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ALLELOPATHIC POTENTIAL OF WHEAT ACCESSIONS

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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

ALLELOPATHIC POTENTIAL OF WHEAT ACCESSIONS

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

BY

JAMES ALTON SPRUELL

Norman, Oklahoma

1984

ALLELOPATHIC POTENTIAL OF WHEAT ACCESSIONS

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF BOTANY AND MICROBIOLOGY

By

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

STYLE USED IN DISSERTATION

This dissertation has been written in the form of two papers. Each paper is to be submitted to *Weed Science* and conforms to the format specified by the editors of *Weed Science*.

ALLELOPATHIC POTENTIAL OF WHEAT ACCESSIONS

PAPER I

GROWTH INHIBITION OF TEST SPECIES

Abstract. Root exudates of 286 accessions of hard red winter wheat (*Triticum aestivum* L.) were compared with that of the commercial strain 'T 64' for their relative ability to inhibit root and shoot growth of Japanese brome (*Bromus japonicus* L.) and common lambsquarters (*Chenopodium album* L.). Five accessions produced root exudates significantly more inhibitory to root growth in indicator plants than the commercial strain. When Japanese brome was grown in the presence and absence of wheat in sand cultures, wheat significantly retarded growth of the brome, with two of the test accessions of wheat significantly more effective than 'T 64' in reducing weed growth. When CI 13633 was grown with Japanese brome on a one-on-one basis in U-tubes containing aerated Hoagland's solution, growth of the brome was approximately 53% of that obtained by growing it with 'T64'. The consistent and superior inhibition of the indicator species by the test accessions indicates a strong allelopathic character which could be incorporated into commercial cultivars.

Additional index words. Allelopathy, biological weed control.

INTRODUCTION

In 1972, Bell and Koeppe (2) postulated that crops possess the potential to suppress the growth of weed seedlings and that the allelopathic agents could serve as natural herbicides. However, in 1974, Putnam and Duke (19) suggested that the allelopathic potential of crops has possibly been reduced or lost during crossing programs selecting for other characters. They screened 538 accessions of cucumber for allelopathic potential and found several wild types that produced exudates more inhibitory to weed germination and growth than 4 commercial varieties. Fay and Duke (11) screened 3000 accessions of oats for their ability to exude scopoletin. They found that 25 of these exuded more blue flourescing material (characteristic of scopoletin) than a standard cultivar. When one of the 25 accessions was grown in close association with wild mustard (Brassica kaber (D.C.) L.C.Wheeler var. pinnatifida (Stokes) L.C. Wheeler), the growth of the weed was significantly lower, with more chlorosis, twisting, and stunting of the plants than that obtained by growing the weed with the standard cultivar. Initial field studies by Lockerman and Putnam (18) demonstrated the ability of selected cultivars of cucumber to reduce the growth of proso millet (Panicum milicaeum L.) more than commercial strains.

The allelopathic potential of wheat straw residue was evaluated by Steinsiek, Oliver, and Collins (21) and found to inhibit seed germination and seedling growth of weeds. Tang and Waiss (22) reported that aqueous extracts of decomposing wheat straw contain salts of acetic, propionic, and butyric acids. Several phenols, including cinnamic, p-coumaric, ferulic, and sinapic acids, have been identified in both living and decaying parts of wheat. Additionally, ferulic and o-coumaric acids have been identified in the root exudates of wheat (23). Because of the high allelopathic potential of fatty acids in inhibiting amylolysis in endosperm (4), and phenols in inhibiting cell elongation and division (5,17), chlorophyll content (9), stomatal opening and closing (8,24), protein synthesis (6), and mineral uptake (7,12,13), it should be possible to identify a strain of wheat of superior allelopathic potential which would reduce the growth of weeds in cultivated fields. As an initial step in investigating this possibility, 286 strains of wheat were compared with a commercial strain for their relative ability to exude compounds inhibitory to weed growth.

EXPERIMENTATION AND RESULTS

Initial study. Two hundred eighty-six accessions of hard red winter wheat were obtained from the U.S. Department of Agriculture Northeastern Plant Introduction Station. In the initial screening, 4 - 6 caryopses[1] of 'T 64' and each test accession were placed on wet filter paper in 9 cm petri dishes and incubated at 28 C for 48 hrs in the dark. Three evenly germinating seeds were selected and planted in 8 cm styrofoam pots containing 350 g of silica sand. The pots were

[1]Although the caryopsis of wheat and brome grass is not technically a seed, for convenience we will employ the terms as synonomous herein.

watered on Day 1 with 120 ml of water, and on Days 3 and 5 with sufficient distilled water to saturate the sand. The amount of water added was carefully controlled to provide not more than 1 ml loss from the bottom of the pot in order to prevent the loss of any allelochemics. The plants were grown in a controlled growth chamber under a 14-hr day (1500 ft-c) at 28 C and a 10-hr night at 21 C. Pots without wheat were periodically included in the study to determine whether the commercial strain 'T 64' had inhibitory activity. On Day 7 the pots were flushed with sufficient 0.02 M phosphate buffer (pH 6.05) to provide 70 ml of leachate. Eighteen milliliters of the leachate were used to water 10 Japanese brome seeds scattered on 80 gm of quartz sand contained in 9 cm petri dishes. The edge of each petri dish was wrapped with parafilm to reduce the variance in root growth due to moisture loss. Seventeen milliliters of the flush were used to water 30 common lambsquarters seeds planted in 80 g of sand in 9 cm petri dishes. Each indicator dish was placed in a growth chamber under conditions described above for a period of 6 days for Japanese brome and 8 days for common lambsquarters. On the 5th day, each petri dish containing common lambsquarters received an additional 5 ml aliquot of water. Germination, root, and shoot length were measured.

No significant differences were observed in the effect of leachate from pots without wheat or from pots with 'T 64'. However, the effect of root exudates from test accessions of wheat varied greatly in their activity on root and shoot growth in the indicator species. The greatest effects were observed on root growth. In common lambsquarters, root growth ranged from 63 to 202 % of control growth and in Japanese brome, it ranged from 42 to 163 %. The effect of the root exudates on shoot growth was smaller, with growth of common lambsquarters varying from 71 to 122 % of control growth and Japanese brome from 79 to 126 %.

To confirm the results, the experiment was repeated 3 - 7 times with selected strains that appeared to be allelopathic. The same procedure was utilized with the exception that all sand was autoclaved and all seeds were washed with a 5 % Chlorox solution for approximately 3 min.

Mean inhibition of root and shoot growth in the replicated studies was less than that observed for the initial study (Table 1). Four accessions inhibited root growth in common lambsquarters by 20 % or more with a maximum of 29 % inhibition. Alternately, 3 accessions inhibited root growth in Japanese brome by 20 % or more with a maximum inhibition of 25 %.The effect of the exudates on shoot growth was inconsistent, with only one accession significantly inhibiting shoot growth.

Side-by-side tests. 'T 64' and four wheat accessions which significantly inhibited root growth of one or both of the indicator species in the initial study were selected for further study. Three wheat seeds of each accession germinated under the conditions described in the initial study were planted with either 10 Japanese brome or 30 common lambsquarters seeds in 8 cm styrofoam pots containing 350 g of autoclaved quartz sand. The wheat was planted in a 5 cm circle with the indicator seeds placed randomly in the pot. All seeds were washed with a 5 % Chlorox solution prior to the test. Each pot received an initial 120 ml of 50 % Hoagland's solution (pH 6.05) and, thereafter on a daily basis, sufficient culture solution to saturate the sand. On Day 16, the plants were harvested and germination, root, and shoot dry wt were determined. Eight replications were utilized per experiment in a Latin square design. The experiment was conducted twice.

Multivariate analysis indicated significant differences between experiment dates. The first trial was conducted in February under slightly drier conditions than the second, which was conducted in March. This difference in humidity probably accounted for the difference in the results of the two trials. Wheat significantly reduced the oven dry weight increments of Japanese brome seedlings, with two of the test accessions of wheat significantly more effective than 'T 64' in retarding weed growth (Table 2). Germination percentages of Japanese brome were largely unaffected by the presence of wheat with only CI 12748 significantly reducing germination of the brome in a single trial. In the February test, seedling growth of common lambsquarters was significantly retarded when grown with either test or commercial accessions of wheat; however, only two of the allelopathic accessions significantly retarded seedling growth on an overall (average) basis (Table 3). Root growth of the indicator forb was significantly lower when grown with CI 12748 and CI 13633 than when grown in the absence of wheat or with 'T 64'. Germination of common lambsquarters was significantly increased in one or more trials by every accession of wheat tested with the largest increases associated with the test accessions of wheat. Mean total weed weight per pot was not significantly different in the presence or absence of wheat. The increase in germination and inhibition of root growth of the forb in the presence of wheat is perhaps a reflection of wheat roots which are known to exude compounds which inhibit and stimulate plant growth (23). Because there were no significant effects of wheat root exudates on germination in the initial study, it appears the stimulatory compound may be only slightly water soluble.

U-tube experiments. Root exudates from commercial and allelopathic strains were tested for their effect on Japanese brome in U-tube experiments designed by Tubbs (20) and modified by AlSaadawi and Rice (1). A weed seedling of uniform root and shoot length was placed in one end of a pyrex U-tube (2.5 cm x 56 cm) painted with aluminum paint and either a test or commercial strain of wheat was placed in the other end. Each seedling was held in place by inserting the stem through a one-hole cork stopper and encasing in cotton. The tubes were filled with 50 % Hoagland's solution and aerated daily for a period of 10 min. Seedlings were grown in a controlled environmental chamber for a period of 3 weeks under conditions previously described . Six seedlings of each accession were tested and the experiment was conducted twice.

The root exudate of one wheat strain significantly reduced overall seedling growth (Table 4,5). It is noteworthy that root growth of Japanese brome was reduced by one or more wheat accessions in all tests, thus providing substantial evidence for allelopathy.

Root growth of Japanese brome was measured every 4 days in the U-tube experiment to more closely determine the timing and release of any inhibitors. Inhibition was not apparent until the 12th day of the experiment, whereupon a sharp reduction in root growth was observed (Figure 1). The pattern of growth indicates that inhibitors were either produced initially between the 8th and 12th day of the experiment or that a physiologically active concentration of the allelochemics was not reached until that time. In considering the shorter experiments conducted earlier in the investigation, the latter would seem more logical. The continued increase in inhibitory activity until the termination of the experiment also supports the second hypothesis.

DISCUSSION

The investigation demonstrated that selected accessions of wheat can inhibit weed seedling growth under laboratory conditions. The combined results from root exudate and total interference studies (side-by-side) suggest that at least some of the wheat accessions have an allelopathic component in their interference. A chemical characterization and isolation of the allelopathic compounds could possibly lead to a synthesis of the compounds or their analogs for use as herbicides (18). Additionally, the incorporation of the character into commercial cultivars through genetic manipulation could provide a basis for biological weed control (18). By judiciously selecting the more allelopathic individuals from an allelopathic strain and by positive assortive breeding with a commercial cultivar, it might be possible to develop a commercial strain which would release kolines as natural herbicides. In the future, it might be possible to more directly incorporate the allelopathic genes into a cultivar through genetic engineering.

Vancura's (23) analysis of the mixed nature of root exudates in wheat is consistent with the simultaneous inhibition of seedling growth and stimulation of germination in common lambsquarters observed in the side-by-side experiment. The presence of inhibitory materials, such as phenols, and plant hormones with both stimulatory and inhibitory effects could promote erratic results. Breeding programs selecting for other characters may have compounded the problem by not only having reduced the natural inhibitory potential of cultivars (19) but possibly may have increased the number and quantity of compounds in root exudates that promote weed growth. An efficient strategy of biological weed control should consider genetic manipulations to reduce compounds in exudates which stimulate weed growth and increase those which inhibit weed growth.

It appears that populations of Japanese brome vary in their response to allelopathic agents. With a variety of potential weed responses, a successful program of biological weed control should consider a rotation of strains with different interference mechanisms, including both allelopathic and competitive components. Hopefully this approach would reduce the development of microbial and weed populations resistent to interference.

The growth inhibition of Japanese brome in U-tube studies by both commercial and test accessions indicates that the commercial cultivar 'T 64' exudes inhibitory compounds also, but the allelopathic potential is less than for several of the test accessions. This suggests that many of the 286 accessions may have had some allelopathic potential but were eliminated from subsequent tests because the inhibitory compounds were not readily leached from the pots. This experiment also suggests that allelopathic genes have not been eliminated from commercial wheat but perhaps are in a low allelic frequency. Future screening programs concentrating on these genotypes could prove fruitful. A survey of wild-type relatives of wheat for genotypes with strong allelopathic potential might prove even more valuable in breeding wheat varieties for allelopathic control of selected serious weeds in the future.

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Table 1. Effects of root exudates from selected accessions of wheat.

	% of Control Growth			
	Japanese brome		Common lambsquarters	
Strain	Root	Shoot	Root	Shoot
CI 11977	88	96	71**	90*
CI 12748	79*	96	79**	97
CI 13633	75*	90	75*	97
CI 13751	77*	90	72*	89
PI 86207	81*	90	92	89

* Significantly different from control at 0.05 probability level

** Significantly different from control at 0.01 probability level

Table 2. Effects of wheat interference on Japanese brome (side by side tests).

		%	Mean Dry Wt (mg)			
Strain	Trial	Germ-ination	Root	Shoot	Whole Plant	Weed wt per pot
No Wheat (control)	1	96	2.1	6.5	8.7	82.8
	2	95	2.3	6.7	9.0	85.5
	Avg.	96	2.2	6.6	8.8	84.2
T 64	1	100	1.9	5.6a	7.5a	74.9
	2	94	2.1	5.4a	7.5a	69.8
	Avg.	97	2.0a	5.5a	7.5a	72.3a
CI 11977	1	100	1.8	5.9	7.7	77.2
	2	93	1.9	5.4a	7.3a	67.6a
	Avg.	97	1.9a	5.7a	7.6a	72.4a
PI 86207	1	100	1.5ab	5.3a	6.7a	67.2a
	2	94	1.8a	4.9ab	6.7ab	62.3a
	Avg.	97	1.7ab	5.0ab	6.7ab	64.8ab
CI 12748	1	100	1.5ab	5.3a	6.8ab	67.9ab
	2	88a	1.7ab	4.7ab	6.4ab	56.2ab
	Avg.	94	1.6ab	5.0ab	6.6ab	62.0ab
CI 13633	1	100	1.6	5.0	6.6a	65.7
	.	.	.	.	.	.
	.	.	.	.	.	.

a. Significantly different from control at the 0.05 probability level.

b. Significantly different from T 64 at the 0.05 probability level.

Table 3. Effects of wheat interference on common lambsquarters (side by side tests).

Strain	Trial	% Germ-ination	Mean Dry Wt (mg) Root	Shoot	Whole Plant	Weed wt per pot
No Wheat (control)	1	50	0.9	5.8	6.7	101.1
	2	48	0.5	3.6	4.1	57.6
	Avg.	49	0.7	4.7	5.4	79.4
T 64	1	65a	0.7	3.8a	4.5a	86.6
	2	47	0.6	3.4	4.0	50.7
	Avg.	56	0.6	3.6	4.2	68.7
CI 11977	1	69a	0.6a	4.1a	4.7a	96.0
	2	43	0.5	3.4	3.9	47.4
	Avg.	56	0.5	3.6	4.1	71.7
PI 86207	1	70a	0.6	3.5a	4.1a	87.0
	2	58a	0.4	2.7	3.1	53.5
	Avg.	64ab	0.5	3.0a	3.5a	70.2
CI 12748	1	75ab	0.6	3.5a	4.1a	92.6
	2	57b	0.4b	2.6a	3.0	50.5
	Avg.	66ab	0.5ab	3.0a	3.5a	71.6
CI 13633	1	69a	0.6ab	3.4a	4.0a	82.9
	.	.	.	.	.	.
	.	.	.	.	.	.

a. Significantly different from control at the 0.05 probability level.

b. Significantly different from T 64 at the 0.05 probability level.

Table 4. Effects of root exudates from selected accessions of wheat on dry weights of Japanese brome in U-tube experiments.

	Mean Dry Weight (mg)*			
Strain**	Root	Shoot	Whole Plant	% of Control
T64	21.4a	59.4a	80.8a	
CI 12748	17.7a	59.6a	77.2a	96
PI 86207	20.0a	59.6a	79.5a	98
T64	24.2a	61.1a	85.2a	
CI 13633	13.3b	31.8b	45.1b	53

* Means with the same letter in each column of each experiment are not significantly different at the 0.05 probability level.

** Grouped by separate experiments.

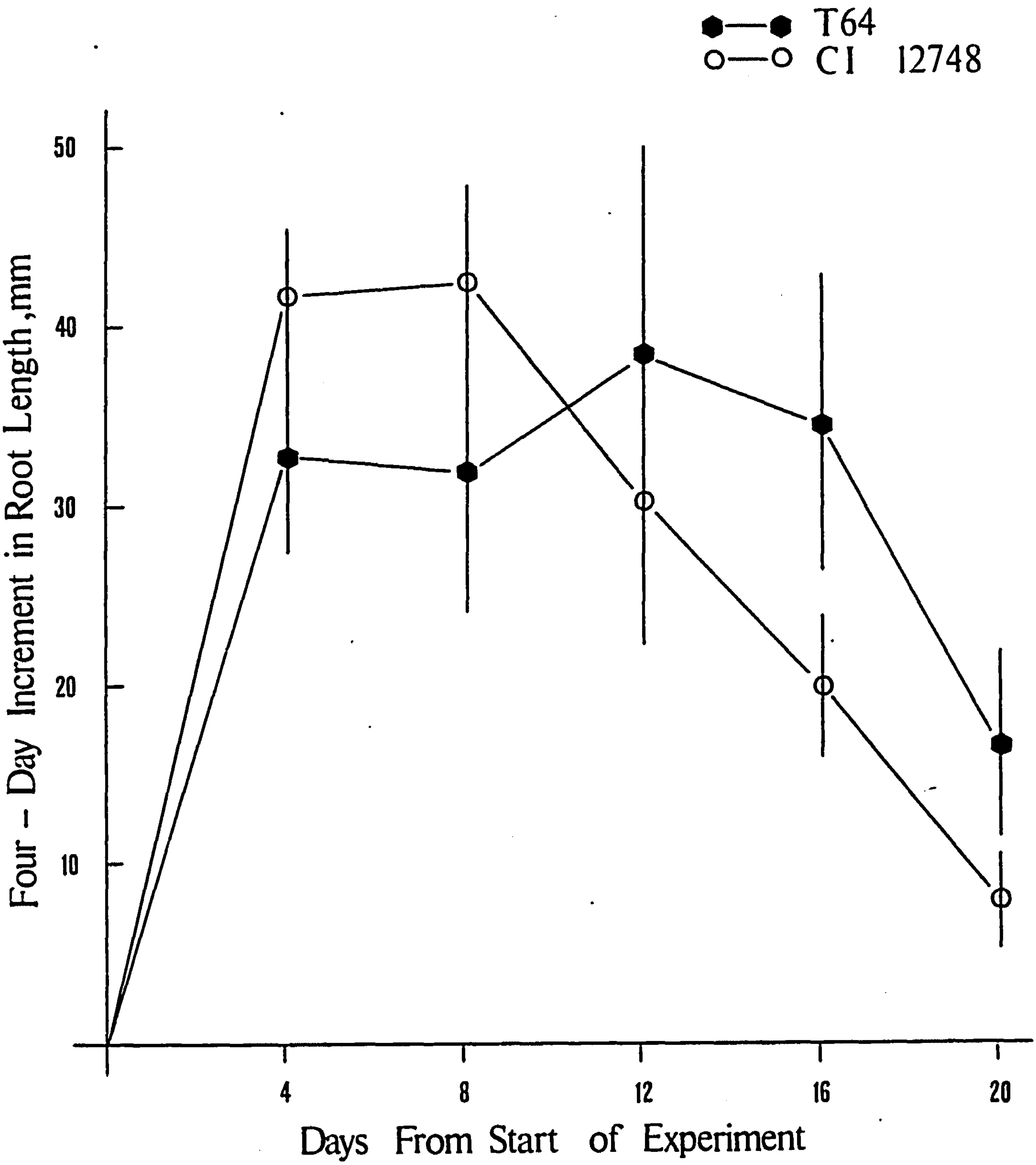
Table 5. Effects of root exudates from selected accessions of wheat on root and shoot lengths of Japanese brome in U-Tube experiments.

	Mean Length (mm)*			
Strain**	Root	Shoot	Whole Plant	% of Control
T64	194a	183a	377a	
CI 12748	172b	177a	348a	92
PI 86207	177b	178a	354a	94
T64	222a	150a	372a	
CI 13633	192b	113b	305b	82

* Means with the same letter in each column of each experiment are not significantly different at the 0.05 probability level.

** Grouped by separate experiment.

Figure 1. Timing of release of inhibitor(s) from roots of CI 12748 and 'T 64' as indicated by growth in root length of Japanese brome.


T64
CI 12748
Four - Day Increment in Root Length, mm
50
40
30
20
10
4
8
12
16
20
Days From Start of Experiment

PAPER II

EFFECTS ON RESPIRATION

Abstract. In an earlier paper, several wheat accessions were identified which produced root exudates significantly more inhibitory to growth of Japanese brome (*Bromus japonicus* L.) and common lambsquarters (*Chenopodium album* L.) than the commercial strain 'T 64'. Two accessions, CI 12748 and PI 86207, were compared with 'T 64' for their relative ability to exude compounds that inhibit respiration of Japanese brome. Respiration rates of roots and shoots of young seedlings and of newly emerged whole seedlings were significantly reduced by root exudates from the allelopathic wheat accessions.

Additional index words. Allelopathy, respiration, biological weed control.

INTRODUCTION

In recent years studies have documented that many allelopathic agents have a pronounced effect on plant respiration. Allelochemics stimulated respiration in such diverse genera as *Chlorella* (2), *Andropogon* (5), *Pinus* (9), and mature *Triticum* (9). On the other hand, phytotoxins inhibited respiration in germinating seeds of *Triticum* and *Hordeum* (9), mitochondrial metabolism of *Phaseolus* (3), and mitochondrial ATPase (4). The integral role of respiration in plant growth makes this action a particularly effective and important allelopathic mechanism.

In a previous study, 286 accessions of hard red winter wheat were compared with a commercial strain for their relative ability to exude compounds that inhibit weed growth (6). Several superior allelopathic strains were identified which consistently inhibited root growth of Japanese brome in root exudate and total interference experiments. As an initial step in examining the potential mechanism of action of the inhibitors, root exudates from allelopathic and commercial accessions of wheat were tested for their effect on respiration of germinating seeds and young seedlings of Japanese brome.

EXPERIMENTATION AND RESULTS

Effects on germinating seeds and newly emerged seedlings. In the previous study, accessions CI 12748 and PI 86207 inhibited root growth of Japanese brome in each of the experiments we conducted and were chosen for further study. Three wheat plants of each accession were grown for 6 days in silica sand contained in a styrofoam pot under conditions described in the initial study section of our earlier work (6). Each pot was then flushed with sufficient 0.02 M phosphate buffer (pH 6.05) to provide 70 ml of leachate. One milliliter of leachate was used to water 20 Japanese brome seeds placed on filter paper in a 25 ml Erlenmeyer flask. The mouth of the flask was covered with parafilm and the flask was placed in a growth chamber for 2-5 days.

Carbon dioxide exchange was measured in an open air system on the 2nd, 3rd, 4th, and 5th day of treatment. Each flask was wrapped with aluminum foil to exclude light and fitted with a two-hole rubber stopper in which glass tubes had been placed. A copper-constantan thermocouple was permanently mounted through the rubber stopper for temperature measurement. A second flask which contained no wheat was prepared without a thermocouple and both flasks were placed in a water bath at 28 C. Air was collected from the overhead vent of the laboratory and passed through an approximately 200 liter sealed vessel to dampen short term fluxuations of CO_2.The stream of air was passed through a 500 ml side-arm flask which contained 300 - 400 ml of water and then through a water-jacketed condensor. The humidified air was conducted by tygon tubing to a Y-fitting where it was divided into two streams. Each end of the Y was connected to a separate flow meter and then respectively to a glass tube of either the sample or reference flask. The remaining tube of each flask was connected to an Anarad Infra Red Gas Analyzer. The flow of air through each flask was maintained at a constant 60 l/hr. Respiratory rates were determined by measuring the differential concentration of CO_2 of air passing through the test and reference flasks. Two replicates of each accession were tested on a given day and the experiment was conducted 3 times. Root exudates of CI 12748 and CI 86207 significantly reduced the CO_2 exchange rates of seedlings on the 4th and 5th day of exposure to leachate (Figure 1).

Effects on roots and shoots. Three wheat plants of each accession were grown for 6 days in silica sand contained in a styrofoam pot under conditions described above. Each pot was then flushed with sufficient 0.02 M phosphate buffer to provide 70 ml of leachate. Five milliliters of leachate were used to water 30 weed seeds placed on filter paper in a 9 cm finger bowl. The top of the bowl was covered with parafilm to prevent drying and the bowl was placed in the growth chamber for 3 to 8 days.

Root respiration was measured on the 1st, 2nd, 3rd, 4th, and 6th day after 50 % or more of the seeds had germinated. Shoot measurements were made on the 2nd, 3rd, 4th, and 6th day after germination. Respiration rates were determined by placing 1.5 cm long root tips or shoot tips with 2.8 ml of 0.18 M phosphate buffer (pH 5.0) in a 15 ml side-arm Warburg flask. Potassium hydroxide and a fluted wick were placed in the center well. The flask was wrapped with aluminum foil to exclude light and was transferred to a differential respirometer for measurement of respiration rates at 28 C. Four measurements of each treatment were made per day and the experiment was conducted twice.

Respiration rates of roots and shoots were reduced when the seeds were germinated in root exudate from allelopathic strains of wheat (Figure 2,3). There were generally no significant differences in treatment effects on any given day; however, the overall treatment effect was significant at the 0.05 probability level for both roots and shoots.

Effects on older seedlings. We previously reported the effect of root exudates on root and shoot growth of Japanese brome grown for 3 weeks with either a commercial or test accession of wheat in U-tube experiments (6). In addition to having measured root and shoot growth in the previous experiment, respiration rates of roots and shoots were determined by loading a Warburg respirometer with either 1 cm sections of roots or shoots and employing the standard manometric procedure described above. Five replications were utilized per strain tested.

No significant differences were observed in root or shoot respiration of Japanese brome grown with root exudates of either 'T 64' or a test strain. Root growth of Japanese brome was previously measured by the authors at 4-day intervals to determine the timing and release of any possible inhibitors. A projection of the line graphs based on four-day growth increments suggested little or no incremental root growth of Japanese brome in root exudates of either 'T 64' or CI 12748 between the 20th and 24th days of the experiment. It is possible that the difference in the effect of exudates from commercial and allelopathic wheat accessions on brome respiration had decreased to non-significant levels by the 20th day of the experiment.

DISCUSSION

The investigation demonstrated that root exudate of allelopathic strains of wheat inhibit respiration of Japanese brome seedlings up to 6 days old. The lower respiration rates may be due to one or more inhibitors. Genetic manipulation to incorporate the active agents into commercial cultivars could enhance the total interference activity of wheat toward weedy species (6).

The large variances in the effect of root exudates on respiration rates in this study is consistent with the large variances observed in plant growth in our previous study. Vancura demonstrated that wheat root exudate contains amino acids, organic acids, sugars, growth hormones, and phenols (8). The mixed nature of the exudate could effect several different physiological processes in plants grown in close association with wheat. The presence of phenols or other allelochemics in the exudate could also inhibit physiological processes which are stimulated by the presence of growth hormones or other compounds. A measured response, in this case respiration, could represent an integration of the action of the individual components in the exudate with possible additive, synergistic, and antagonistic interactions. An effective biological control should consider genetic manipulation that would accent the synergistic action of weed specific kolines in exudates and reduce compounds which might stimulate weed growth or interfere with the action of the kolines.

Respiration may contribute energy and intermediates to metabolic events which involve synthesis of new tissue and events which involve tissue replacement or maintenance (1). Thornley's model for plant growth directly related plant growth to respiration (7). Allelopathic agents which inhibit growth respiration in emerging seedlings would be particularly effective and consistent with the observations made in this study. On the other hand, as plants matured, the increase in structural dry matter would require a greater proportion of respiration to be devoted to maintenance components. Allelopathic agents that increase maintenance respiration in older plants would be effective at this point. Weaver and Klarich (9) found that vapors from <u>Artemisia</u> <u>tridentata</u> inhibited respiration of germinating seeds of wheat and stimulated respiration of mature leaves. This suggests that the same allelopathic mechanism may act differentially on growth and maintenance respiration. In young plants in which structural dry matter has increased and growth respiration has decreased a cross over point might be reached where allelochemics with pronounced effects on respiration may go unnoticed because of experiments that measure only total respiration.

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Figure 1. Effects of root exudates from wheat on respiration of germinating seeds and newly emerged whole seedlings of Japanese brome.

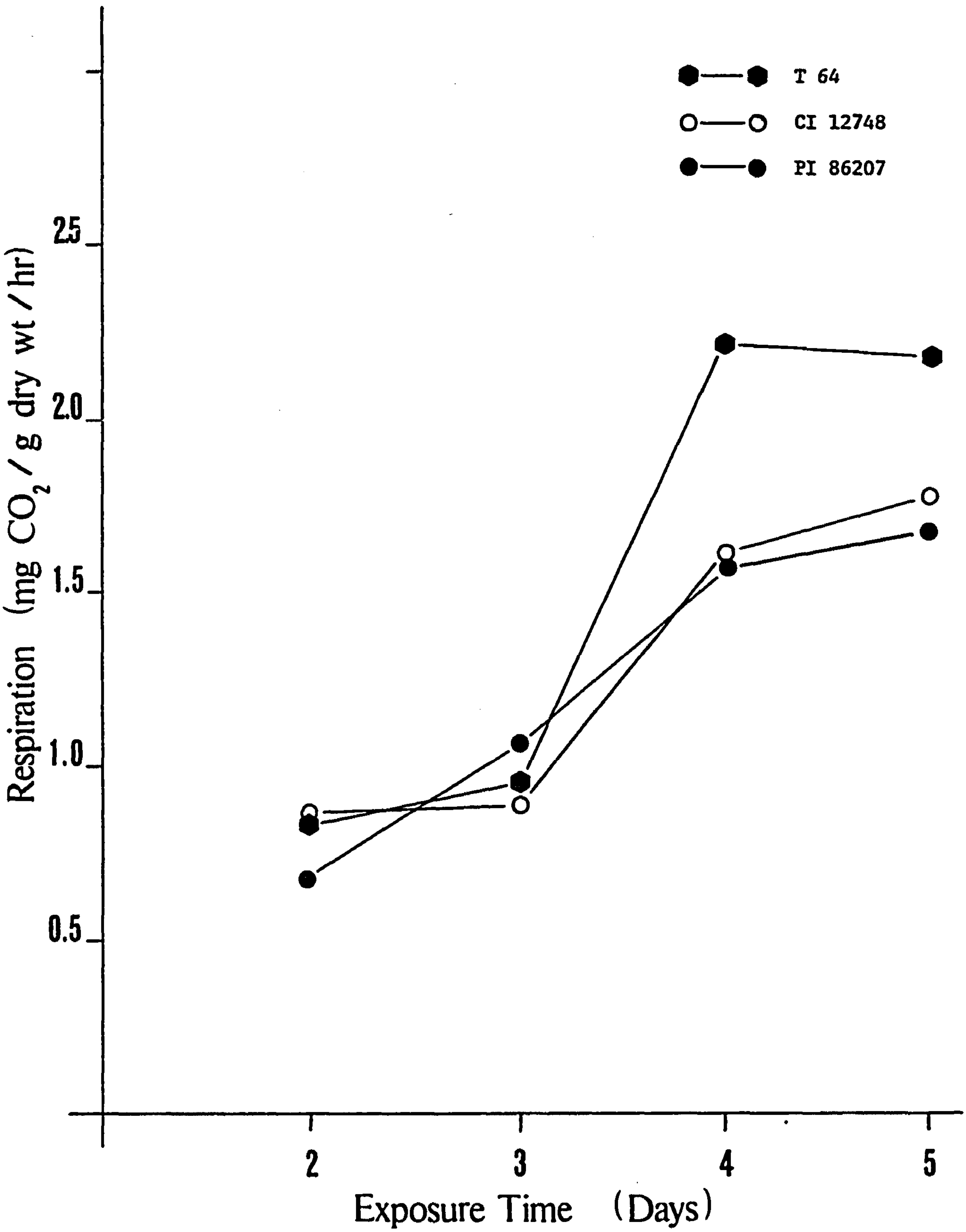

T 64
CI 12748
PI 86207
Respiration (mg CO_2 / g dry wt / hr)
2.5
2.0
1.5
1.0
0.5
2
3
4
5
Exposure Time (Days)

Figure 2. Effects of root exudates from wheat on respiration of roots of newly emerged seedlings of Japanese brome.

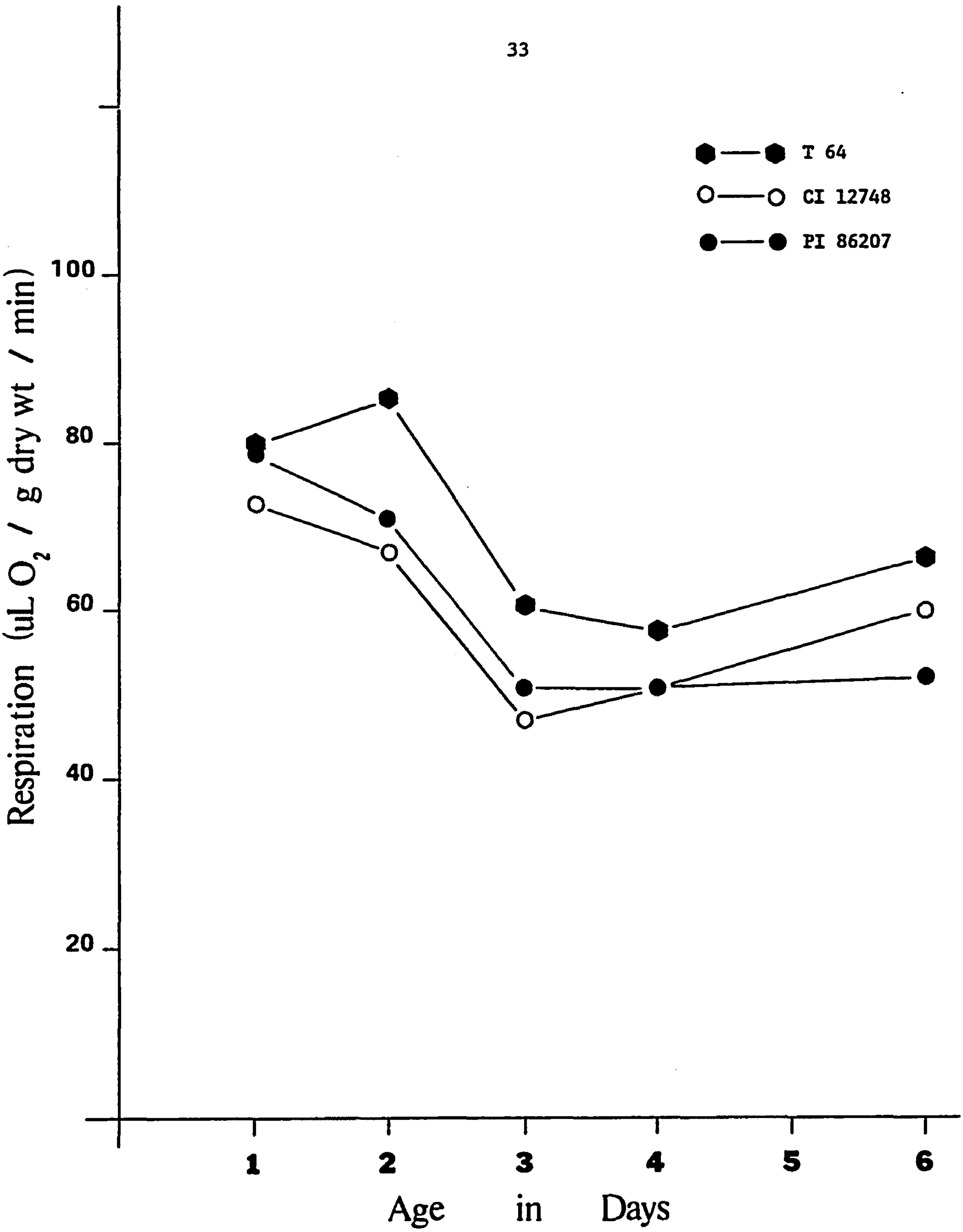
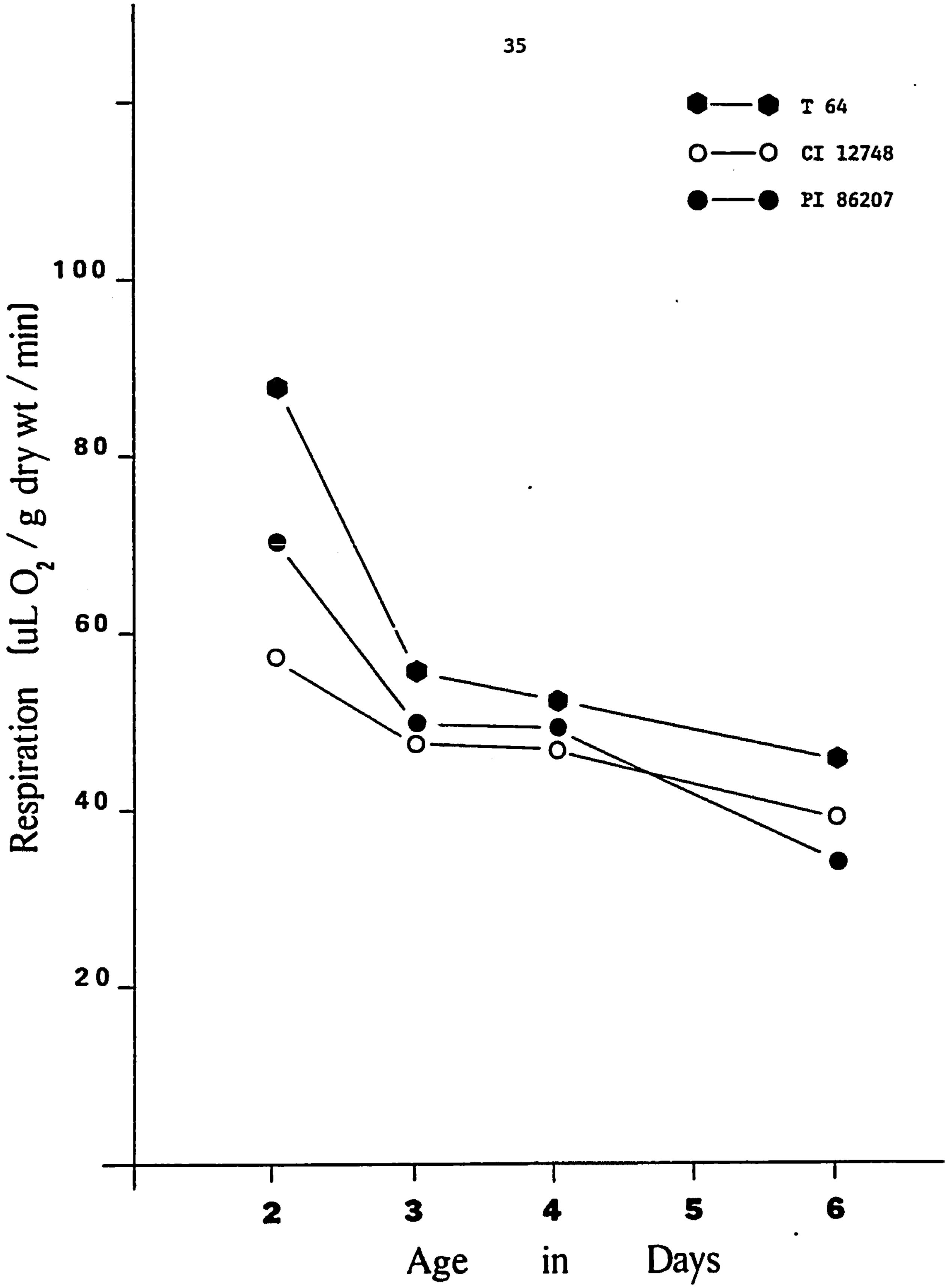

T 64
CI 12748
PI 86207
Respiration (uL O2 / g dry wt / min)
100
80
60
40
20
1
2
3
4
5
6
Age in Days

Figure 3. Effects of root exudates from wheat on respiration of shoots of newly emerged seedlings of Japanese brome.


T 64
CI 12748
PI 86207
Respiration (uL O_2 / g dry wt / min)
100
80
60
40
20
2
3
4
5
6
Age in Days