste-Foy, Québec, Canada, G1V 2J3

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Abstract—Organic acids are major water-soluble allelochemicals found in soil infested with quackgrass and are involved in several processes that are important in plant growth and development. This study was carried out to gain more information on the effects of benzoic acid (BEN) and *trans*-cinnamic acid (CIN) on growth, mineral composition, and chlorophyll content of soybean [*Glycine max* (L.) Merr. cv. Maple Bell] grown in nutrient solution. The two allelochemicals reduced root and shoot dry biomass of soybean. Treated plants had fewer lateral roots and tended to grow more horizontally compared to the untreated plants. Lateral roots were stunted and less flexible. The amounts of P, K, Mg, Mn, Cl^-, and SO_4^{2-} were lower, and Zn and Fe contents were higher in roots of plants grown with BEN or CIN as compared to untreated plants. Shoots of plants grown with the allelochemical showed greater accumulation of Ca, Mg, and Zn, whereas P and Fe contents were reduced. The BEN and CIN also caused reductions in leaf chlorophyll content. The BEN and CIN may be responsible for negative allelopathic effects of quackgrass on soybean by inhibiting root growth, by altering ion uptake and transport, and by reducing chlorophyll content.

Key Words—Allelochemical benzoic acid, *trans*-cinnamic acid, mineral uptake, quackgrass, *Elytrigia repens*, root morphology, soybean, *Glycine max*.

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*To whom correspondence should be addressed.

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INTRODUCTION

Quackgrass [*Elytrigia repens* (L.) Nevski] is a widespread weed that causes significant crop yield reductions in the temperate zone. The detrimental effects of quackgrass have been associated with production of toxic substances by living or decaying tissues (Rice, 1984). Root and shoot residues of quackgrass were shown to be phytotoxic to several crops including soybean [*Glycine max.* (L.) Merr.], navybean (*Phaseolus vulgaris* L.) and alfalfa (*Medicago sativa* L.) (Weston and Putnam, 1986).

Phenolic compounds are the major allelochemicals found in soil infested with quackgrass (Whitehead et al., 1982; Bobnick and Hagin, 1985). More recently, high concentrations of benzoic acid (BEN) and *trans*-cinnamic acid (CIN) (Figure 1) were identified in the rhizosphere of quackgrass, ranging from 50 to 250 μM (Baziramakenga et al., 1994). These organic acids inhibit germination and plant growth when applied exogenously in millimolar concentrations (Chou and Patrick, 1976; Lynch, 1980; Ramirez and Garraway, 1982; Ueda, 1989). However, the physiological and biochemical aspects of how these compounds affect growth remains obscure. Glass (1974a) found that the absorption of K by excised roots of barley (*Hordeum vulgar* L. cv. Karlsberg) was inhibited by the two compounds. Benzoic acid also inhibited P uptake by excised roots of barley (Glass, 1973, Glass and Dunlop, 1974). Tillberg (1970) observed that CIN has no effect on P uptake by *Scenedesmus obtusiusculus*. None of the above studies was conducted on intact root systems. The BEN and CIN were also reported to reduce chlorophyll content in wheat (*Triticum aestivum*) (Mattagajasingh and Kar, 1989) and soybean (Patterson, 1981).

The objective of this research was to describe the effects of BEN and CIN on growth and chlorophyll and mineral contents of intact seedlings of soybean [*Glycine max* (L.) Merr.] grown hydroponically in order to contribute to the understanding of the mechanisms by which quackgrass affects soybean growth.

METHODS AND MATERIALS

Plant Material. Soybean [*Glycine max.* (L.) Merr. cv Maple Bell] seeds were sterilized for 30 min with 5% hypochlorite, rinsed with distilled water, and placed on sterilized vermiculite saturated with 10 mM $CaSO_4$. The plants

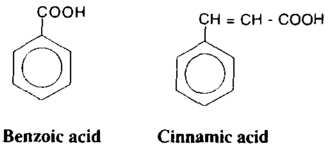

Fig. 1. Structure of benzoic and cinnamic acids.

were maintained in a growth chamber with a 28:20°C day-night temperature, a light-dark regime of 16:8 hr, an irradiance of 280 μmol/m^2/sec and a 70% relative humidity.

Mineral Uptake. Two-week-old seedlings were transferred into an Erlenmeyer containing 100 ml of nutrient solution of the following composition (μM): 750 KNO_3, 325 $Mg(NO_3)_2$, 10 KH_2PO_4, 1000 $CaSO_4$, 8 H_3BO_3, 0.2 $MnSO_4$, 0.2 $ZnSO_4$, 0.2 $CuSO_4$, and 0.2 $(NH_4)_6Mo_7O_{24}$ (Cakmak and Horst, 1991). After three days of acclimatization, the seedlings were transferred into nutrient solutions containing BEN or CIN at concentrations ranging from 0 to 250 μM and adjusted to pH 5.8 with 0.01 M NaOH or 0.01 N HCl. The nutrient solution was replaced every two days because more than 70% of the acids disappeared within three days by plant uptake or microbial degradation (Blum and Dalton, 1985) and to avoid a fall in pH of the nutrient solution.

Seedlings were harvested after four weeks and separated into roots and shoots. Dry weights were obtained after drying the plant parts for 24 hr at 50°C in a forced-air oven. Dried samples were heated in a glass beaker for 3 hr at 450°C in a muffle furnace, and then ground into a fine powder with a Willey mill (20-mesh screen). Ash residue was dissolved in 5 ml of 0.5 N HCl. The solution was filtered through Whatman No. 42 filter paper, and the filtrate was adjusted to 25 ml with distilled water. The K, Ca, Mg, Cu, Fe, Mn, and Zn contents were determined by atomic absorption spectroscopy on a Perkin-Elmer atomic absorption spectrometer 3300. Phosphorus content was measured colorimetrically using a phosphovanadomolybdate complex color on a Hitachi U-1000 Spectrophotometer (Murphy and Riley, 1962).

Anions were extracted according to Cataldo et al. (1975). Briefly, plant tissues (100 mg) were incubated with 10 ml of distilled water for 1 hr at 45°C. The suspensions were filtered through Whatman No. 2 filter paper. The Cl^-, NO_3^-, and SO_4^{2-} contents were measured by ion chromatography (Dionex 4000i, Dionex Corp., Sunnyvale, California) using an anion exchange column (Dionex IonPac AS4A) isocratically eluted with 3 mM $NaHCO_3$ and 2.4 mM Na_2CO_3. Anions were detected by suppressed conductivity (Dionex Micromembrane Suppressor using 0.025 N H_2SO_4 at 5 ml/min as conductivity suppressor).

Determination of Chlorophyll Contents. Fully expanded leaves were taken randomly from seedlings treated with BEN or CIN at 0, 50, 100, and 200 μM. Their petioles were removed, and fresh weights determined. The chlorophyll pigments were extracted by 95% methanol for 16 hr in the dark. Absorbance of the extracts was read at 649 and 665 nm on a Hitachi U-1000 Spectrophotometer. Chlorophyll *a* and *b* contents were calculated using formulas of Knudson et al. (1977):

$$\frac{\text{Chlorophyll } a(\mu\text{g})}{\text{Solution (ml)}} = [(13.70)(A_{665\,\text{nm}})] - [(5.76)(A_{649\,\text{nm}})]$$

$$\frac{\text{Chlorophyll } b(\mu\text{g})}{\text{Solution (ml)}} = [(25.80)(A_{649\,\text{nm}})] - [(7.60)(A_{665\,\text{nm}})]$$

Each experiment was carried out according to a completely randomized design with three replicates and was repeated twice. The data of root and shoot biomass, chlorophyll *a* and *b*, and elemental concentration were submitted to standard analysis of variance after testing for homogeneity of variance. For each compound, the selected concentration treatments were compared to the untreated control using a *t* test.

Root Morphology. In an additional experiment, root morphology was examined. Both aromatic acids were used at 0, 50, 100, 200, and 250 μM. Three days after germination, soybean seedlings were transferred into an Erlenmeyer containing 40 ml of the nutrient solution for 24 hr and then the allelochemicals were added. The Erlenmeyer flasks were kept as previously described for 14 days. At the end of the experiment, root morphology was evaluated visually.

RESULTS

Seedling Growth and Root Morphology. Both BEN and CIN reduced soybean root and shoot dry biomass (Figure 2). A significant reduction of shoot and root biomass occurred for plants subjected to 150 μM of CIN, whereas significant reduction was observed at 200 μM for BEN. When BEN was used at 250 μM, root biomass was reduced by 40% and shoot biomass by 35% compared to the control. The corresponding reductions were respectively 25 and 32% for CIN. Visual differences in soybean root systems were also apparent (Figures 3 and 4). Primary root elongation and the number and length of secondary roots were inhibited by the two allelochemicals. Lateral roots were stunted and less flexible.

Mineral Absorption and Translocation. Each of the two allelochemicals consistently affected the soybean mineral content, the effect being dependent on the concentration of allelochemicals and on the mineral element. Root absorption of P, K, and Mg was severely inhibited by BEN (Table 1). The Ca and Cu absorption was found to be unaffected by BEN. The BEN at concentrations higher than 150 μM strongly enhanced the Fe absorption compared to the control. Low concentrations of BEN (50 and 100 μM) slightly stimulated the uptake of Mn, but larger concentrations were inhibitory. The BEN (250 μM) significantly enhanced Zn root content.

Absorptions of P, K, Mg, and Mn were severely depressed by CIN (Table 1). For example, at 250 μM of CIN, K uptake was inhibited by 64%, P uptake by 42%, and Mg and Mn uptake by 74%. The CIN significantly promoted the absorption of Zn and Fe in soybean roots. The Cu content of roots increased in the presence of low concentrations of CIN. Root absorption of Ca was not affected by CIN.

The BEN treatments did not result in statistically significant changes in

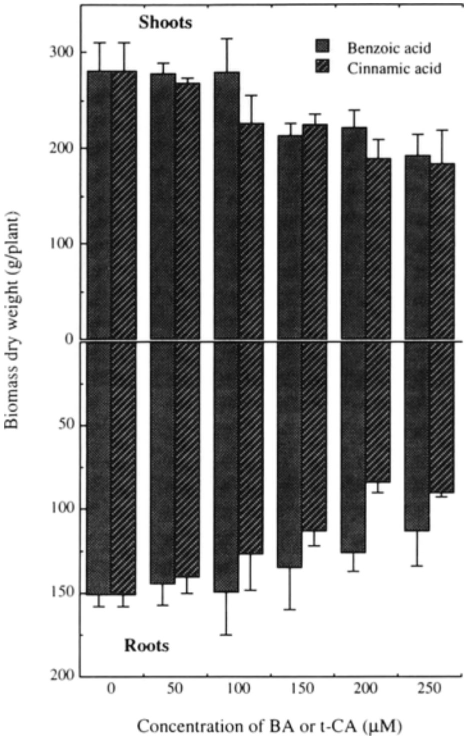

Fig. 2. Effects of benzoic and cinnamic acids on root and shoot dry biomass of soybean.

shoot K and Cu contents. The highest concentrations of BEN significantly promoted the shoot Ca, Mg, and Zn contents while the opposite effect was observed for P and Fe (Table 2). The Mn content of shoots was raised at 100 μM of BEN, as compared with untreated plants.

The amounts of K, Ca, Zn, and Mn measured in the shoots were not changed by the treatments with CIN (Table 2). The shoot Mg content was significantly enhanced by CIN. A significant reduction in shoot P and Fe content was observed in seedlings treated with CIN. Higher concentrations of CIN raised the amount of Cu in soybean shoots.

The shoot Cl^- content was reduced by CIN or BEN (Figure 5). Only CIN depressed the root Cl^- concentration (Figure 6). The contents of SO_4^{2-} in root decreased with increasing rates of the two allelochemicals. Low concentrations of BEN or CIN stimulated the translocation of SO_4^{2-} to the shoots, while the

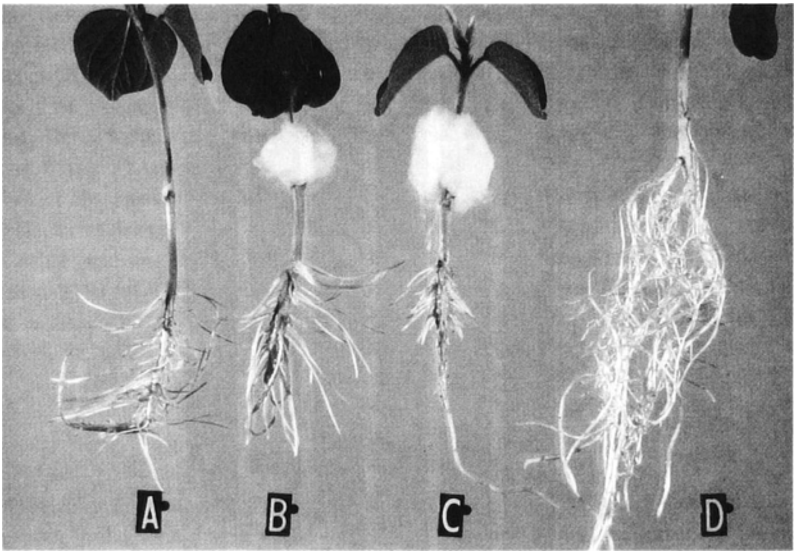

Fig. 3. Soybean root system as affected by benzoic acid: (A) 50 μM, (B) 100 μM, (C) 200 μM, and (D) control.

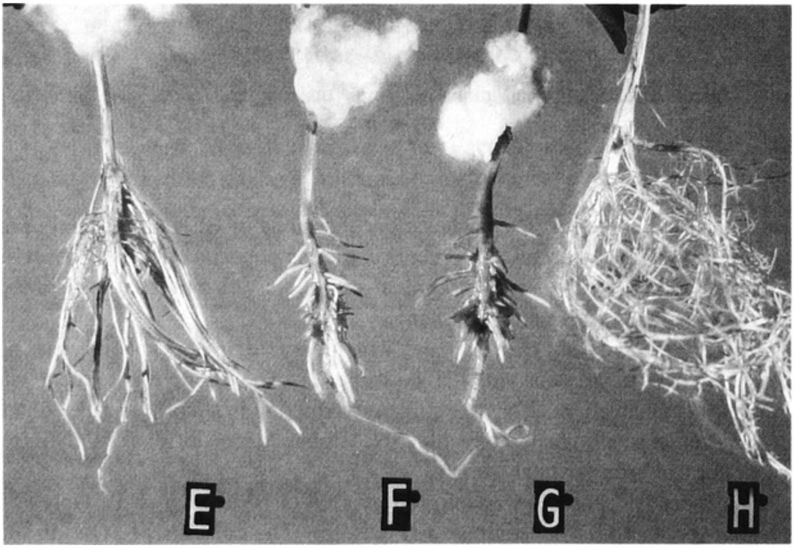

Fig. 4. Soybean root system as affected by cinnamic acid: (E) 50 μM, (F) 100 μM, (G) 200 μM. Control at right.

TABLE 1. EFFECTS OF BENZOIC ACID (BEN) AND *trans*-CINNAMIC ACID (CIN) ON NUTRIENT CONTENT OF ROOTS OF SOYBEAN SEEDLINGS[a]

	Nutrient concentration							
	μmol/g dry wt				nmol/g dry wt			
Treatment	P	K	Ca	Mg	Cu	Zn	Mn	Fe
Control	123	949	94	179	376	354	1412	2435
BEN								
50 μM	120	877	79	155*	265	326	1605	2307
100 μM	102**	823	75	133*	254	313	1464	2596
150 μM	92**	804	77	128**	308	407	1249	3486
200 μM	78**	731*	75	110**	434	465	1071*	4593**
250 μM	72**	721**	80	104**	470	531*	884**	9092**
CIN								
50 μM	117	817	75	151*	409	409	1331	2305
100 μM	107*	739*	79	118**	532*	539*	1281	2842
150 μM	98**	608**	87	96**	489	514*	962**	3745*
200 μM	71**	451**	96	66**	460	674**	593**	6302**
250 μM	71**	343**	111	48**	476	731**	367**	6876**

[a] Levels of significance (compared to the untreated control): $*0.01 < P < 0.05$; $**P < 0.01$.

highest concentrations produced the inverse effect. Concentrations larger than 150 μM promoted the accumulation of NO_3^-; this effect was much more noticeable in roots than in shoots.

Chlorophyll Content. Seedlings grown in the presence of BEN or CIN showed chlorosis, especially at concentrations higher than 100 μM; this was reflected in the chlorophyll content (Figures 7 and 8). At lower concentrations, there was a slight increase in chlorophyll content. Chlorophyll *a* content was affected to a greater extent than chlorophyll *b*. At 200 μM, chlorophyll *a* declined by 37% with BEN and by 27% with CIN. Only BEN at a concentration greater than 100 μM decreased chlorophyll *b*.

DISCUSSION

The growth of soybean seedlings and the formation of lateral roots were inhibited by BEN and CIN, and the extent of inhibition was related to the concentration of the allelochemicals. Vaughan and Ord (1990) also observed that BEN and CIN derivatives altered root morphology in pea (*Pisum sativum*). Our data could explain the results of Weston and Putnam (1986) who reported quackgrass inhibition of legume root hair formation. The allelopathic substance

TABLE 2. EFFECTS OF BENZOIC ACID (BEN) AND *trans*-CINNAMIC ACID (CIN) ON NUTRIENT CONTENT OF SHOOTS OF SOYBEAN SEEDLINGS

	Nutrient concentration							
	µmol/g dry wt				nmol/g dry wt			
Treatment	P	K	Ca	Mg	Cu	Zn	Mn	Fe
Control	91	437	213	73	101	480	441	1125
BEN								
50 µM	89	449	218	87*	97	503	516*	1080
100 µM	82	462	217	87*	92	525	490	1028
150 µM	75**	466	238	105**	135	573	484	982
200 µM	67**	431	253*	106**	138	629*	417	827*
250 µM	66**	422	250*	109**	136	700**	382	784*
CIN								
50 µM	88	485	214	92*	126	511	446	934
100 µM	81*	465	239	96**	131	577	487	850*
150 µM	73**	500	215	97**	154**	575	431	817*
200 µM	73**	398	202	101**	156**	570	416	812*
250 µM	65**	381	216	104**	196**	581	401	833*

[a] Levels of significance (compared to the untreated control): *$0.01 < P < 0.05$; **$P < 0.01$.

may interfere with the root meristematic processes, resulting in impaired cell division (Vaughan and Ord, 1990). Alternation of hormonal balance, such as that of indoleacetic acid (IAA), is one likely mechanism by which allelopathic compounds affect plant growth (Rice, 1984). The BEN and CIN derivatives, depending on the extent and pattern of substitution, influence IAA concentrations in plant tissues by stimulating or inhibiting enzymes involved in IAA synthesis and destruction (Vaughan and Ord, 1991). This mechanism could also be operative for the two allelochemicals used in the present study. Several BEN and CIN derivatives were reported to interfere with metabolic processes such as cell-wall extension, protein synthesis, enzymatic activities, mitochondrial respiration, and plant–water relations (Rice, 1984; Tan et al., 1992; Sato et al., 1982; Dube et al., 1992).

Results from the present work indicate that BEN and CIN affect mineral uptake and their translocation from roots to shoots in soybean. This direct effect on mineral composition constitutes another possible explanation for the inhibition of soybean growth by BEN or CIN. Inhibitions of the same order of magnitude have been reported for soybean and sorghum (*Sorghum bicolor* L. Moench) exposed to ferulic acid (McClure et al., 1978; Kobza and Einhellig, 1987).

The mechanisms of inhibition of ion uptake are still unclear. Glass (1974b)

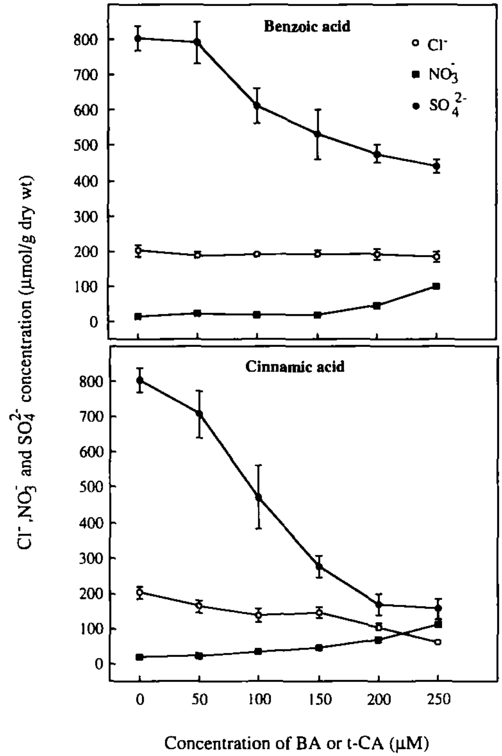

Fig. 5. Effects of benzoic and cinnamic acids on the concentration of Cl^-, NO_3^-, and SO_4^{2-} in shoots of 14-day-old soybean seedlings.

indicated that the inhibitory effects of benzoic and cinnamic derivatives are strongly correlated with their lipid solubilities as reflected by their octanol–water partition coefficients. BEN and CIN can depolarize the root cell membrane, causing a generalized increase in membrane permeability and dysfunction. BEN depolarized the electrical potential of oat coleoptiles (Bates and Goldsmith, 1983) and membranes of epidermal cells of barley roots (Glass and Dunlop, 1974). In contrast, Macri et al. (1986) concluded that BEN had no effect on depolarization of pea stem mitochondria. Rice (1984) noted that phenolic compounds could affect respiration and mitochondrial metabolism, thus limiting ATP synthesis; however, BEN has no effect on mitochondrial ATPase (Macri et al., 1986) and a small inhibitory effect on the respiration of tomato slices (Baker et al., 1978). A recent study with *Saccharomyces cerivisiae* suggests that BEN lowers ATP content as a result of high ATP utilization rather than

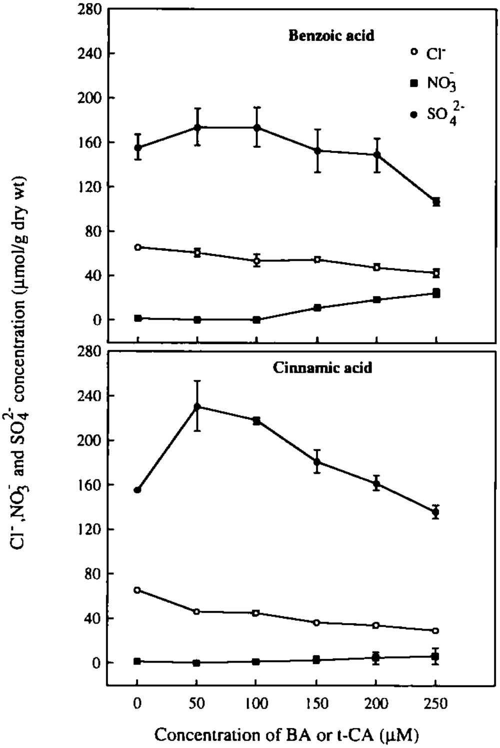

Fig. 6. Effects of benzoic and cinnamic acids on the concentration of Cl^-, NO_3^-, and SO_4^{2-} in roots of 14-day-old soybean seedlings.

from inhibition of its synthesis (Warth, 1991). Tillberg (1970) noted an increase in ATP content for cells of *Scenedesmus* treated with CIN.

The current study showed that NO_3^- accumulated in roots treated with BEN or CIN. It is difficult to speculate on the reason for this accumulation. It could be related to inhibition of enzymes involved in nitrate metabolism, lack of reducing power, or antagonism between nitrates and other anions. The limited availability of information in this area indicates that some BEN and CIN derivatives inhibited nitrate reductase (Pospisil and Sindearova, 1981).

Our results indicate that low concentrations of BEN and CIN can promote chlorophyll content, whereas larger concentrations produced the inverse effect. These results are in accordance with Mattagajasingh and Kar (1989), who concluded that BEN (100 µM) raised the chlorophyll content in wheat. Patterson (1981) reported that CIN (1 mM) reduced the chlorophyll content of soybean.

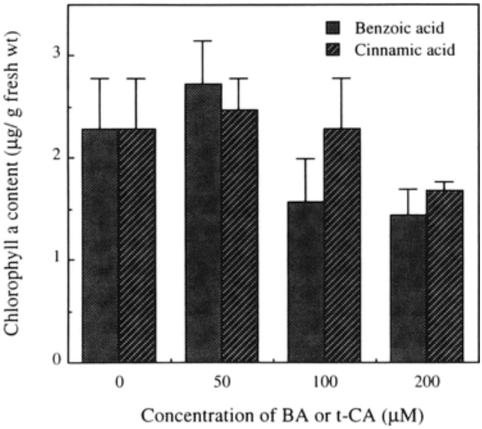

Fig. 7. Effects of benzoic and cinnamic acids on chlorophyll *a* content of 14-day-old soybean seedlings.

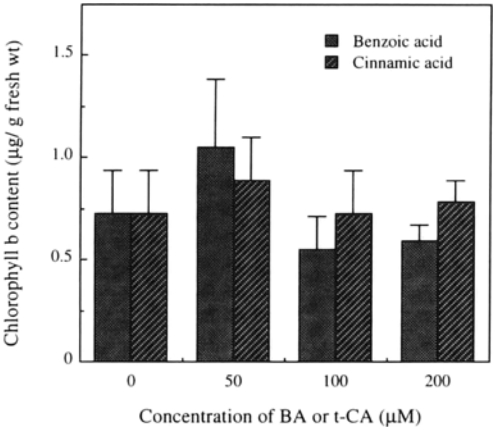

Fig. 8. Effects of benzoic and cinnamic acids on chlorophyll *b* content of 14-day-old soybean seedlings.

Since the chlorophyll content is closely related to plant dry matter production (Buttery and Buzzell, 1977), any reduction in leaf chlorophyll content would limit net photosynthesis and thus diminish total plant growth. The present study does not establish whether reduction in the chlorophyll content is due to a reduction in synthesis or to an allelochemical-induced degradation. The involvement of minerals in chlorophyll synthesis suggests that allelochemicals could influence its synthesis by limiting the supply of these ions. For instance, our data show that Fe was reduced in shoots treated with BEN.

Results from the present work indicate that BEN and CIN affect plant growth, particularly root growth and morphology, alter the uptake and transport of ions, and reduce the chlorophyll content. BEN and CIN may be responsible for the allelopathic effects of quackgrass on crops and weeds under field conditions. As suggested by Einhellig (1986), inhibition of seedling growth might better be regarded as a tertiary effect, with perturbation of mineral nutrition as a secondary effect and the cause of such inhibitions the true primary effect. Cell membranes are the prime targets for alleochemicals and further investigations could clarify the mechanisms by which inhibition of growth is related to changes in membrane properties.

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REFERENCES

BAKER, J.E., LIEBERMANN, M., and ANDERSON, J.D. 1978. Inhibition of ethylene production in fruit slices by a rhizobitoxine analog and free radical scavenger. *Plant Physiol.* 61:886–888.

BATES, G.W., and GOLDSMITH, M.H.M. 1983. Rapid response of the plasma-membrane potential in oat coleoptiles to auxin and other weak acids. *Planta* 159:231–237.

BAZIRAMAKENGA, R., SIMARD, R.R., and LEROUX, G.D. 1994. Determination of organic acids in soil extracts by ion chromatography. *Soil Biol. Biochem.* In press.

BLUM, U., and DALTON, B.R. 1985. Effects of ferulic acid, an allelopathic compound, on leaf expansion of cucumber seedlings grown in nutrient culture. *J. Chem. Ecol.* 11:279–301.

BOBNICK, S.J, and HAGIN, R.D. 1985. Allelopathic effects of vanillin and its glucoside on germinating legume seeds. *Proc. 39th Annu.* Meeting of NWSS, p. 76 (abstract).

BUTTERY, B.R., and BUZZELL, R.I. 1977. The relationship between chlorophyll content and rate of photosynthesis in soybeans. *Can. J. Plant. Sci.* 57:1–5.

CAKMAK, I., and HORST, W. 1991. Effect of aluminum on lipid peroxidation, superoxide dismutase, catalase and peroxide activities in root tips of soybean (*Glycine max*). *Physiol. Plant.* 83:463–468.

CATALDO, D.A., HAROOM, M., SCHRADER, L.E., and YOUNGS, V.L. 1975. Rapid colorimetric determination of nitrate in plant tissue by titration of salicylic acid. *Commun. Soil Sci. Plant Anal.* 6:71–80.

CHOU, C.-C. and PATRICK, Z.A. 1976. Identification and phytotoxic activity of compounds produced during decomposition of corn and rye residues in soil. *J. Chem. Ecol.* 2:369–387.

DUBE, A., BHARTI, S., and LALORAYA, A.M. 1992. Inhibition of anthocyanin synthesis by cobaltous ions in first internode of *Sorghum bicolor* L. Moench. *J. Exp. Bot.* 43:1379–1382.

EINHELLIG, F.A. 1986. Mechanisms and modes of action of allelochemicals, pp. 171–205, *in* A.R. Putnam and C.-S. Tang (eds.). *The Science of Allelopathy*. John Wiley & Sons, New York.

GLASS, A.D.M. 1973. Influence of phenolic acids on ion uptake I. Inhibition of phosphate uptake. *Plant Physiol.* 51:1037–1041.

GLASS, A.D.M. 1974a. Influence of phenolic acids on ion uptake III: Inhibition of potassium uptake. *J. Exp. Bot.* 25:1104–1113.

GLASS, A.D.M. 1974b. Influence of phenolic acids upon ion uptake. II. A structure-activity study of the inhibition of phosphate uptake by benzoic acid derivatives, pp. 159–164, *in* R.L. Bieleski, A.R. Ferguson, and M.M. Cresswell (eds.). Mechanisms of Regulation of Plant Growth, Bulletin 12. The Royal Society of New Zealand, Wellington.

GLASS, A.D.M., and DUNLOP, J. 1974. Influence of phenolic acids on ion uptake. IV. Depolarization of membrane potentials. *Plant Physiol.* 54:855–858.

KNUDSON, L.L., TIBBITTS, T.W., and EDWARDS, G.E. 1977. Measurement of ozone injury by determination of leaf chlorophyll concentration. *Plant Physiol.* 60:606–608.

KOBZA, J., and EINHELLIG, F.A. 1987. The effects of ferulic acid on the mineral nutrition of grain sorghum. *Plant Soil* 98:99–109.

LYNCH, J.M. 1980. Effects of organic acids on the germination of seeds and growth of seedlings. *Plant, Cell Environ.* 3:255–259.

MACRI, F., VIANELLO, A., and PENNAZIO, S. 1986. Salicylate-collapsed membrane potential in pea stem mitochondria. *Physiol. Plant.* 67:136–140.

MATTAGAJASINGH, S.N., and KAR, M. 1989. Changes in the antioxidant system during the greening of etiolated wheat leaves. *J. Plant Physiol.* 134:656-660.

MCCLURE, P.R., GROSS, H.D., and JACKSON, W. 1978. Phosphate absorption by soybean varieties: The influence of ferulic acid. *Can. J. Bot.* 56:764–767.

MURPHY, J., and RILEY, J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 27:31-36.

PATTERSON, D.T. 1981. Effects of allelopathic chemicals on growth and physiological responses of soybean (*Glycine max*). *Weed Sci.* 29:53–59.

POSPISIL, F., and SINDEAROVA, M. 1981. The effect of phenolic acids on metabolism and nutrient uptake of roots, pp. 253-257, *in* R. Brouwer, O. Gasparikova, J. Kolek and B.C. Loughman (eds.). Structure and Function of Plant Roots. Martinus Nijhoff Dr W. Junk Publishers, The Hague.

RAMIREZ, A.M.E., and GARRAWAY, J.L. 1982. Plant growth inhibitory activity of extracts of raw and treated pig slurry. *J. Sci. Food Agric.* 33:1189–1196.

RICE, E.L. 1984. Allelopathy, 2nd ed. Academic Press, Orlando, Florida, 422 pp.

SATO, T., KIUSHI, F., and SANKAWA, U. 1982. Inhibition of phenylalanine ammonia-lyase by cinnamic acid derivatives and related compounds. *Phytochemistry* 21:845-850.

TAN, K.S., HOSON, T., MASUDA, Y., and KAMISAKA, S. 1992. Effect of ferulic and coumaric acids in *Oryza* coleoptile growth and the mechanical properties of cell walls. *J. Plant Physiol.* 140:460-465.

TILLBERG, J.-E. 1970. Effects of abscisic acid, salicylic acid and *trans*-cinnamic acid on phosphate uptake, ATP-level and oxygen evolution in *Scenedesmus*. *Physiol. Plant.* 23:647-653.

UEDA, J. 1989. Promotive effect of capillarol and related compounds on root growth. *Physiol. Plant.* 76:42–46.

VAUGHAN, D., and ORD, B.G. 1990. Influence of phenolic acids on morphological changes in roots of *Pisum sativum*. *J. Sci. Food. Agric.* 52:289-299.

VAUGHAN, D., and ORD, B.G. 1991. Extraction of potential allelochemicals and their effects on root morphology and nutrient content, pp. 399–421, *in* D. Atkinson (ed.). Plant Root Growth: An Ecological Perspective. Blackwell Scientific, London.

WARTH, A.D. 1991. Effect of benzoic acid on glycolitic metabolite levels and intracellular pH in *Saccharomyces cerevisiae*. *Appl. Environ. Microbiol.* 57:3415-3417.

WESTON, L.A., and PUTNAM, A.R. 1986. Inhibition of legume seedling growth by residues and extracts of quackgrass (*Agropyron repens*). *Weed Sci.* 34:366-372.

WHITEHEAD, D.C., DIBB, H., and HARTLEY, R.D. 1982. Bound phenolic compounds in water extracts of soils, plant roots and leaf litter. *Soil Biol. Biochem.* 15:133–136.