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INTERACTIONS OF TEMPERATURE AND FERULIC ACID STRESS ON GRAIN SORGHUM AND SOYBEANS

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Abstract—Experiments were conducted to test the hypothesis that allelopathic effects of ferulic acid (FA) may be altered by the temperature conditions of the growth environment. Growth of grain sorghum and soybean seedlings over a 10-day treatment period showed that a significant interaction effect occurred between environmental temperatures and FA treatments. Sorghum grown with an average day temperature of 37°C and soybeans grown at 34°C had greater dry weight reductions caused by FA than when the respective environments were 8°C and 11°C lower. The threshold concentration for inhibition of sorghum growth was 0.2 mM FA under the hot conditions and 0.4 mM FA with the cooler conditions. Soybeans were more sensitive than sorghum, and these inhibition thresholds for the hot and cool environments were 0.1 and 0.25 mM FA. These results demonstrate that temperature stress enhances allelochemical inhibition and indicate that interactions with the environment are an important consideration for understanding allelopathy.

Key Words—Ferulic acid, allelopathy, temperature stress, sorghum, soybean.

INTRODUCTION

Biochemical interference among plants (allelopathy) occurs in a variety of plant communities, and it is apparent that many plants can contribute toxins to the environment (Rice, 1974, 1979). The biological activity of allelochemicals depends on the presence of sensitive plant species, the degree of toxicity of the specific substances, the combination of allelochemicals present, and their residence time. Aspects of the environment are also important in allelopathy. Moisture conditions and soil type influence the availability

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and persistence of allelochemicals (Patrick et al., 1964; Wang et al., 1971; McCalla and Norstadt, 1974). The level of synthesis and accumulation of allelochemicals in donor plants may be raised by mineral deficiencies, temperature stress, ultraviolet light, and osmotic stress (Koeppe et al., 1969, 1970; Armstrong et al., 1970; del Moral, 1972; Lehman and Rice, 1972). However, many other environmental interactions have not been investigated.

Benzoic and cinnamic acids are frequently implicated in allelopathy. Vanillic, *p*-hydroxybenzoic, *p*-coumaric, caffeic, and ferulic acids are common ones identified in soil extractions where allelopathy is investigated. Quantities in the rhizosphere are extremely variable, with amounts reported for specific compounds ranging from less than 10 ppm to over 1000 ppm (Whitehead, 1964; Guenzi and McCalla, 1966; Wang et al., 1967; Lodhi, 1975, 1978; Turner and Rice, 1975; Chou and Patrick, 1976). The extent of soil binding and inactivation of phenolic acids also remains a complex unknown. Therefore, a persistent question in allelopathy has been whether the small amounts of allelochemicals that are often reported can be functional in regulation of germination and growth.

Part of the rationale supporting the regulatory role of small quantities of allelochemicals is that several different substances often act in cooperative ways (Rasmussen and Einhellig, 1977, 1979; Einhellig and Rasmussen, 1978; Einhellig et al., 1982; Williams and Hoagland, 1982). Allelopathic effects may also be viewed as a type of stress. Thus, it is plausible that additional environmental conditions may be important dimensions that modify growth interference from allelochemicals. Stowe and Osborn (1980) found that nitrogen and phosphorus availability influenced phytotoxicity of vanillic and *p*-coumaric acids. We have observed that under greenhouse conditions with adequate nutrients, there is considerable variation in response of bioassay plants to treatments with a known allelochemical.

The conjecture of these experiments was that when an allelochemical is near its threshold for inhibition of seedling growth, temperature of the growth environment would alter the allelopathic effect. High temperatures, yet growth temperatures still within the normal range of tolerance, create some stress on plant metabolism. Experiments were designed to determine if temperature stress would interact with and alter allelochemical effects from ferulic acid.

METHODS AND MATERIALS

Grain sorghum (*Sorghum bicolor* Moench., Dekalb Hybrid DK28) and soybeans [*Glycine max* (L.) Merr. cv. Corsoy] seedlings were used as the test plants in these experiments. Both are crop species which may be subjected to interference from allelochemicals released from weeds or decom-

position of crop residue (Colton and Einhellig, 1980; Schon and Einhellig, 1982; Einhellig and Schon, 1982), and they are sensitive to phenolic acids (Einhellig and Rasmussen, 1978, 1979). Seeds were germinated in vermiculite in the greenhouse, and after 6 days they were individually transplanted to opaque plastic vials containing nutrient solution. Containers for sorghum held 80 ml and those for soybeans held 120 ml. The nutrient solution consisted of 5 mM $Ca(NO_3)_2$, 5 mM KNO_3, 2 mM $MgSO_4$, 0.9 mM $NH_4H_2PO_4$, 0.1 mM $(NH_4)_2HPO_4$, standard Hoagland's micronutrients (Hoagland and Arnon, 1950), and 72 μM iron supplied as sodium ferric diethylene-triamine pentaacetate (Sequestrene 330).

Seedlings were selected for uniformity after one day of acclimatization and treated with ferulic acid (Sigma Chemical Co.) dissolved in fresh nutrient solution. Ferulic acid (FA) was chosen as an allelochemical because of its common occurrence. Treatment levels for sorghum were 0, 0.1, 0.2, and 0.4 mM FA, and soybean treatments were 0, 0.1, and 0.25 mM FA. Each treatment utilized 24–30 seedlings which were divided into two subgroups with one subgroup placed in a higher temperature environment than the other.

Different greenhouses were utilized to obtain the two temperature environments for grain sorghum experiments. This allowed one environment to have a temperature stress while both retained full-sun growth conditions. The hot environment averaged 8°C above the cool from 1000 to 2000 hr, with 37°C (34–41) the mean (and range) for the hot environment, compared to 29°C (29–33) for the cooler environment. Night temperatures (2200–800 hr) averaged 20°C (18–23) and 18°C (16–19), respectively. These were the averages obtained by taking hourly temperatures during the 10-day treatment period for sorghum. The two environments also had some differences in humidity. The average day–night relative humidity for the hot environment was 24 and 56%, and it was 41 and 64% for the cooler environment. Soybeans were injured by the hot environment used for sorghum, and temperatures used with soybeans were lower. Soybean experiments were conducted in matched growth chambers using a 16:8 hr light–dark cycle with a light intensity of 300 $\mu E/sec/m^2$ (Lamba Instruments, L1-170 Quantum/Radiometer/Photometer). The accompanying temperature cycles during the light and dark were 34 and 29°C and 23 and 14°C, respectively, for the hot and cool environments. The chambers had no regulation of relative humidity and the averages were 40 and 53% and 63 and 73%.

The original treatment solution was replenished on the fifth day after treatment and abaxial leaf diffusive resistance was taken on this day using a Li-Cor model LI-1600 steady-state porometer. Abaxial resistances were obtained from the largest leaf of sorghum and from soybean unifoliates. Experiments were terminated after 10 days of treatment. At harvest, sorghum plants were measured for width of the largest leaf and base to tip shoot and

root lengths. Sorghum shoot and root dry weights were obtained after 48 hr at 104°C and shoot–root ratios were calculated. Soybean harvest consisted of taking the leaf area and dry weight for each seedling. Data of each experiment were analyzed by two-way analysis of variance (ANOVA). Within each environment a one-way ANOVA with Duncan's multiple-range test was applied. Each experiment was duplicated.

RESULTS

Sorghum seedlings treated with FA in the two temperature environments exhibited several differences in appearance and in dry weights by the end of the experiments. The overall comparison of temperature effects using the two-way ANOVA showed that plants grown under the hot conditions had significantly lower root weight and total plant weight, resulting in a higher shoot-root ratio (Table 1). The two-way ANOVA summation of FA effects across the two environments showed that the FA treatments caused significant alterations in dry matter accumulation in roots, shoots, and the total plant. Interaction effects between temperature and FA treatments also occurred. All sorghum weights and the shoot–root ratio showed a significant interaction of these two variables. Since the stress variables had a significant interaction on sorghum, further analysis of the effects of FA within each temperature was logical.

Ferulic acid inhibition of growth in each of the two temperature regimes was verified using a one-way ANOVA with Duncan's multiple-range test (Table 1). However, perhaps the most important observation concerning effects on dry weight is that seen by comparing FA inhibition in the hot regime to inhibitory effects under the cooler temperatures. This comparison demonstrates that the 0.2 mM FA treatment significantly reduced root, shoot, and total plant weights below the corresponding control with hot growth conditions, but the 0.2 mM FA treatment had no effect with cooler conditions. While 0.4 mM FA treatments inhibited seedling dry weights in both environments, these reductions were considerably greater with higher temperatures. Dry weights of sorghum grown in the hot regime with 0.4 mM FA were also significantly reduced below the inhibition caused by 0.2 mM FA. These comparisons were similar in the duplicate experiment (not shown).

Visual differences between sorghum seedlings grown in the two temperatures were evident. The shoots of seedlings grown with the hot conditions had a darker green color and the leaves were more narrow. This temperature effect on leaf width was verified by the significant probability obtained using the two-way ANOVA (Table 2). Plants in the hot environment also had a reduced root length and an increase in diffusive resistance when compared to those in the cool environment. A consideration of FA treatments irrespec-

TABLE 1. INTERACTION OF TEMPERATURE AND FERULIC ACID (FA) STRESS ON SORGHUM SEEDLINGS

Treatment	Dry wt[a] *in mg* ± SE (and % of control)			Ratio shoot–root
	Root	Shoot	Plant	
Hot[b] (37°C)				
Control	80.2 ± 4.5a	145.6 ± 8.3a	225.8 ± 12.1a	1.82 ± .06a
0.1 mM FA	81.9 ± 7.2a (102.1)	150.0 ± 16.9a (103.0)	231.9 ± 24.0a (102.7)	1.83 ± .05a
0.2 mM FA	66.4 ± 3.9b (82.8)	84.2 ± 5.5b (57.8)	150.6 ± 9.3b (66.7)	1.27 ± .02b
0.4 mM FA	26.0 ± 2.9c (32.4)	49.2 ± 4.1c (33.8)	75.2 ± 6.7c (33.3)	1.89 ± .14a
Cool (29°C)				
Control	102.7 ± 4.1a	123.5 ± 6.3a	226.2 ± 8.9a	1.20 ± .03a
0.1 mM FA	103.6 ± 5.4a (100.9)	116.6 ± 9.2a (94.4)	220.2 ± 14.5a (97.3)	1.12 ± .04ab
0.2 mM FA	109.0 ± 6.1a (106.1)	116.9 ± 7.3a (94.7)	225.9 ± 13.4a (99.9)	1.07 ± .03b
0.4 mM FA	72.6 ± 4.0b (70.7)	79.3 ± 4.8b (64.2)	151.9 ± 8.6b (67.2)	1.09 ± .02b
	Two-way ANOVA *F* value (and probability)			
Temperature	89.2 (0.0001)	0.1 (0.7621)	13.7 (0.0004)	224.9 (0.0001)
FA	33.8 (0.0001)	29.8 (0.0001)	31.5 (0.0001)	18.6 (0.0001)
Temp–FA	3.4 (0.0204)	8.2 (0.0001)	6.7 (0.0005)	13.9 (0.0001)

[a]Column means within a temperature regime that are not followed by the same letter are significantly different, $P < 0.05$, ANOVA with Duncan's multiple-range test.
[b]Day temperature mean. See text for details.

tive of temperature conditions demonstrated that FA affected diffusive resistance and each of the morphological parameters, as shown by the two-way ANOVA. Interaction effects between temperature and FA were significant for both root and shoot length.

Ferulic acid effects on seedling morphology occurred in both temperatures, but definite differences are apparent when FA treatments under the hot environment are compared to those under the cool (Table 2). These differences in morphology parallel effects found on dry weight. In the hot environment, 0.2 mM FA-treated seedlings had significantly reduced leaf width, root length, and shoot length below the corresponding control, but

TABLE 2. INTERACTION OF TEMPERATURE AND FERULIC ACID (FA) STRESS ON SORGHUM SEEDLING MORPHOLOGY AND DIFFUSIVE RESISTANCE[a]

Treatment	Day 5 abaxial resistance (sec/cm)	Leaf width (mm)	Root length (cm)	Shoot length (cm)
Hot (37°C)				
Control	2.1 ± 0.2a	13.9 ± 0.5a	18.9 ± 0.6a	24.0 ± 0.8a
0.1 mM FA	2.7 ± 0.3ab	13.3 ± 0.5a	17.7 ± 0.9a	24.4 ± 2.0a
0.2 mM FA	3.6 ± 0.4b	11.9 ± 0.6b	14.5 ± 1.0b	17.6 ± 1.1b
0.4 mM FA	3.7 ± 0.9b	8.6 ± 0.3c	7.6 ± 1.4c	8.9 ± 1.2c
Cool (29°C)				
Control	1.3 ± 0.2a	18.5 ± 0.5a	21.3 ± 0.9a	21.5 ± 0.8a
0.1 mM FA	2.5 ± 0.2b	18.2 ± 0.6a	20.0 ± 0.4a	20.0 ± 1.2a
0.2 mM FA	2.1 ± 0.1bc	17.1 ± 0.6a	21.0 ± 0.6a	21.0 ± 0.8a
0.4 mM FA	2.9 ± 0.2c	15.7 ± 0.7b	16.8 ± 0.4b	14.7 ± 0.7b
	Two-way ANOVA F value (and probability)			
Temperature	17.40 (0.0001)	188.62 (0.0001)	83.43 (0.0001)	0.80 (0.3767)
FA	11.91 (0.0001)	22.67 (0.0001)	37.70 (0.0001)	40.50 (0.0001)
Temp–FA	2.40 (0.0766)	2.45 (0.0671)	8.67 (0.0001)	9.72 (0.0001)

[a]Column means within a temperature regime that are not followed by the same letter are significantly different, $P < 0.05$, ANOVA with Duncan's multiple-range test.

this inhibition did not occur with the cooler temperature. In both temperatures, 0.4 mM FA reduced these morphological features, but effects were greater in the hot environment. In contrast, an increase in diffusive resistance was measured for all FA treatment levels under cool conditions, but only 0.2 and 0.4 mM FA caused an increase in resistance in the hot environment.

The general response of soybean seedlings to FA and temperature stresses used in these studies was similar to that found with sorghum. The two-way ANOVA probabilities demonstrated that both temperature and FA treatment had significant effects on leaf area and plant dry weight (Table 3). There was also a significant temperature–FA interaction on soybean leaf area and plant weight. Abaxial leaf resistance taken on day 5 was significantly higher under the hot regime, and a significant probability was also obtained from comparing all FA treatments without regard to the tempera-

TABLE 3. INTERACTION OF TEMPERATURE AND FERULIC ACID (FA) STRESS ON SOYBEAN SEEDLINGS[a]

Treatment	Day 5 abaxial resistance[b] (sec/cm)	Leaf area[b] (cm^2)	Dry weight[b] (mg)
Hot[c] (34°C)			
Control	3.5 ± 0.5a	70.9 ± 2.1a	410.0 ± 7.7a
0.1 mM FA	2.7 ± 0.2ab	71.0 ± 1.8a	349.0 ± 11.8b
		(100.2)	(85.1)
0.25 mM FA	2.1 ± 0.1b	40.2 ± 2.2b	259.4 ± 8.4c
		(56.7)	(63.3)
Cool (23°C)			
Control	1.3 ± 0.1a	52.6 ± 2.4a	393.5 ± 11.8a
0.1 mM FA	1.4 ± 0.1a	50.0 ± 1.8a	392.5 ± 12.7a
		(95.10)	(99.7)
0.25 mM FA	1.4 ± 0.1a	36.4 ± 2.6b	328.1 ± 14.8b
		(69.2)	(83.4)
	Two-way ANOVA F value (and probability)		
Temperature	59.6	63.4	11.7
	(0.0001)	(0.0001)	(0.0010)
FA	4.4	73.04	47.21
	(0.0175)	(0.0001)	(0.0001)
Temp–FA	6.6	8.85	7.3
	(0.0028)	(0.0004)	(0.0012)

[a]Values are the mean ± SE (and % of control).
[b]Column means within a temperature regime that are not followed by the same letter are significantly different, $P < 0.05$, ANOVA with Duncan's multiple-range test.
[c]Day temperature mean. See text for details.

ture. The interaction of the two stresses was further studied by comparisons of analyses within each temperature.

Soybeans grown at a day temperature of 34°C were significantly reduced in dry weight by 0.1 mM FA and plants grown with 0.25 mM FA had even lower weight (Table 3). In contrast, 0.1 mM FA did not alter the dry weight of soybeans at 23°C. Only the 0.25 mM FA treatment reduced growth in this temperature. At harvest, soybean leaf areas of the 0.25 mM FA groups were below the controls in both temperatures. Ferulic acid did not alter diffusive leaf resistance when soybeans were grown at 23°C, whereas at 34°C the 0.25 mM FA plants had a significant reduction in diffusive resistance. Data from the replicate experiment (not shown) were similar to effects shown in Table 3.

DISCUSSION

The data support the hypothesis that allelopathic effects of FA may be altered by environmental temperatures. The threshold for FA inhibition of seedling growth was significantly lower when plants were grown at temperatures near the higher end of their range of tolerance. Two previous reports have suggested an interaction of allelochemical inhibition with temperature. Glass (1976) noted that the effects of a mixture of phenolic acids on excised barley roots varied under several temperature regimes. Steinsiek et al. (1982) reported that the inhibitory action of extracts from wheat on weed-seed germination and growth was temperature-dependent, and several of the weeds they tested had the greatest inhibition at 35°C. Thus, allelopathic inhibition is closely tied with this aspect of the environment.

While FA-induced inhibition of both grain sorghum and soybean seedling growth was enhanced by temperature stress, there were some differences in response between the two test species. Inhibition of soybean seedlings was achieved by lower FA treatment levels than with sorghum, and soybeans were stressed by lower temperatures. In concert with temperature stress, 0.1 mM FA reduced soybean growth, while twice this concentration was required for inhibition of sorghum. These results illustrate that a combination of allelopathic and environmental conditions may alter growth of one species but not affect another. Such a differential in response to allelochemical action among species fosters allelopathic regulation in plant communities.

Grain sorghum seedlings treated with FA had an elevated diffusive resistance in all treatments except one. This stomatal effect was found at the lowest levels of FA treatment in the cool environment even though these treatments did not alter growth. Ferulic acid alteration of stomatal function reinforces previous work, suggesting one mechanism of allelopathic action may be an interference with plant water balance (Einhellig and Muth, 1980; Einhellig and Schon, 1982). However, the soybean plants in the hot environment that were inhibited in growth most strongly by FA had a decrease in diffusive resistance. This opposite response was unexpected, but it may have resulted from the interrelationship with heat stress. It is likely that both FA and temperature stress modify several different aspects of metabolism.

The fact that the action of an allelochemical such as FA is modified by another factor of the growth environment is extremely important for understanding allelopathy. Certainly several environmental variables influence plant growth, and it is seldom that all growth conditions are at their optimum. Other stresses, such as the temperature conditions, are a likely occurrence accompanying the presence of allelochemicals. The results of this study demonstrate that temperature stress enhances allelochemical inhibition, thus the magnitude of allelopathic action is directly related to the total conditions. A consideration of such interactions, along with the fact that

several different allelochemicals may be acting together, further clarifies the process of allelopathy under field conditions.

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