Soluble Sugars and Free Amino Acids of *Poa pratensis* Exposed to Chlorophenoxy Herbicides and Pathogenesis by *Drechslera sorokiniana*

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ABSTRACT

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The influence was evaluated of two postemergence herbicides, 2-(2-methyl-4-chlorophenoxy)propionic acid (MCPP) and 2-(2,4,5-trichlorophenoxy)propionic acid (2,4,5-TP), on total and individual soluble sugars and free amino acids of leaves of herbicide-tolerant *Poa pratensis* and on the severity of leaf spot induced by *Drechslera sorokiniana*. The incidence of leaf spot of plants growing in soil treated with MCPP was more severe than leaf spot of the untreated controls. 2,4,5-TP had no influence on the severity of the leaf spot. Leaves of plants growing in soil treated with either herbicide had lower sucrose and total sugar amounts than did control leaves. The decrease in sucrose and total soluble sugars in uninoculated leaves of herbicide-treated plants was significantly correlated with increased leaf spot severity of inoculated leaves of herbicide-treated plants. No differences existed in sugar content among infected leaves of control or herbicide-treated plants. The results are discussed relative to previous classification of Drechslera leaf spot on *P. pratensis* as a "low sugar" disease. MCPP and 2,4,5-TP had little effect on the total free amino acids in uninoculated leaves. Inoculated leaves of control and MCPP-treated plants had greater amounts of total free amino acids than did uninoculated leaves of respective plants. No difference existed in total free amino acid content between uninoculated and inoculated leaves of 2,4,5-TP-treated plants. No meaningful significant correlations existed between free amino acid content and leaf spot severity.

Additional key words: Bipolaris sorokinianum, Helminthosporium sativum, Kentucky bluegrass, mecoprop, silvex.

Leaf spot of Kentucky bluegrass (*Poa pratensis* L.) caused by *Drechslera sorokiniana* (Sacc.) Subram. and Jain (= *Helminthosporium sativum* P. K. and B.) is influenced by cultural practices such as nitrogen fertilization (5,31) and mowing height (7,11) and by such environmental factors as light (26) and temperature (15). Postemergence herbicides also influence the severity of leaf spot of *P. pratensis* (13). Chlorophenoxy herbicides generally stimulate leaf spot, but a few chlorophenoxy herbicides selectively stimulate or inhibit leaf spot, depending upon concentration of the herbicide and method of application (13).

Management of grasses used for turf includes applications of selective postemergence chlorophenoxy herbicides to herbicide-tolerant perennial grass species. The herbicides are absorbed and inactivated in tolerant plants by degradation, hydroxylation of the aromatic ring, or conjugation with plant constituents (25). Chlorophenoxy herbicides generally function as auxin analogs and can influence sugar and amino acid metabolism of treated herbicide-sensitive plants (1,18,22,24,28,37). Sugar content in leaves of herbicide-treated, sensitive plants is decreased as a result of increased respiration and the inhibition of photosyntheses (18,24,28,37). Chlorophenoxy herbicides decrease the protein and amino acid content in leaves of sensitive plants (1,22). The effect of chlorophenoxy herbicides on the soluble sugar and free amino acid content of leaves of a herbicide-tolerant species such as *P. pratensis* is largely unknown.

Infection by fungal pathogens also affects the soluble sugar and free amino acid content of leaves. A metabolic sink may form at infection sites, resulting in increased translocation of sugars and amino acids to infected leaves (9,17,34). Fungal enzyme activity and the stimulation of host respiration also influence sugar content (4,19). The amount of free amino acids in leaves generally decreases initially with infection by *Drechslera halodes* but later increases supposedly due to the activity of proteolytic enzymes of the pathogen (8).

The content of soluble sugars and free amino acids in plants has been postulated to directly influence susceptibility to diseases caused by *Drechslera* sp. (16,34,36). Leaf spot of *P. pratensis* has been termed a "low sugar" disease on the basis of correlations of low leaf sugar content with severe leaf spot (23). Some writers have questioned the direct effect of sugar content on Drechslera leaf spot (6,10,31). Because chlorophenoxy herbicides affect the severity of leaf spot of *P. pratensis* and probably influence soluble sugar and free amino acid content, an investigation into the relations of the two herbicide-mediated effects is warranted. Research was conducted to evaluate the effects of selected postemergence chlorophenoxy herbicides on soluble sugars and free amino acids in leaves of herbicide-tolerant *P. pratensis* and subsequent leaf spot severity as a preliminary step in determining the role of chlorophenoxy herbicides in pathogenesis by *D. sorokiniana*.

MATERIALS AND METHODS

P. pratensis 'Newport' was vegetatively propagated in a steamed mixture of loam and peat (2:1, v/v) in 7.6-cm-square plastic pots. Plants were grown in the greenhouse with 16 hr of light daily (daylight supplemented with incandescent lights) for 60 days preceding treatment. Cultures of *D. sorokiniana* were maintained on 20 ml of 1% Czapek Dox broth in 3% (v/v) Bacto-agar in 100 × 15-mm sterile plastic petri dishes. Virulence of cultures was maintained by isolating hyphal tips from diseased leaf tissue of *P. pratensis* obtained by periodic inoculations. Only 20-day-old cultures were used in this study (12).

Plants were treated with 40 ml (20 ml each, 4 and 2 days before incubation) of 10^{-4} M 2-(2-methyl-4-chlorophenoxy)propionic acid (MCPP), or 2-(2,4,5-trichlorophenoxy)propionic acid (2,4,5-TP) or with distilled water (control) applied to the soil. The four youngest visible leaves of one shoot were inoculated with 5–10 conidia suspended in 0.02 ml of sterile, distilled water at five positions, 1 cm apart, along a 10-cm length of the leaf beginning

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approximately 5 cm from the leaf tip in a special inoculation apparatus (30). Uninoculated plants received 0.02 ml of sterile, distilled water as a control. The concentration of conidial suspensions was determined with a particle counter (High Accuracy Products Corp., Montclair, CA 91763). Each treatment consisted of 17 individual shoots with four leaves each and was replicated three times. Plants were incubated for 6 days at 24 C under continuous fluorescent light (80–90 $\mu E \cdot M^{-2} \cdot sec^{-1}$) and then evaluated for disease severity and sampled for sugar and amino acid extraction. Disease severity was evaluated on 10-cm lengths of leaf blades of inoculated plants by the method described by Hodges (14). Estimated lesion area was expressed as a percentage of the area of four leaves from one shoot. The values from the 17 shoots of each treatment were averaged to determine the disease severity of each treatment replication. The data presented are the means of these values for three replicates of each treatment.

Soluble sugars and free amino acids were determined in leaf tissues from inoculated and uninoculated plants. The 10-cm leaf sections from each replicate were freeze-dried at −50 C for 48 hr and ground in a Wiley mill fitted with a 420-μm (40-mesh) screen. One hundred milligrams dry weight of ground tissue was used per sample for sugar analyses. Sugars were extracted in a microsoxhlet apparatus with 12 ml of 80% ethanol for 4 hr. The extract was evaporated, and chlorophyll was removed by partioning with 20 ml of ethyl ether:water (1:1, v/v). The aqueous phase was filtered through decolorizing charcoal and a Millipore filter (0.45 μm) and prepared for thin-layer chromatography (3,21). Sugars were applied to plates of kieselguhr G (20 × 20 cm by 250-μm thick) buffered with 0.02 M sodium acetate. Sucrose, glucose, and fructose were separated with a mixture of ethyl acetate and 65% isopropanol (65:35, v/v), and raffinose was separated with a mixture of *n*-propanol, ethyl acetate, and water (40:50:10, v/v). All sugars were visualized with aniline-diphenylamine-phosphoric acid reagent (21). Sugars were referenced to authentic standards of known concentrations, and relative quantities of extracted sugars were determined with a scanning diffuse-reflectance densitometer (model K-49500; Kontes, Vineland, NJ 08360) and a computing integrator (model SP4100; Spectra-Physics, Santa Clara, CA 95051).

Free amino acids were extracted from 100 mg (dry weight) samples with 95% ethanol for 24 hr and in three aliquots of 80% ethanol for 24 hr. Ethanol extracts were pooled and air-dried. Chlorophyll was removed by partioning with 30 ml of a mixture of ethyl ether and water (1:1, v/v). The aqueous phase containing free amino acids was demineralized on a column of AG 50W-X8-H^+ ion-exchange resin 74- to 38-μm (200- to 400-mesh) (Bio-Rad Laboratories, Richmond, CA 94804) and eluted with 2 N ammonium hydroxide. The eluate was air-dried and analyzed on an amino acid analyzer. Data were analyzed as a 3 × 2 factorial design for the mean percentage of diseased leaf tissue, individual soluble sugars and their total, and individual free amino acids and their total in leaves of one shoot of each treatment. Mean comparisons were made using Duncan's multiple range test (DMRT).

RESULTS

The mean percentage of diseased area of leaves of control plants not treated with herbicides and inoculated with *D. sorokiniana* was 22.3. Inoculated leaves of plants growing in soil to which 10^{-4}M MCPP had been applied has significantly greater diseased area of 28.4% (DMRT, $P = 0.05$). The percentage of diseased area of inoculated leaves of plants growing in soil treated with 10^{-4}M 2,4,5-TP was 25.6 and was not significantly different from either the control or MCPP-treated plants (DMRT, $P = 0.05$).

Both herbicides decreased the total soluble sugar content in leaves of uninoculated plants (Table 1). Only sucrose decreased in leaves of uninoculated plants after applications of MCPP or 2,4,5-TP. No differences in sugar content existed in leaves among nonherbicide- and herbicide-treated plants inoculated with *D. sorokiniana*.

Differences in content of soluble sugar existed between uninoculated and inoculated leaves (Table 1). Relative to uninoculated control plants, sucrose decreased and fructose increased in leaves of nonherbicide-treated control plants inoculated with *D. sorokiniana*. Inoculated leaves of MCPP- or 2,4,5-TP-treated plants increased in glucose, fructose, and total soluble sugars compared with leaves of uninoculated plants treated with MCPP or 2,4,5-TP. Raffinose remained unchanged in all treatments.

MCPP and 2,4,5-TP had little effect on the free amino acid content of uninoculated leaves (Table 2). MCPP decreased Ala, Lys, and His, and 2,4,5-TP decreased Lys compared with uninoculated controls. Herbicide-treated plants inoculated with *D. sorokiniana* exhibited greater variation in free amino acid content. Asp increased in MCPP-treated plants, and Ser, Gly, Ala, Val, Ile, Leu, Tyr, His, Arg, and total free amino acids decreased in 2,4,5-TP-treated plants compared with the inoculated control.

Infection by *D. sorokiniana* affected the content of free amino acids in leaves of *P. pratensis* (Table 2). Inoculated leaves of control plants that received no herbicide exhibited higher contents of Ser, Glu, Gly, Ala, Val, Ile, Leu, His, and total free amino acids than did uninoculated controls; conversely, Lys decreased relative to uninoculated controls.

Correlation coefficients were calculated for comparisons of soluble sugar and free amino acid amounts with the percentage of diseased leaf area of nonherbicide- and herbicide-treated plants. The correlation for sucrose versus diseased area was $r = -0.78$ and for total soluble sugars versus diseased area was $r = -0.68$. No significant correlations occurred between amino acids and disease, $P = 0.05$.

DISCUSSION

In a previous study, soil application of 10^{-4}M MCPP increased the severity of leaf spot caused by *D. sorokiniana* on *P. pratensis*, whereas 10^{-4}M 2,4,5-TP reduced disease severity (14). The results presented here using the same concentration and method of application support the stimulatory effect of MCPP. However, in the present study, the percentage diseased leaf area of 2,4,5-TP-

TABLE 1. Mean content of soluble sugars of leaves of control and herbicide-treated *Poa pratensis*, both uninoculated and inoculated with *Drechslera sorokiniana*[x]

	Soluble-sugar content (μmoles/g dry wt)					
	Uninoculated			Inoculated		
Sugars	Control	MCPP	2,4,5-TP[y]	Control	MCPP	2,4,5-TP
Sucrose	7.7 a/a[z]	4.5 b/a	4.6 b/a	4.5 a/b	5.3 a/a	5.0 a/a
Glucose	1.8 a/a	1.5 a/b	1.3 a/b	2.3 a/a	2.2 a/a	2.7 a/a
Fructose	0.7 a/b	0.4 a/b	0.4 a/b	1.8 a/a	1.4 a/a	1.3 a/a
Raffinose	0.5 a/a	0.4 a/a	0.5 a/a	0.5 a/a	0.4 a/a	0.3 a/a
Total	10.7 a/a	6.9 b/b	6.8 b/b	9.2 a/a	9.3 a/a	9.3 a/a

[x] Mean content of soluble sugars in the average of three replications from the analysis of tissue from four leaves of 17 shoots each.
[y] Both herbicides are 10^{-4}M concentration in 20 ml of water applied to the soil 4 and 2 days before incubation.
[z] Within each row, letters left of the slash indicate differences between the three values (control, MCPP, and 2,4,5-TP) within the uninoculated or inoculated groups; letters right of the slash indicate differences between the two values for control, two values for MCPP, or two values for 2,4,5-TP in the uninoculated and inoculated groups. Numbers followed by the same letters are not significantly different according to Duncan's multiple range test.

TABLE 2. Mean content of free amino acids of leaves of control and herbicide-treated *Poa pratensis*, both inoculated and inoculated with *Drechslera sorokiniana*[x]

	Free amino acid content (μmoles/g dry wt)					
	Uninoculated			Inoculated		
Amino acids	Control	MCPP	2,4,5-TP[y]	Control	MCPP	2,4,5-TP
Proline	1.02 a/a[z]	0.46 a/b	0.47 a/a	1.36 a/a	1.13 a/a	0.99 a/a
Histidine	0.20 a/b	0.12 b/b	0.17 a/b	0.28 a/a	0.29 a/a	0.21 b/a
Lysine	0.39 a/a	0.33 b/a	0.30 b/a	0.32 ab/b	0.37 a/a	0.29 b/a
Arginine	0.34 a/a	0.27 a/b	0.33 a/a	0.40 a/a	0.34 ab/a	0.27 b/a
Glycine	0.31 a/b	0.29 a/b	0.31 a/a	0.37 a/a	0.35 a/a	0.30 b/a
Threonine	1.12 a/a	1.16 a/a	1.25 a/a	1.06 a/a	1.07 a/a	0.83 a/b
Alanine	3.39 a/b	2.91 b/b	3.49 a/a	4.14 a/a	3.86 a/a	2.88 b/b
Valine	0.71 a/b	0.70 a/b	0.78 a/a	0.87 a/a	0.91 a/a	0.67 b/a
Serine	2.75 a/b	3.03 a/b	3.04 a/a	3.67 a/a	3.78 a/a	2.64 b/a
Isoleucine	0.32 a/b	0.35 a/a	0.35 a/a	0.40 a/a	0.42 a/a	0.31 b/a
Leucine	0.24 a/b	0.25 a/a	0.24 a/a	0.29 a/a	0.29 a/a	0.21 b/a
Aspartic acid	0.27 a/a	0.30 a/b	0.27 a/a	0.30 b/a	0.41 a/a	0.30 b/a
Glutamic acid	1.31 a/b	1.56 a/a	1.35 a/a	1.66 ab/a	1.79 a/a	1.43 b/a
Phenylalanine	0.58 a/a	0.52 a/a	0.54 a/a	0.51 a/a	0.50 a/a	0.38 a/b
Tyrosine	0.38 a/a	0.33 a/a	0.37 a/a	0.36 a/a	0.33 a/a	0.22 b/b
Total	13.33 a/b	12.60 a/b	13.27 a/a	16.01 a/a	15.85 a/a	11.96 b/a

[x] Mean content of free amino acids is the average of three replications from the analysis of tissue from four leaves of 17 shoots each.
[y] Both herbicides are 10^{-4}M concentration in 20 ml of water applied to the soil 4 and 2 days before incubation.
[z] Within each row, letters left of the slash indicate differences beetween the three values (control, MCPP, and 2,4,5-TP) within the uninoculated or inoculated groups; letters right of the slash indicate differences between the two values for control, two values for MCPP, or two values for 2,4,5-TP in the uninoculated and inoculated groups. Numbers followed by the same letters are not significantly different according to Duncan's multiple range test.

treated plants was not different from that of the control. The relatively high virulence of the isolate of *D. sorokiniana* used in this study (22% diseased leaf area of the control) could have negated the inhibitory influence of 2,4,5-TP.

Both MCPP and 2,4,5-TP caused a decrease in total soluble sugars of uninoculated leaves of *P. pratensis* (Table 1). This corresponds with previous reports of sugar loss from leaves of plants sensitive to MCPP and 2,4,5-TP, and probably is associated with increased respiration and decreased photosynthesis (18,24,28,37). Therefore, decreases in the sugar content of leaves of MCPP- and 2,4,5-TP-treated plants seem to be independent of sensitivity or tolerance to the herbicides. The results also support the contention that sugar loss is not the principal cause of death in herbicide-treated plants (35).

The decreased content of sucrose and total soluble sugars of uninoculated leaves of herbicide-treated plants was significantly correlated with the increased percentage of diseased leaf area of inoculated plants. This lends support to the contention that this disease is promoted by low sugar levels (23). However, the effect of leaf sugar content on leaf spot caused by *D. sorokiniana* probably is not a direct relationship (6,10,31). The metabolism of sugars within herbicide-treated, infected leaves is complex. Respiration, photosynthesis, translocation, enzyme activity, and the pathogen's utilization of sugars interact to influence sugar content in such leaves (4,18,19,24,28,37). Treatments that decreased sugars preceding inoculation resulted in more severe leaf spot. High sugar levels inhibit the induction of cell-wall-degrading enzymes in some host-parasite interactions (20,33). The lower levels of sugars in leaves of herbicide-treated plants at the time of inoculation might permit increased production of cell-wall-degrading enzymes after inoculation and facilitate early pathogenesis. However, an interpretation of leaf sugar data is difficult.

Infection by *D. sorokiniana* resulted in a decrease in sucrose and an increase in fructose, with no change in total soluble sugars compared with the uninoculated control (Table 1). Increased respiration is common to fungal infection (4,19). Sucrose may be hydrolyzed to glucose and fructose before entry into respiration pathways. Some pathogens alter translocation of low-molecular-weight metabolites, such as sugars, to form metabolic sinks at infection sites (9,17). The apparent lack of a herbicide effect on total sugars of infected leaves may be due to the formation of a sink in the heavily infected leaves of herbicide-treated plants (Table 1).

Application of 10^{-4}M MCPP or 2,4,5-TP to *P. pratensis* had little effect on the free amino acid content of uninoculated leaves (Table 2). The herbicides generally decrease free amino acids in leaves of herbicide-sensitive plants by inducing metabolic sinks elsewhere in the plants; ie, stems, roots, or apices (1,22). Decreased rates of translocation of herbicides in tolerant species could delay or limit herbicide-induced decreases in free amino acids in leaves (25). Measurement of free amino acids in selected tissues of *P. pratensis* at time intervals after herbicide application would be informative in future studies.

Free amino acids of leaves of *P. pratensis* increased after inoculation with *S. sorokiniana* (Table 2). Similar increases have been noted in various host-parasite interactions (8). The increase could be due to proteolysis or to increased translocation of amino acids to the infected leaves (8,9,17,29).

MCPP-treated, inoculated plants had greater amounts of total amino acids in their leaves than did leaves of MCPP-treated, uninoculated plants (Table 2). However, 2,4,5-TP-treated, inoculated plants had total free amino acid levels in their leaves not different from those in leaves of uninoculated 2,4,5-TP-treated plants (Table 2). The two herbicides behaved uniformly in most other comparisons of effects on sugars or amino acids. Soil application of various concentrations of 2,4,5-TP results in erratic effects on leaf spot severity (14). The degree of inactivation of herbicides in *P. pratensis* could be responsible for these effects (2,22,27,32). However, the difference in the free amino acid content of infected leaves of MCPP-treated plants compared to 2,4,5-TP-treated plants may be of interest in understanding how chlorophenoxy herbicides may influence pathogenesis by *D. sorokiniana*. Further study is required to clarify any possible role of amino acids in this relationship.

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