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Biochemical Basis for Wheat Seedling Allelopathy on the Suppression of Annual Ryegrass (*Lolium rigidum*)

HANWEN WU,*,†,‡ TERRY HAIG,†,‡ JAMES PRATLEY,†,‡ DEIRDRE LEMERLE,‡,§ AND MIN AN#

Farrer Centre for Conservation Farming and Environmental and Analytical Laboratories, Charles Sturt University, Locked Bag 588, Wagga Wagga, NSW 2678, Australia; NSW Agriculture, Wagga Agricultural Institute, Wagga Wagga, NSW 2650, Australia; and Cooperative Research Centre for Weed Management Systems

The chemical basis for wheat seedling allelopathy on the growth of annual ryegrass was investigated by the identification and quantification of multiple allelochemicals from wheat seedlings. Results indicated that 58 wheat accessions differed significantly in seedling allelopathy and inhibited the root growth of ryegrass from 10 to 91%, depending on accession. Analysis of allelochemicals by GC/MS/MS indicated that allelopathy was significantly correlated with the levels of measured allelochemicals in the shoots and roots of young wheat seedlings. Ryegrass root growth was also negatively correlated with the levels of *p*-hydroxybenzoic, vanillic, and *trans*-ferulic acids in root exudates. Wheat allelopathic potential was negatively correlated with the levels of the eight known allelochemicals quantified in the shoots, roots, and water−agar medium, with multiple regression coefficients (r) of −0.61, −0.71, and −0.71, respectively. In comparison with weakly allelopathic accessions, strongly allelopathic accessions produced significantly higher amounts of allelochemicals in the shoots and roots of the wheat seedlings and also exuded larger quantities of allelochemicals into the growth medium. Wheat accessions with strong seedling allelopathy might be useful for management of weeds during the establishment stage, thereby reducing the need for commercial herbicides in early-season application.

KEYWORDS: Allelochemicals; allelopathy; phenolic acids; root exudates; weed suppression; annual ryegrass (*Lolium rigidum* Gaud.)

INTRODUCTION

Modern agriculture relies heavily on synthetic herbicides in weed management (*1*). However, the continued use of herbicides may threaten sustainable agricultural production and has resulted in serious ecological and environmental problems, such as the increased incidence of resistance in weeds to important herbicides and increased environmental pollution and health hazards (*2*). The incidence of resistance in weeds to herbicides has increased dramatically (*3*). Some weeds, such as annual ryegrass, have evolved multiple resistances to a number of herbicide classes (*4*, *5*). The adverse impacts of herbicides on agricultural production systems, and the ineffectiveness of herbicides on resistant weed species, have prompted the search for nonherbicidal innovations to manage weed populations (*6*). Allelopathy is an alternative weed control method that could be incorporated into an integrated weed management package, thereby reducing the dependence on herbicides and extending the commercial life of valuable chemicals (*6*).

The potential for using allelopathy in weed management has been well documented (*6*−*8*). The application of crop allelopathy in weed suppression involves two crop growth stages, that is, vegetative stage and postharvest stage (*9*). At the vegetative growth stage, crop seedling allelopathy could be exploited to suppress weeds. Crop seedling allelopathy occurs through the exudation of phytotoxins by crop plants into the growth environment. These phytotoxins reduce the growth of weeds in the vicinity. Therefore, crop seedlings with allelopathic activity could reduce the need for early-season application of commercial herbicides, with late-season weed control provided by the heightened advantages of crop competitiveness (*9*). At the postharvest stage, crop residue allelopathy could aid in weed suppression. Allelochemicals present in crop residues may leach into the soil and affect the germination and growth of nearby weeds.

Wheat (*Triticum aestivum* L.), one of the world's most important crops, has been extensively studied for its allelopathic potential in weed management (*9*−*17*). Steinsiek et al. (*10*) reported that aqueous extracts of wheat residues affected the

* Author to whom correspondence should be addressed (e-mail hwu@csu.edu.au).
† Farrer Centre for Conservation Farming, Charles Sturt University.
‡ Cooperative Research Centre for Weed Management Systems.
§ NSW Agriculture.
# Environmental and Analyical Laboratories, Charles Sturt University.

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germination and growth of ivyleaf morning glory [*Ipomoea bederacea* (L.) Jacq.], velvetleaf (*Abutilon theophrasti* Medic.), prickly sida (*Sida spinosa*), and hemp sesbania [*Sesbania exaltata* (Raf.) Cory]. Wheat aqueous extracts are also allelopathic to pitted morning glory (*Ipomoea lacunosa* L.) and common ragweed (*Ambrosia artemisiifolia* L.) (*18*), to a herbicide-susceptible biotype of annual ryegrass (*Lolium rigidum*) (*12*), and to an annual ryegrass biotype resistant to herbicide groups 1−3 and 5−7 (*17*). Research has also shown that root exudates of wheat seedlings are allelopathic to the growth of annual ryegrass (*13*). In an evaluation of 453 wheat accessions originating from 50 countries, Wu et al. (*9*) found that wheat accessions differed significantly in their seedling allelopathy. Further research showed that wheat accessions varied significantly in the production of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and *p*-hydroxybenzoic, vanillic, *cis*-*p*-coumaric, syringic, *cis*-ferulic, *trans*-*p*-coumaric, and *trans*-ferulic acids in the shoots and roots (*15*, *16*, *19*). Wheat seedlings also exuded these compounds into an agar growth medium, and the amounts of released allelochemicals differed among accessions (*19*, *20*). Such significant variations in the production and exudation of allelochemicals among wheat accessions suggest a chemical basis to wheat seedling allelopathy in affecting the growth of annual ryegrass (*9*).

The objectives of this study were to (1) evaluate the allelopathic activity of root exudates from 58 selected wheat accessions on the growth of annual ryegrass, (2) identify and quantify 8 known allelopathic compounds in root exudates released from 17-day-old wheat seedlings, and (3) determine the chemical basis for the differential allelopathic activity among wheat accessions.

MATERIALS AND METHODS

Evaluation of Wheat Allelopathic Activity. A worldwide collection of 58 wheat accessions from the Australian Winter Cereals Collection was selected and screened for allelopathic potential on the growth of annual ryegrass by the equal-compartment-agar method described previously (*13*). Briefly, 12 germinated wheat seeds (surface-sterilized) of each accession were uniformly selected and aseptically sown on an agar surface in three rows on half of a glass beaker prefilled with 30 mL of 0.3% water−agar. The beaker was covered with a piece of Parafilm and placed in a controlled-growth cabinet with a daily light/dark cycle of 13 h/11 h and a temperature cycle at 25 °C/13 °C. After the wheat seedlings had grown for 7 days, 12 germinated seeds of ryegrass were sown on the other half of the agar surface in three rows. A paperboard was used to divide the entire beaker into two equal compartments, each occupied separately by wheat and ryegrass seedlings. The beaker was again covered with Parafilm and placed in the growth cabinet for 10 more days. Ryegrass was grown alone as a control. After 10 days of cogrowth of ryegrass with wheat, the longest root lengths of the ryegrass seedlings were measured. A randomized complete block design with three replicates was used. In addition, 58 wheat-alone experiments (one for each accession) were simultaneously run alongside the above phytotoxicity experiments, for the purpose of collecting shoot, root, and growth-medium samples required for the analysis of allelochemical content.

Preparation of Tissue Samples. Preparation of shoot or root samples was identical to the procedure described previously (*21*). Shoots or roots of 17-day-old wheat seedlings were harvested for each accession and immediately freeze-dried. An amount of 0.1 g of shoots or roots was cut into 2 mm lengths, ground into powder, macerated with 3 mL of 0.001 M HCl, sonicated at 5 °C for 15 min, and centrifuged at 20000 rpm at 10 °C for 15 min. The supernatant was collected and extracted three times with 10 mL portions of diethyl ether. The ether was evaporated under reduced pressure at 35 °C.

Collection of Root Exudates from the Agar Medium. Wheat seedlings were uprooted from the water−agar medium and the roots rinsed twice with 5 mL portions of distilled water to remove the residual agar. The washings were pooled into the agar medium. The growth medium was collected, adjusted to pH 3.0 by dropwise addition of 0.06 M HCl, stirred thoroughly, and sonicated at 5 °C for 15 min. The agar medium was extracted three times with 60 mL portions of diethyl ether. The combined ether layers were then evaporated under reduced pressure at 35 °C.

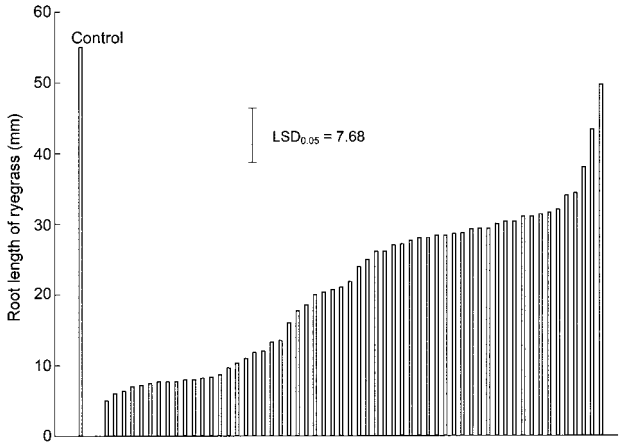

Figure 1. Effects of root exudates from 58 wheat accessions on the growth of annual ryegrass. The 58 wheat accessions were ranked from strongly allelopathic (left) to weakly allelopathic (right) as Tasman, Khapli, Wattines, AUS 12627, Triller, SST 6, AUS 18060, Tunis 2, AUS 18056, Meering, Virgilio, SST 16, Canada 56, Sunstar, AUS 18364, CD 87, RAC 820, Batavia, Cranbrook, Janz, Egret, Opata, Altar 84, Jing Hong, Sunco, Kite, Currawong, Cadoux, Halberd, Bernina, Batten, Canada 4125, Lamar, Studena, Matong, Hartog, Emika, Federation, Insignia, Trident, Dollarbird, Eretria, Robin, Wakanui, Afghanistan 9, Baroota Wonder, Sudan 8, WG-357, Canada 3740, AUS 12788, Sunstate, RAC 710, Excalibur, Afghanistan 19, L 1512-2721, HY-65, Canada 51, and PF 8716.

Derivatization, Quantitation, and GC/MS/MS Analysis. Methods for derivatization and quantitation of wheat samples were identical to those described previously (*21*). All samples were silylated by adding 1.0 mL of MSTFA (Alltech Australia) at 60 °C for 30 min. The silylated samples were directly analyzed by GC/MS/MS (gas chromatography and tandem mass spectrometry), which was carried out on a Varian 3400 CX gas chromatograph coupled with a Varian Saturn 2000 ion trap mass spectrometer. The GC/MS/MS conditions for the analysis of wheat samples were identical to those reported previously (*21*). The DIMBOA and phenolic acids were identified and quantified by comparing retention time and product ion spectra with those in the user library created from the standard compounds. Quantitative analysis was performed by the internal standard method (*21*). All samples were run in triplicate. Results were reported in units of milligrams per kilogram of dry matter for shoot and root tissues and in micrograms per liter for water−agar.

Statistical Analysis. All experimental data were subjected to analysis of variance using Genstat 5 (release 3.2), and the treatment means were tested separately for least significant difference (LSD) at a 5 or 1% level of probability. Correlation analyses of the root growth of annual ryegrass were conducted with each individual allelochemical and each group of allelochemicals in wheat shoots, roots, and root exudates. Multiple regression analysis of the root growth of annual ryegrass was also conducted with all eight allelochemicals determined.

RESULTS AND DISCUSSION

Significant differences in wheat seedling allelopathy in the growth of annual ryegrass were observed in a worldwide collection of 58 wheat accessions. Root exudates from wheat accession Tasman caused the strongest inhibition on ryegrass root growth, with a mean root length of only 5.0 mm. In contrast, the accession PF 8716 yielded the least inhibitory root exudates, with a mean root length of 49.7 mm, which was not significantly

Table 1. Comparison of the 10 Most and 10 Least Allelopathic Wheat Accessions and Allelochemical Contents in Their Shoots,[a] Roots,[a] and Root Exudates[b]

	wheat accessions								
	10 most allelopathic			10 least allelopathic			LSD = 0.01[c]		
allelochemical	shoots	roots	exudates	shoots	roots	exudates	shoots	roots	exudates
p-hydroxybenzoic acid	34.34	57.58	11.15	28.15	54.53	4.39	3.15**	6.32	0.65**
vanillic acid	52.66	71.09	10.92	36.40	50.01	4.53	4.83**	3.49**	0.47**
cis-coumaric acid	4.40	9.53	1.96	3.71	5.65	0.54	0.25**	0.29**	0.27**
syringic acid	36.19	10.62	21.66	8.45	7.41	18.62	3.02**	0.22**	1.25**
cis-ferulic acid	4.73	18.25	4.34	3.97	5.13	2.30	0.49**	1.67**	0.49**
trans-coumaric acid	43.96	91.86	9.70	25.08	48.17	4.96	4.54**	7.57**	0.75**
trans-ferulic acid	105.0	120.9	13.94	33.41	78.02	5.35	3.44**	4.10**	0.84**
DIMBOA	559.7	611.8	na[d]	238.4	551.4	na	20.56**	13.70**	na
average root length of ryegrass (mm)		7.00			35.62			2.45**	

[a] Data presented are the means (mg kg^{-1} of dry matter) of 10 selected wheat accessions. [b] Data presented are the means (μg L^{-1} of water–agar) of 10 selected wheat accessions. [c] **, significant difference at $P < 0.01$. [d] na, not applicable.

Table 2. Correlations of Each Allelochemical with Wheat Allelopathic Potential against the Root Growth of Annual Ryegrass[a]

	wheat		
allelochemical	shoots	roots	root exudates
p-hydroxybenzoic acid	–0.28*	–0.28*	–0.57**
vanillic acid	–0.45**	–0.60**	–0.52**
cis-coumaric acid	–0.10	–0.42**	–0.25
syringic acid	–0.48**	–0.29*	–0.02
cis-ferulic acid	–0.11	–0.53**	–0.15
trans-coumaric acid	–0.33*	–0.44**	–0.24
trans-ferulic acid	–0.44**	–0.26*	–0.43**
DIMBOA[b]	–0.35**	–0.18	na[c]
total[d]	–0.61**	–0.71**	–0.71**

[a] Data expressed as the correlation coefficient between each allelochemical and the root length of annual ryegrass with significance at $P < 0.05$ (*) or 0.01 (**). [b] DIMBOA refers to 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one. [c] na, not applicable. [d] Multiple regression of all allelochemicals with the root length of annual ryegrass.

different from the nil-wheat control (**Figure 1**). Among the 58 wheat accessions, the 10 most allelopathic wheat accessions (allelopathic group) significantly inhibited the root growth of annual ryegrass by 87%, whereas the 10 least allelopathic accessions (nonallelopathic group) reduced the root growth of ryegrass by 35% (**Table 1**). The allelopathic group consisted of Tasman, Khapli, Wattines, AUS 12627, Triller, SST 6, AUS 18060, Tunis 2, AUS 18056, and Meering, and the nonallelopathic consisted of Canada 3740, AUS 12788, Sunstate, RAC 710, Excalibur, Afghanistan 19, L 1512-2721, HY-65, Canada 51, and PF 8716. Wu et al. (*9*) reported that seedling allelopathy differed significantly among wheat accessions. Of the 453 wheat accessions screened, 63 wheat accessions produced root exudates inhibiting root length of ryegrass by >80%. Spruell (*11*) found that 5 of 286 wheat accessions produced root exudates significantly more inhibitory to the root growth of Japanese brome (*Bromus japonicus* L.) and common lambsquarters (*Chenopodium album* L.) than a commercial cultivar T64. When accession CI13633 was grown with Japanese brome on a one-to-one basis in U-tubes containing aerated Hoagland's solution, growth of the weed was ~47% less than when grown with T64.

The allelochemical basis for the varied wheat seedling allelopathy was investigated by identifying and quantifying eight known allelochemicals in the shoots and roots of 17-day-old wheat seedlings and in their associated water−agar growth medium (**Table 2**). Results showed that root length of annual ryegrass was negatively correlated with most of the allelochemicals contained in the shoots or roots of young wheat seedlings. However, the root length of ryegrass was not significantly correlated with the levels of *cis*-*p*-coumaric and *cis*-ferulic acids accumulated in wheat shoot tissues or with the level of DIMBOA in wheat root tissues.

Allelochemicals produced in wheat shoots and roots and released by wheat seedlings as root exudates into the agar growth medium form the chemical basis for wheat allelopathic inhibition on ryegrass. Wu et al. (*19*, *20*) found that there were no significant correlations between root exudates and shoots or roots in the levels of each allelochemical determined, although significant correlation was found between the roots and shoots (*15*). The present study showed that the root length of ryegrass was significantly and negatively associated with only *p*-hydroxybenzoic, vanillic, and *trans*-ferulic acids in the water−agar medium. In addition, no clear association was found between the level of exuded DIMBOA and wheat seedling allelopathy, although 11 of the 58 wheat accessions exuded varied amounts of DIMBOA through wheat living roots into the growth medium (*19*).

Multiple-regression analysis showed that the combination of eight compounds in the shoots, roots, and water−agar medium was significantly associated with wheat allelopathic potential on the root growth of annual ryegrass (**Table 2**). These results demonstrated that each individual allelochemical in wheat root exudates might not be significantly associated with wheat allelopathic activity but that the eight allelochemicals examined jointly showed significant association with wheat allelopathic activity, indicating probable additive or synergistic effects among allelochemicals. Allelopathic effects are mostly seen to be the result of synergistic, additive, or partially antagonistic activity among a group of allelochemicals rather than of a single compound (*22*, *23*).

Grouped data also showed that the root length of ryegrass significantly correlated with the amounts of benzoic and cinnamic acid derivatives, total ferulic, and total *p*-coumaric acids contained in the shoots and roots of wheat seedlings, and in their associated water−agar medium, with the exception of total coumaric acid in root exudates, which did not significantly correlate to root growth of ryegrass (**Table 3**). Syringic acid exuded by the living roots of wheat seedlings had little impact on wheat seedling allelopathy (**Table 2**). After the exclusion of syringic acid from the group of benzoic acid derivatives in the agar medium, a better correlation ($r = -0.60$**) was

Table 3. Correlations of Each Group of Allelochemicals with Wheat Allelopathic Potential against the Root Growth of Annual Ryegrass[a]

	wheat		
allelochemical[b]	shoots	roots	root exudates
benzoics	–0.54**	–0.54**	–0.36**
cinnamics	–0.44**	–0.39**	–0.36**
total COU	–0.31*	–0.46**	–0.26
total FER	–0.43**	–0.32*	–0.37**

[a] Data expressed as the correlation coefficient between each group of allelochemicals and the root length of annual ryegrass significance at $P < 0.05$ (*) or 0.01 (**). [b] Benzoics refers to the benzoic acid derivatives, including *p*-hydroxybenzoic, syringic, and vanillic acids; cinnamics refers to the cinnamic acid derivatives, including *cis*- and *trans*-*p*-coumaric and *cis*- and *trans*-ferulic acids; total COU includes the *cis*- and *trans*-*p*-coumaric acids; total FER includes the *cis*- and *trans*-ferulic acids.

obtained between the remaining benzoic acid derivatives and wheat allelopathic potential.

Comparative chemical data between the allelopathic wheat group and the nonallelopathic group are outlined in **Table 1**. Chemical analysis showed that the allelopathic group produced significantly higher amounts of the eight allelochemicals analyzed in the shoots than the nonallelopathic group. The concentrations of syringic acid, *trans*-ferulic acid, and DIMBOA in the shoots of the allelopathic group were over 4, 3, and 2 times higher than those of the nonallelopathic group, respectively. Except for *p*-hydroxybenzoic acid, concentrations of the other seven compounds were significantly higher in the roots of the allelopathic group than in the nonallelopathic group. It was also found that wheat seedlings of the allelopathic group exuded higher concentrations of allelochemicals into the agar growth medium than the nonallelopathic group (**Table 1**). The concentrations of *p*-hydroxybenzoic, vanillic, *cis*-coumaric, *trans*-coumaric, and *trans*-ferulic acids in the root exudates of the allelopathic group were >2 times higher than those of the nonallelopathic group. These results suggest wheat accessions with high concentrations of allelochemicals in plant tissues and in root exudates might possess strongly allelopathic activity against weeds. Mattice et al. (*24*) recommended that analysis of allelochemicals by certain analytical techniques such as high-performance liquid chromatography (HPLC) be used to predict allelopathic potential among different rice accessions against barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.].

The exuded phenolic acids and DIMBOA identified in the present study do not completely account for all of the observed cultivar-specific allelopathic activity. Together, the eight allelochemicals in the shoots, roots, or water−agar medium explained only 38, 51, and 51% of the variation in the growth inhibition of annual ryegrass, respectively. Similar findings have been obtained in rice allelopathy (*25*) and sorghum allelopathy (*26*). In evaluating the allelopathic potential of sorghum aqueous extracts by using wheat as a bioassay species, Ben-Hammouda et al. (*26*) found that wheat radicle length was negatively correlated with each of the five phenolic acids contained in the aqueous sorghum extracts. Although significant individually, associations were small, accounting for <20% of the variation in inhibition. Together, the five phenolic acids accounted for 72% of the variability in inhibition of wheat radicle growth.

Wheat plants are known to produce many allelochemicals of structurally distinct groups, such as fatty acids, hydroxamic acids, and other bioactive compounds (*27*−*29*). Wheat seedlings that inhibit ryegrass root growth may therefore contain other active, but as yet unknown, allelochemicals in addition to those examined in this study. These bioactive compounds could form a complex allelochemical mixture to exhibit combined effects with much greater allelopathic activity than that of each individual compound (*23*). Further research in determining the relationship between wheat seedling allelopathy and other allelopathic compounds is required prior to the implementation of wheat seedling allelopathy for integrated weed management.

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