EFFECTS OF IMPOSED MOISTURE STRESS ON FOUR FOLIAR APPLIED HERBICIDES AND THE EFFECT OF QUIZALOFOP-ETHYL AND FLUAZIFOP-BUTYL ON PROTEIN SYNTHESIS

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Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
December, 1986

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ACKNOWLEDGEMENTS

The author wishes to express his appreciation to his major adviser Dr. Donald S. Murray for his training, advice, and helpful criticisms as well as for his valued personal friendship throughout the course of the author's training at Oklahoma State University. A special note of thanks is also given to Dr. Eddie Basler who gave specific suggestions, guidance, and invaluable training throughout this research as well as providing laboratory space for the research. The author also wishes to express appreciation to the other members of his committee Dr. Jim F. Stritzke, and Dr. John F. Stone for their time and suggestions on this research.

Appreciation is also extended to the Departments of Agronomy and Botany at Oklahoma State University for the use of the facilities and equipment which made this research possible. The author also wishes to acknowledge the support of Dow Chemical Company, ICI Americas Inc., DuPont Chemical Company, and BASF-Wyandotte Corporation. Thanks are also expressed to the author's fellow graduate students for input into this research as well as for their friendship. A very special thanks goes to Trina Wheless, Jean Winters, Kim Nunley, and Roberto Machaddo for their valuable assistance in the laboratory.

Great appreciation is expressed to the author's family for their kind understanding, encouragement, and love during the years of graduate study. A special note of thanks is expressed to the author's wife for her moral support, and helpful criticisms in the preparation of this manuscript.

This thesis is dedicated to my wife Sandra D. Reynolds.

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Each of the two parts of this thesis is a separate manuscript to be submitted for publication in WEED SCIENCE, the journal of the Weed Science Society of America.

PART I

EFFECTS OF IMPOSED MOISTURE STRESS ON THE ABSORPTION AND TRANSLOCATION OF FOUR FOLIAR APPLIED HERBICIDES

EFFECTS OF IMPOSED MOISTURE STRESS ON THE ABSORPTION AND TRANSLOCATION OF FOUR FOLIAR APPLIED HERBICIDES

Abstract. Laboratory experiments were conducted utilizing grain Sorghum [Sorghum bicolor (L) "Acco BRY 90"] as an indicator species to determine the effects of imposed moisture stress on the absorption and translocation of the butyl ester of fluazifop {(±)-2-[4-[[5-(trifluoromethyl)-2-pyridinyl]oxy]phenoxy]propanoic acid}, sethoxydim {2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one}, methyl ester of haloxyfop {2-[4-[[3-chloro-5-(trifluoromethyl)-2-pyridinyl]oxy]phenoxy]propanoic acid}, and the ethyl ester of quizalofop {2-[4-[(6-chloro-2-quinoxalinyl)oxy]-phenoxy]-propionic acid, ethyl ester}.

The absorption and percent recovery were calculated as well as acropetal and basipetal translocation of the absorbed ^{14}C-herbicide. With the exception of quizalofop the percent recovery for all herbicides was significantly less at the 48 h time interval when compared to the 3 and 6 h treatment interval. Herbicide recovery was not affected by imposed moisture stress. Imposed moisture stress affected the ^{14}C-herbicide absorption when plants were exposed to the stress for 48 h but stress did not affect

herbicide absorption by plants exposed to stress for 3 or 6 h. The percent absorption of the ^{14}C herbicide was greatest at the 48 h time interval for all herbicides. Moisture stress did not affect the acropetal translocation of any herbicide at the 6 or 48 h time interval; however, differences existed among herbicides. The basipetal translocation for all herbicides was affected similarly by imposed moisture stress. Moisture stress caused approximately an 18% decrease in basipetal translocation of all herbicides. Differences in basipetal translocation also existed among the herbicides. The data also indicates that on a percent basis, acropetal and basipetal translocation occurs rapidly with these compounds with the total amount translocated being dependent upon herbicide absorption.

Additional index words. water stress, acropetal, basipetal, psychrometers, graminicides, haloxyfop-methyl, fluazifop-butyl, quizalofop-ethyl, sethoxydim.

INTRODUCTION

A number of selective postemergence applied grass herbicides has recently been introduced. Four of these herbicides include fluazifop-butyl, sethoxydim, haloxyfop-methyl, and quizalofop-ethyl. These herbicides can effectively control perennial and annual grass species when applied in a timely manner under favorable growing conditions (2,8,12,16). Postemergence applied herbicides provide another control option and in some instances are replacing the conventional preplant incorporated and

preemergence herbicides. However, the degree of control can be quite variable (8,13,16). These herbicides appear to be significantly affected by environmental conditions, as shown with other herbicides (6,14,17,20,21).

Retzinger et al. (16) showed that the degree of johnsongrass [Sorghum halepense (L.) Pers. #[1] SORHA] control with sethoxydim was more dependent on rainfall 5 days before and after herbicide application than size of johnsongrass. Conversely, Chernicky et al. (8) reported that moisture stress did not affect the control of large crabgrass [Digitaria sanguinalis (L.) # DIGSA] with sethoxydim. Kells et al. (13) have shown that the control of quackgrass [Agropyron repens (L.) Beauv. # AGRRE] with fluazifop was significantly reduced by moisture stress. They showed with radioautographs that fluazifop was better distributed throughout the plant when plants were not under moisture stress.

Fluazifop, haloxyfop, quizalofop, and sethoxydim appear to produce similar injury symptoms on susceptible plants. Treated leaves become reddish-purple probably due to anthocyanin production resulting from the increased accumulation of free sugars in the leaves (1,18). Associated with this, necrosis is initially in the meristematic tissue and ultimately the entire leaf tissue

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1. Letters following this symbol area a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark St., Champaign, IL 61820

dies (1,10,18). Fluazifop and haloxyfop appear to undergo hydrolysis and are translocated as free acids in both xylem and phloem tissue to their respective sites of action (3,9,13,19). Sethoxydim has been shown to be transformed into six major products when in aqueous media and upon exposure to light (4). Less than 2% of the original parent compound was detected after 3 h thus indicating that one of the more stable end products is the herbicidal active form (4,5).

Fluazifop, haloxyfop, and sethoxydim caused significant reductions in corn [Zea mays (L.)] yields when applied at sublethal concentrations (7). This was attributed to their effects on respiration (1,11), protein synthesis (15), or apparent photosynthesis (10).

These herbicides have been extensively investigated in field situations for their effectiveness; however, little information is available on their responses to moisture stress alone. The research that is conducted in field situations in which the plants are stressed is usually a net effect of several stress factors such as intense light, low humidity, and high temperatures. The objective of this research was to evaluate the effect of imposed moisture stress on the absorption and translocation of fluazifop, haloxyfop, quizalofop, and sethoxydim independently of other factors associated with stress.

MATERIALS AND METHODS

Grain sorghum seedlings were utilized to determine absorption and translocation parameters of these herbicides because of their susceptibility (2) and genetic uniformity. The experimental design of this experiment was a 3 by 2 by 4 factorial with 4 replications. The three time intervals of translocation (3, 6, and 48 h) were the fixed components of one factor. The two levels of stress imposed were the components of the second factor and were actually random components of the model as each stress level was not exactly the same. The four herbicides were the levels of the third factor and were analyzed as fixed components of the model as they were always constant. This experiment was repeated one time. In both experiments, the plants were established and maintained similarly. The bioassay media was a Teller fine sandy loam (fine-loamy mixed thermic Udic Argiustoll). The soil was taken from the top 15 cm of the soil profile, passed through a 2 mm soil sieve and stored in polyethylene containers until needed. The soil analysis was conducted on a composite soil sample taken from the storage containers. The soil contained 50, 149, and 502 kg/ha of nitrogen, phosphorus, and potassium, respectively and had 0.8% organic matter and a pH of 5.9. Ten seeds were planted per 8.5 (top diameter) by 14 (height) cm styrofoam cup containing 575 g of air dry soil. After emergence the seedlings were thinned to a density of 1 seedling per cup. The plants were grown in a controlled environment chamber at 80% RH with a

temperature regime of 29 C days and 21 C nights and a 12 h photoperiod at an average photosynthetic photon flux density (PPFD) of 241 $\mu E \cdot m^{-2} \cdot s^{-1}$. The growth chamber had horizontal air movement perpendicular to the treatment replications. Imposed moisture stress. The water holding capacity of the soil within the cups was determined prior to the initiation of the experiment. A cup with bottom drainage holes was filled with 575 g of air dry soil, and then saturated by applying water to the surface of the soil. The uncovered cup was placed on a large piece of absorbent paper which was covered with a small amount of soil and allowed to drain for 12 h. The cup and soil were reweighed to determine the water holding capacity of the soil contained in the cup.

At the time of planting the cups were subirrigated in order not to disturb the planted seeds. The plants were then watered every other day on a gravimetric basis to ensure uniformity of the population in terms of soil water availability. Six days prior to herbicide application, one-half of the entire population was no longer watered in order to impose a high degree of moisture stress (6). The remaining one-half of the population was watered up to and including the day of herbicide application. At the time of herbicide application, leaf-cutter thermocouple psychrometers[2] were utilized to quantify leaf water potentials. A leaf disc was taken from the first fully

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2. J. R. D. Merrill Specialty Equipment, Logan, Utah 84321.

expanded leaf 3 cm above the leaf collar. Preliminary experimentation showed no significant difference in leaf water potential between the first and second true leaves. The leaf samples were enclosed in the thermocouple chambers and placed in a water bath at 30 C for at least 4 hours prior to reading. After the thermocouples were equilibrated, they were attached to a microprocessor-controlled Wescor HP-115 Water Potential Data System,[3] and microvolt readings were taken. The thermocouples' measuring junctions were cooled by passing a 5 mA current through it for 5 s followed by a 5 s delay; the measuring junction was then monitored for 15 s.

Herbicides and herbicide application. All herbicides were labeled with ^{14}C. Herbicide specific activity and labeled positions are as follows: fluazifop (21.5 Ci/M), quizalofop (8.1 Ci/M,phenol-^{14}C), haloxyfop (10.6 Ci/M, phenoxy UL-^{14}C), and sethoxydim (13.06 Ci/M, H-4-^{14}C). A treatment solution of each herbicide was prepared by dissolving each in acetone and Triton X100 (Oxtoxynol) to bring the herbicides to a concentration of approximately 0.05 µCi/µl with 0.47% Triton X100. Standards from each treatment solution were taken before, during, and after herbicide applications in order to quantify the exact amount of ^{14}C-herbicide applied to the plants. Two 1-µl drops of each respective herbicide were applied to the second most fully expanded true leaf 2 cm above the collar. The plants were

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3. Wescor Inc. 459 South Main, Logan, Utah 84321.

then placed back into the controlled environment chamber without watering and allowed to continue growth for either 3, 6, or 48 hours.

At the time of harvest the plants were sectioned into 6 components. The treated leaf was removed from the plant at the collar and dissected into 3 components: a 2 cm section between the treated area and the collar of the treated leaf; a 2 cm section where the herbicide was applied; and the portion of the treated leaf above the treated area. The remainder of the plant was sectioned into 3 components: the roots of the plant; plant parts (minus roots) below where the collar of the treated leaf was attached; and plant parts above where the collar of the treated plant was attached. At harvest, the 2 cm treated area section was excised from the treated leaf and washed in 10 ml of 95% ethanol for 30 s to remove any unabsorbed material from the leaf surface.

The dissected plant parts were lyopholized and weighed. The tissue was then homogenized with an electronic tissue homogenizer in a total volume of 10 ml of 95% ethanol. An aliquot of the leaf wash, as well as each homogenate, was analyzed by liquid scintillation spectrophotometry utilizing a Beckman LS 5801[4]. The samples were corrected for background, dilution, and quench; thus, data reported are calculated from corrected disintegrations per minute (DPM) values.

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4. Beckman Instruments, P.O. Box C-19600, Irvine, California 92713.

The percent recovery was calculated as the percentage of the amount of ^{14}C-herbicide applied that can be accounted for in the total of the plant fractions as well as the leaf wash of the treated area. Herbicide absorption was calculated as the percent of the recovered ^{14}C which was not removed in the leaf wash of the treated leaf. Acropetal translocation was calculated as the percentage of the ^{14}C absorbed by the plant that moved into the leaf tissue above the treated area. Basipetal translocation is the percentage of the total ^{14}C found in leaves, stems, and the roots below the treated area.

All studies were repeated and data presented are means of two experiments. Means were separated using a model with the error term nested within runs [Run(Time Herb Stress)] in order to evaluate the treatment means which have unequal variances between experiments. By assigning groupings of stressed or non-stressed to the plants, the data were analyzed with stress as a fixed effect instead of using each individual stress value which was a random effect.

The data were also subjected to regression analysis utilizing the individual values of water potential as one of the independent variables along with time and herbicide. The regression analysis was also conducted with the stress and non-stressed plants being evaluated as fixed effects as previously described. The dependent variables evaluated

were percent recovery, absorption, and acropetal and basipetal translocation.

RESULTS AND DISCUSSION

Imposed moisture stress. These data were analyzed with respect to stress level and it was determined that stress levels were significantly different, whereas, the stress levels were not significantly different between individual treatments of herbicides or time. The values presented are the mean values combined over herbicides, time interval, and experiments. The terminology of high and low stressed plants will for the remainder of this discussion be indicative of leaf water potential mean values of -680 (±274) and -363 (±133) kPa, respectively.

Herbicides and herbicide application. The percent absorption was the only parameter to show a good correlation with the independent variables when using the individual water potential values as well as the groupings of water potentials. The R^2 values for each herbicide's absorption as a quadratic function of stress and time ($\hat{y} = \beta_0 + \beta_1*time + \beta_2*time^2 + \beta_3*stress + \beta_4*stress^2 + \beta_5*time*stress + \beta_6*time*stress^2 + \beta_7*stress*time^2$) was 0.91, 0.82, 0.75, and 0.88 for haloxyfop, fluazifop, quizalofop, and sethoxydim, respectively. The analysis of variance for the percent recovery of herbicides applied resulted in a significant time by herbicide interaction (Table 1) with no other interactions or individual parameters being significant to the model. These data indicate that the percent recovery of

the herbicides was not different between 3 and 6 h for any given herbicide. The percent recovery for all herbicides with the exception of quizalofop was significantly lower at the 48 h time interval than at either the 3 or 6 h time intervals. Quizalofop exhibited no change on percent recovery at any of the time intervals as did the other herbicides. Sethoxydim exhibited the highest percent recovery of any herbicide at the 3 and 6 h interval. At the 48 h time interval quizalofop exhibited the highest percent recovery of 88% followed by sethoxydim at 76% and haloxyfop and fluazifop at 65 and 66%, respectively. There was no significant effect on recovery of the herbicides by stress level. The reason for a decrease in percent herbicide recovery due to time may be explained by the fact that by 48 h some of the ^{14}C-herbicide may have been exuded into the soil in which the plants were growing or due to incomplete recovery of the roots from the soil. Analysis of the soil however, failed to provide significant quantities of ^{14}C-herbicide upon extraction with ethanol or hexane.

The percent of recovered herbicide absorbed by the plants exhibited a significant time by stress interaction (Table 2) as well as a significant time by herbicide interaction (Table 3). The percent absorption of the herbicides was not different between 3 and 6 h nor were they affected by stress at these time intervals. All herbicides exhibited a significantly greater absorption of herbicide at the 48 h time interval than at the 3 or 6 h time interval

under both stressed and non-stressed conditions. At the 48 h time interval the stressed plants exhibited a significant increase in the absorption of herbicides.

The effects of time on each herbicide (Table 3) also indicates that all herbicides exhibit a greater absorption at the 48 h time interval than at the 3 or 6 h time interval. Fluazifop had the greatest amount of absorption at the 48 h time interval followed by haloxyfop and sethoxydim with quizalofop having the least amount of absorption. Herbicides differed little, if any, among the 3 and 6 h time intervals. The increase in absorption of the herbicides with respect to time is explainable provided the herbicide stays in contact with the tissue, allowing more to enter. The reason that the higher stress levels appear to further increase absorption is not easily explained. This result may be due to increased adsorption to the leaf surface which by our methodology is indistinguishable from absorption. In general, all herbicides would be expected to exhibit an increase in absorption with respect to time as was shown by regression. The other possibility is the same amount of herbicide was absorbed at all time intervals but due to decreased recovery of ^{14}C-herbicides with respect to time the percentage of the recovered herbicide absorbed would appear to be significantly greater even though the actual quantity of herbicide present in the plant is constant.

The acropetal movement of these herbicides exhibited a time by herbicide by stress interaction (Table 4). These data indicate that stress caused significantly more acropetal movement with fluazifop and sethoxydim and significantly less acropetal movement with quizalofop at the 3 h time interval. Stress did not significantly affect acropetal movement at the other time intervals. Sethoxydim had the greatest acropetal translocation of any of the herbicides at the 48 h time interval under the stressed condition. In general, sethoxydim had the greatest acropetal movement of all the herbicides.

Basipetal translocation is an important factor in considering the effectiveness of these herbicides, especially for deep rooted perennial species. The statistical analysis of this parameter indicates that the significant factors were time, herbicide, and stress with no interactions being present. The data show 19, 17, 13, and 10 % basipetal translocation for sethoxydim, haloxyfop, fluazifop, and quizalofop, respectively with a least significant difference (LSD α=0.05) of 5.0. The stressed plants exhibited significantly less basipetal translocation than the non-stressed plants. The stressed plants had 12.5 % of the absorbed ^{14}C translocated basipetally while the non-stressed plants had 15.3 % translocated basipetally. This accounts for an 18.3 % reduction in the amount of basipetal translocation for the moisture stressed plants in comparison with the non-stressed plants. A significance in

basipetal translocation also existed with respect to time. The percent basipetal translocation was 15, 11, and 16% at 3, 6, and 48 h, respectively. This indicates that the downward translocation of these herbicides occurs in a few hours. It should be noted, however, that if 15% of the material in the tissue is translocated basipetally, the actual quantity translocated is directly affected by the amount absorbed which increases with time. The percentage of ^{14}C present in the root fractions was not affected by stress or herbicide. The Observable Significance Level (OSL) for the time parameter resulted in a value of 0.07 indicating that time would be a significant factor if evaluated by analysis of variance at an alpha level of 0.1.

These data indicate that differences do exist as to how many of these products enter the plants in both stressed and non-stressed conditions as was shown by the absorption and recovery data. These data showed that stress affected their distribution within the plants at these stress levels. The data also indicates that all herbicides reacted in a similar fashion with respect to the reduction of basipetal translocation due to moisture stress, although the actual quantities of herbicide translocated varied among herbicides. These data alone do not explain variable responses to herbicidal applications in field situations. It should be noted that under field conditions, stressed plants are usually under a variety of different stresses. Plants under moisture stress are generally also subjected to

high temperatures, low relative humidity, and intense sunlight. All of these environmental stresses can have an effect on some of these herbicides as shown by previous research (8,13,16,21). There are also possibilities that these factors may have an interaction with each other such that no one factor can be singled out to explain the variable performance of these herbicides in field situations when applied to stressed plants.

ACKNOWLEDGMENTS

Appreciation is expressed to Basf Wanydotte Co., Dow Chemical Co., E. I. DuPont de Nemours and Co., and ICI Americas for supplying radiolabled sethoxydim, haloxyfop-methyl, quizalofop-ethyl and fluazifop-butyl, respectively.

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Table 1. Percent of ^{14}C-herbicide applied to grain sorghum recovered in plant tissue and wash.

	Treatment time interval (hours)		
Herbicide	3	6	48
	% recovery		
haloxyfop	88 bc	83 b-d	65 e
fluazifop	86 b-d	80 cd	66 e
quizalofop	85 bc	80 cd	88 bc
sethoxydim	99 a	92 ab	76 d

Means Separated by LSD ($\alpha = 0.05$) = 10.

Table 2. Percent of recovered ^{14}C-herbicide absorbed by grain sorghum as affected by moisture stress and time.

Stress level	Treatment time interval (hours)		
	3	6	48
	% absorption		
high	8 c	11 c	53 a
low	8 c	8 c	42 b

Means Separated by LSD ($\alpha = 0.05$) = 5.

Table 3. Percent of recovered ^{14}C-herbicide absorbed by grain sorghum as affected by herbicide and time.

	Treatment time interval (hours)		
Herbicide	3	6	48
	% absorption		
haloxyfop	7 ef	8 d-f	50 b
fluazifop	9 d-f	11 d-f	65 a
quizalofop	4 f	5 ef	25 c
sethoxydim	12 de	15 d	52 b

Means separated by LSD ($\alpha = 0.05$) = 7.

Table 4. Percent of absorbed ^{14}C-herbicide translocated acropetally from the treated area as affected by herbicide, time, and moisture stress.

	Treatment time interval (hours)					
	3		6		48	
	Stress level					
Herbicide	high	low	high	low	high	low
	% acropetal translocation					
haloxyfop	7 c-e	10 c-e	6 de	5 e	11 c-e	11 c-e
fluazifop	15 a-c	5 e	9 c-e	7 c-e	12 b-e	13 b-e
quizalofop	11 c-e	19 ab	13 b-d	6 de	10 c-e	10 c-e
sethoxydim	20 ab	7 de	11 c-e	9 c-e	23 a	20 ab

Means Separated by LSD ($\alpha = 0.05$) = 8.

PART II

EFFECTS OF QUIZALOFOP-ETHYL, FLUAZIFOP-BUTYL, DICYCLOHEXYLCARBODIIMIDE, AND PH ON PROTEIN SYNTHESIS

EFFECTS OF QUIZALOFOP-ETHYL, FLUAZIFOP-BUTYL, DICYCLOHEXYLCARBODIIMIDE, AND PH ON PROTEIN SYNTHESIS

Abstract. Laboratory experiments with grain sorghum [Sorghum bicolor (L) "Acco BRY 90"] were conducted to determine the effects of the butyl ester of fluazifop {(±)-2-[4-[[5-(trifluoromethyl)-2-pyridinyl]oxy]phenoxy]propanoic acid}, the ethyl ester of quizalofop {2-[4-[(6-chloro-2-quinoxalinyl)oxy]-phenoxy]-propionic acid, ethyl ester}, dicyclohexylcarbodiimide, and pH on the absorption and incorporation of ^{3}H-L-leucine into protein.

The recovery of the applied ^{3}H-L-leucine was not significantly different among treatments or pH. Fluazifop at 100 µM concentration at pH 4.5 resulted in less absorption of leucine from the incubation media than the check. The 100 µM concentration of quizalofop at pH 4.5 and 7.5 also resulted in less absorption than the check. The percent incorporation of absorbed leucine was significantly greater at the 6.5 pH level for the check and the 100 µM concentration of fluazifop in comparison to each's respective pH levels. Fluazifop at 100 µM enhanced ^{3}-H-L-leucine incorporation into protein at pH 4.5 and 6.5 over that of the check at the same pH value. Quizalofop at a 1

µM concentration exhibited a higher incorporation value than the check at pH 7.5 as did 100 µM quizalafop at pH 4.5 and 7.5. Fluazifop caused an over all significant reduction in the synthesis of protein at both concentrations as did DCCD. Neither concentration of quizalofop resulted in a reduction of protein content.

Additional index words. Leucine, amino acid, pH, DCCD.

INTRODUCTION

Several postemergence-over-the-top applied herbicides have recently been developed for the control of annual and perennial grass species. The list of such herbicides include fluazifop-butyl and quizalofop-ethyl. These herbicides give good control of many grass species when applied in a timely manner under favorable growing conditions (7,19,20,28). These herbicides cause similar visual injury symptoms to susceptible species. Initially the plant's leaves will become red to purple in coloration followed by the necrosis of the meristematic regions of the growing plant and ultimately the necrosis and death of the entire plant. The red color of leaves caused by applications of sethoxydim {2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one}, has been reported (1) to be due to the accumulation of free sugars which causes anthocyanin production thus resulting in the coloration of the plant. This increase in accumulation is possibly due to a reduction in respiration (1).

Fluazifop-butyl and haloxyfop-methyl {2-[4-[[3-chloro-5-(trifluoromethyl)-2-pyridinyl]oxy]phenoxy]propanoic acid} appeared to undergo hydrolysis and were translocated as free acids to their respective sites of action (3,11,20,30). Fluazifop-butyl, and haloxyfop-methyl were shown to be mobile in both xylem and phloem tissue (5,11,20).

Fluazifop-butyl, haloxyfop-methyl, and sethoxydim caused significant reductions in corn [Zea mays (L.)] yields when applied at sub-lethal concentrations to 70- to 80-cm corn (6). This may be attributed to the effects of these herbicides on respiration (1,15), protein synthesis (24), or apparent photosynthesis (14).

The effects of various herbicides on protein synthesis has been extensively investigated (13,16,18,22,23,27). Fluazifop-butyl has been reported to inhibit protein synthesis in concentrations of 1 X 10^{-4} to 1 x 10^{-6} M. The reduced incorporation effects due to fluazifop were found to be reduced by 2 x 10^{-6} M concentrations of 2,4-D [(2,4-dichlorophenoxy)acetic acid] (24). Haloxyfop-methyl did not significantly affect protein synthesis in cultured cells of corn as indicated by ^{14}C-leucine incorporation and did not result in an increase in the uptake of the free ^{14}C-leucine (9). However, fatty acid synthesis was greatly reduced. A major effect of diclofop-methyl was to inhibit ATP synthesis and the translocation of photosynthate to the roots of wild oats [Avena fatua (L.) # AVEFA] a susceptible species while the effects were not as pronounced in barley [Hordeum

vulgare (L.)] a resistant species (10). The utilization of leucine to evaluate protein synthesis has been extensively researched and established as a reliable means of protein synthesis determination (2,8,17,25,29).

Fluazifop, haloxyfop-methyl, and sethoxydim have been investigated more than has quizalofop; however, more information is needed to understand the specific mode of action of these herbicides. The objectives of this research were to determine the effects of fluazifop and quizalofop on protein synthesis and to compare those results with that of a known H^+ extrusion inhibitor DCCD (4,12,26) and to determine if the results would be altered by pH gradients.

MATERIALS AND METHODS

The following methodology utilized to determine protein synthesis was a slightly modified technique from that described by Gruenhagen and Moreland (17).

Tissue preparation. Grain sorghum a susceptible species to these herbicides (19), was used to obtain tissue for incubation. Grain sorghum seeds were washed for 3 h in an aerated screen cage with fresh tap water being added constantly. The seeds were then placed in three rows on germination paper, rolled up, and wrapped with polyethylene. One end of the polyethylene wrapped germination paper was then placed into a styrofoam cup containing one-half strength Hoagland's solution, such that no seeds were submerged below the Hoagland's solution surface. The cups containing the Hoagland's solution and germination papers

were then placed into a controlled environment chamber with a 24 h darkness period at a temperature of 25 C.

The seeds were allowed to germinate for 4 days with nutrient solution being added as needed. On the fourth day 1 cm sections of mesocotyl tissue were excised just below the coleoptile node. Ten 1 cm sections were weighed and placed in test tubes for each data observation.

Incubation Media. The incubation media consisted of 2.50 ml of 0.02 M potassium phosphate buffer, (pH of 4.5, 6.5, or 7.5), 1.00 ml of 5% (w:v) sucrose, 1.25 ml of distilled water, 0.20 ml of ^{3}H-L-leucine[5] (1.0 µCi/ml), and 0.05 ml stock solution of technical grade fluazifop, quizalofop, DCCD, or 95% ethanol. The fluazifop and quizalofop stock solutions were prepared at concentrations of 1×10^{-2} and 1×10^{-4} M in 95 % ethanol and the DCCD stock solution was prepared in ethanol at a concentration of 5×10^{-2} M.

Incubation and Analysis of Tissue. The tissue was placed in test tubes with all components of the media present and the radiolabeled leucine and the fluazifop, quizalofop, DCCD, or ethanol was added last. The tubes were then placed into a continuously shaking 30 C water bath and allowed to incubate for 3 hr.

The incubation media was removed from the tissue by decanting the media and tissue into an ASTM suction funnel such that the incubation media was caught in a test tube

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5. ICN Radiochemicals, P.O. Box 19536, Irvine,CA 92713 (2,3,4,5-^{3}H sp. act. 115 Ci/mmole)

inside the suction flask. The tissue was subsequently washed with two 5 ml aliquots of unlabeled leucine (200 µg/ml) to remove any unabsorbed ^{3}H-L-leucine. The washes were added to the original incubation media. The tissue was then stored at -20 C until analysis were made. After thawing the tissue was homogenized in 10 ml of 95% ethanol utilizing a hand-held glass tissue homogenizer. The homogenate containing the ethanol precipitated protein was centrifuged for 10 min at 8x with the supernatant being decanted into another tube. The pellet, consisting of cellular debris and protein, was washed 2 times by resuspending in 5 ml aliquots of ethanol and centrifuging as before. The washes and supernatant were combined. The supernatants contained the ^{3}H-L-leucine taken up by the tissue but not incorporated into protein. The pellet was subsequently resuspended in 1.2 ml of 0.5 N NaOH and left for 1.0 h in order to solubilize the protein. This fraction was then centrifuged for 10 min at 8x. The resulting supernatant containing the NaOH-soluble protein was utilized in 0.50 ml aliquots to determine the amount of radiolabeled leucine present in the protein fraction and for protein determinations. The pellet also was analyzed to determine the amount of ^{3}H-L-leucine present in the cellular debris.

An aliquot of each homogenate as well as the incubation media was analyzed by liquid scintillation spectrophotometry

utilizing a Beckman LS 5801[6]. The aliquots from aqueous based fractions such as the incubation media, protein fraction, and pellet were frozen and lypholized[7] in order to minimize insolubility with the scintillation cocktail utilized[8]. The samples were corrected for background, dilution, and quench; thus, data reported are corrected disintegrations per minute (DPM) values.

The percent recovery of the applied leucine was calculated by totaling the DPM present in all fractions and dividing it by DPM applied to the medium. The percent of the total DPMs absorbed that was present in individual fractions was calculated by dividing the number of DPMs absorbed in a given fraction by the total number of DPMs absorbed and multiplied by 100.

Protein determinations were made using the Lowry method (21). After color development for 30 min spectrophotometric readings were taken at 750 nm. The amount of protein present was determined by comparison to standard curves prepared with bovine albumin serum.

Experiment I statistical design and analysis. This research was divided into two separate experiments. Experiment I consisted of the evaluation of 1 and 100 µM fluazifop and DCCD at a concentration of 500 µM. Each of these treatments

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6. Beckman Instruments, P.O. Box C-19600, Irvine, California 92713.
7. Virtis Freezemobile 12, The Virtis Company Incorporated, Gardiner, New York 12525.
8. 3a70 Complete Counting Cocktails, Research Products International Corporation, 410 N. Business Center Drive, Mount Prospect, Illinois 60056.

were evaluated in 0.01 M potassium phosphate buffers at pH 4.5, 6.5, and 7.5. The experimental design was a randomized complete block design with a 4 by 3 factorial arrangement of treatments with 4 replications. This experiment was conducted three times. The data presented were pooled for analysis and data reported are the means of the three experiments.

Experiment II statistical design and analysis. Experiment II was conducted identically to experiment I with the exception that quizalofop was utilized instead of fluazifop. The concentrations of quizalofop evaluated were also at 100 and 1 μM. The same buffer concentrations and pHs were utilized for this experiment. The experimental design was a randomized complete block design with a 4 by 3 factorial arrangement of treatments with 4 replications. This experiment was conducted twice and the data were pooled for analysis. The data presented are the means for the two experiments.

RESULTS AND DISCUSSION

Experiment I. The percent recovery of the ^{3}-H-L-leucine applied for tissue uptake did not vary significantly between treatments or pH units (data not shown). The absorption of ^{3}H-L-leucine showed a significant treatment by pH interaction (Table 1). The DCCD, as expected caused the greatest reduction in leucine absorption of any treatment. The absorption of leucine was not significantly, affected by either herbicide concentration at pH 6.5 or 7.5 in

comparison to the check. There was, however, significantly less absorption at pH 4.5 for fluazifop at a concentration of 100 µM but not at 1 µM. The lowest pH value of 4.5 provided significantly greater absorption of leucine than at 7.5 for the check and 100 µM fluazifop treatments. There were no differences between the pH levels for the DCCD or 1 µM fluazifop treatments.

The percent of the absorbed ^{3}H-L-leucine incorporated into the protein fraction had a significant pH by treatment interaction (Table 2). These data present the percent incorporation of absorbed leucine by the tissue. The check treatment resulted in a significantly higher percentage of incorporation at the intermediate level of pH as did 100 µM fluazifop in comparison to the other pH levels. Fluazifop at the 1 µM concentration had significantly less incorporation of leucine at the 4.5 than at either the 6.5 or 7.5 pH level.

The amount of ^{3}H-L-leucine (pg) present in the protein per gram of fresh tissue is shown in Table 3. On this basis, fluazifop at 100 µM enhanced ^{3}-H-L-leucine incorporation into protein at pH 4.5 and 6.5 over that of the check. There was no significant effects of pH on ^{3}H-L-leucine incorporation into protein in the absence of fluazifop although at 100 µM concentration of fluazifop, less ^{3}H-L-leucine was incorporated at pH 7.5 than at pH 6.5 or 4.5. The 1 µM concentration of fluazifop had no affect on leucine incorporation when compared to the check. The

DCCD treatment caused significantly less leucine incorporation than any other treatment.

The quantities of protein present per gram of fresh tissue reveals the overall net effects of fluazifop on synthesis and degradation of protein. There were no interactions present for this parameter nor was pH significant (Table 4). These data show that DCCD had the most dramatic effect of any treatment on protein content although both concentrations of fluazifop caused significant reductions in protein content when compared to that of the check.

Experiment II. There was no significant effect by quizalofop treatments or pH on ^{3}-H-L-leucine recovery. The percent of the recovered herbicide absorbed by the tissue (Table 1) was significantly less than that of the check for 100 µM quizalofop and DCCD at the 4.5 and 7.5 pH levels but not at the intermediate pH level of 6.5. The 1 µM quizalofop treatment did not significantly differ in absorption from that of the check.

The percentage of the absorbed leucine incorporated into the protein fraction was affected by quizalofop and DCCD and had a significant treatment by pH interaction (Table 2). These data indicate that DCCD did not significantly affect the percentage of incorporation from that of the check. Quizalofop at the 100 µM concentration at pHs 4.5 and 7.5 as well as quizalofop at 1 µM pH 7.5,

exhibited an increase in the percentage of leucine present in the protein fraction over that of the check.

The quantity of ^{3}H-L-leucine incorporated (pg/g fresh weight) indicates no significant affect by DCCD or quizalofop from that of the 100 µM concentration (Table 3). Quizalofop exhibited a higher incorporation value than the check at the 1 µM concentration at the 7.5 pH level.

The actual milligrams of protein present per gram of fresh tissue (Table 4) indicates that protein synthesis was not affected by quizalofop at any concentration. DCCD, as in the first experiment had a significant reduction in protein synthesis. The pH also had an affect on protein synthesis but no pH, treatment interaction was present. The amount of protein present per g of fresh tissue (mg/g) was 173 177, and 152 (LSD α=0.05 = 13) for pH 4.5, 6.5, and 7.5, respectively. These data show that protein content was higher for all treatments at the 4.5 or 6.5 level of pH.

The data from these experiments indicate that protein content is inhibited by 1 and 100 µM fluazifop but not by 1 and 100 µM quizalofop. These data shows that although protein content is inhibited by fluazifop that the percentage of ^{3}H-L-leucine present in the protein fraction is greater in the presence of 100 µM fluazifop. These data also indicate that fluazifop does not act the same as DCCD, a know H^{+} efflux inhibitor. These data also indicate that the incorporation of ^{3}H-L-leucine was the highest at pH 6.5 for the check as well as for the 100 µM fluazifop.

These data appear to indicate that as protein content is decreased the utilization of an exogenous source of leucine increases. This possibly means that a precursor to protein synthesis is being inhibited or that the degradation of the protein is being stimulated. It also indicates that although incorporation of leucine into protein is pH sensitive that the net effect on protein content was a reduction by the fluazifop treatments. Another possible reason for an increased utilization of leucine is that although overall protein content is being decreased that synthesis of proteins rich in leucine are being stimulated.

ACKNOWLEDGMENTS

Appreciation is expressed to E. I. DuPont de Nemours and Co., and ICI Americas for providing technical grade quizalofop-ethyl and fluazifop-butyl, respectively.

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Table 1. Effects of fluazifop, quizalofop, DCCD, and pH on percent of recovered ^{3}H-L-leucine absorbed by grain sorghum mesocotyl tissue.

Treatment	pH of incubation media		
	4.5	6.5	7.5
Experiment I[1]			
	% absorbed		
Check	5.22 e	3.68 cd	3.16 bc
Fluazifop (1 µM)	4.40 de	3.31 b-d	4.01 cd
Fluazifop (100 µM)	4.02 cd	4.23 c-e	2.26 ab
DCCD (500 µM)	1.48 a	1.60 a	1.50 a
Experiment II[2]			
	% absorbed		
Check	3.95 de	2.94 b-d	3.70 c-e
Quizalofop (1 µM)	3.46 cd	3.12 cd	4.83 e
Quizalofop (100 µM)	2.51 a-c	2.91 b-d	1.63 ab
DCCD (500 µM)	1.48 a	1.76 ab	1.72 ab

[1]Means separated by LSD (α = 0.05) = 1.15.

[2]Means separated by LSD (α = 0.05) = 1.32.

Table 2. Effects of fluazifop, quizalofop, DCCD, and pH on percent of absorbed ^{3}H-leucine incorporated into protein fraction of grain sorghum mesocotyl tissue.

Treatment	pH of incubation media		
	4.5	6.5	7.5
Experiment I[1]			
	% incorporation		
Check	22 abc	38 fg	31 c-e
Fluazifop (1 µM)	26 bc	32 d-f	33 d-f
Fluazifop (100 µM)	36 ef	40 g	34 ef
DCCD (500 µM)	27 b-d	22 ab	19 a
Experiment II[2]			
	% incorporation		
Check	21 a	27 a-c	21 a
Quizalofop (1 µM)	21 a	31 b-e	38 e
Quizalofop (100 µM)	32 c-e	34 c-e	33 c-e
DCCD (500 µM)	28 a-d	32 c-e	24 ab

[1]Means separated by LSD ($\alpha = 0.05$) = 6.

[2]Means separated by LSD ($\alpha = 0.05$) = 8.

Table 3. Effects of fluazifop, quizalofop, DCCD, and pH on the amount of ^{3}H-leucine incorporated per gram of fresh grain sorghum mesocotyl tissue (pg/g).

Treatment	pH of incubation media		
	4.5	6.5	7.5
Experiment I[1]			
	pg/g		
Check	290 b	370 bc	313 b
Fluazifop (1 µM)	366 bc	349 b	386 bc
Fluazifop (100 µM)	470 cd	522 d	325 b
DCCD (500 µM)	144 a	133 a	111 a
Experiment II[2]			
	pg/g		
Check	195 a-c	215 bc	178 a-c
Quizalofop (1 µM)	192 a-c	238 bc	416 d
Quizalofop (100 µM)	252 bc	272 c	156 ab
DCCD (500 µM)	108 a	182 a-c	115 a

[1]Means separated by LSD ($\alpha = 0.05$) = 119.

[2]Means separated by LSD ($\alpha = 0.05$) = 97.

Table 4. Effects of fluazifop, quizalofop, and DCCD on quantity of protein per gram of fresh grain sorghum mesocotyl tissue (mg/g).

treatment	
Experiment I[1]	
	mg/g
check	149 a
Fluazifop (1 µM)	135 b
Fluazifop (100 µM)	134 b
DCCD (500 µM)	114 c
Experiment II[2]	
	mg/g
check	169 a
Quizalofop (1 µM)	178 a
Quizalofop (100 µM)	179 a
DCCD (500 µM)	144 b

[1]Means separated by LSD ($\alpha = 0.05$) = 11.

[2]Means separated by LSD ($\alpha = 0.05$) = 15.

VITA

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Doctor of Philosophy

Thesis: EFFECTS OF IMPOSED MOISTURE STRESS ON FOUR FOLIAR APPLIED HERBICIDES AND THE EFFECT OF QUIZALOFOP-ETHYL, AND FLUAZIFOP-BUTYL, ON PROTEIN SYNTHESIS

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