

Reprinted from *WEEDS*
Vol. 14, No. 2, April 1966

Influence of Temperature and Humidity on Foliar Absorption, Translocation, and Metabolism of 2,4,5-T by Mesquite Seedlings¹

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Abstract. Foliar absorption of carboxyl-labeled 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) by mesquite [*Prosopis juliflora* var. *glandulosa* (Torr.) Cockerel] seedlings was continuous throughout a 72-hr period. Approximately 50% of the 2,4,5-T applied to a single leaf was absorbed when 5 to 100 µg were applied. No significant differences were found in the amounts of 2,4,5-T absorbed at 70 and 85 F, but an increase occurred at 100 F after 72 hr. Only slight differences in absorption were found at different humidity levels. Translocation was primarily basipetal from the point of application at 70 F, both acropetal and basipetal at 85 F, and only a short distance acropetal at 100 F. The quantities of 2,4,5-T translocated into untreated tissues at 100 F were less than at 70 and 85 F. The highest concentrations of 2,4,5-T were found in tissues with highest soluble sugar concentrations. From 3 to 27% of the 2,4,5-T absorbed by mesquite leaves was subsequently detected in untreated stem, leaf, and root tissues.

Approximately 80% of the 2,4,5-T absorbed by mesquite leaves was metabolized after 24 hr. Moving the seedlings to a different environment at the time of treatment increased the rate of 2,4,5-T metabolism. Metabolism of 2,4,5-T was completely inhibited at 50 F and a lower rate of metabolism was noted at 100 than at 70 and 85 F. No important differences in metabolism were found at different humidity levels.

INTRODUCTION

SEVERAL authors have described the influence of environment on the absorption, translocation, metabolism, and lethal action of the substituted phenoxy acids by higher plants (2, 5, 14, 19, 25); however, few studies have dealt directly with 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) and woody plants (9, 16). Barrier and Loomis (2) and Rice (20) have shown that increases in temperature between 15 and 30 C result in increased uptake of 2,4-dichlorophenoxyacetic acid (2,4-D) in beans and soybeans. The influence of temperature on the metab-

olism of substituted phenoxy acids by higher plants has been investigated only indirectly (23). Several workers have reported that high humidity increased foliar absorption of 2,4-D, urea, maleic hydrazide, and other organic compounds (5, 19, 25). Clor *et al.* (5, 6) report that relative humidity increases translocation of urea, 2,4-D, and 3-amino-1,2,4-triazole (amitrole) in cotton and oaks.

This paper describes experiments designed to investigate the influence of temperature and humidity on the absorption, translocation, and metabolism of 2,4,5-T by mesquite seedlings. Specific objectives of the study were to determine the influence of temperature and relative humidity on the rate of 2,4,5-T absorption and metabolism by mesquite leaves, and translocation and accumulation of 2,4,5-T in untreated tissues.

MATERIALS AND METHODS

Seedlings of mesquite (*Prosopis juliflora* var. *glandulosa* (Torr.) Cockerel) were grown in 5-in clay pots filled with washed sand in the greenhouse to an approximate height of 20 cm. Mineral nutrients were added by means of the nutrient solution made with distilled water described by Mitchell *et al.* (18). Seedlings were subjected to the desired environmental conditions in growth cabinets previously described (3), or they were kept in the greenhouse. Temperature and humidity levels were varied in the cabinets, but the seedlings were exposed to 14 hr of light at an intensity of approximately 1500 foot-candles and 10 hr of darkness each day. Temperatures in the greenhouse fluctuated from as low as 74 at night to as high as 100 F during the day. Relative humidity in the greenhouse was maintained at 90 to 100% at all times except during a period of approximately 6 hours during midday when it dropped to as low as 80%.

The treating solutions were made by dissolving carboxyl-labeled 2,4,5-T, which had a specific activity of 0.57 millicurie per millimole, in absolute ethanol. Then suf-

¹Received for publication June 23, 1965. Cooperative investigations of the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, and the Texas Agricultural Experiment Station.

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ficient distilled water containing a blended surfactant³ was added to make a 50% ethanol solution containing 1 µg 2,4,5-T per µl and 0.1% (v/v) surfactant concentration. Five replications were treated in all experiments.

Measured quantities of the treating solution were pipetted on the upper surface of the leaves for specific periods. The treated leaves then were rinsed in three 5-ml portions of 80% ethanol, and the rinsing solutions composited. Duplicate, 1-ml samples of the composited rinsing solutions were pipetted into 1-in planchets, dried under a heat lamp, and assayed for radioactivity under a D-47 Geiger-Müller detector equipped with a micromil window and operated in an atmosphere of 98.7% helium and 1.3% butane while attached to a scaler. The same quantity of 2,4,5-T applied to the experimental leaves also was applied to leaves which were immediately harvested and rinsed. The rinsing solutions of these treated leaves served as standards for the calculation of absorption. No radioactivity was detected in the ethanol extracts or the tissue residues of leaves which were rinsed immediately after treatment. The difference in the amount of 2,4,5-T applied to the leaf and the amount found in the rinsing solution was considered to be the amount absorbed by the leaf. Losses of 2,4,5-T due to volatilization were negligible under the conditions of this study.

The amounts of radioactivity in tissues of mesquite seedlings were determined by homogenizing the tissues in a blender with 80% ethanol for 1.5 min, filtering the homogenate, and assaying the filtrate for radioactivity. After correcting for self-absorption, the amounts of C¹⁴ were calculated; and the results expressed as counts per min per 0.1 g of fresh weight of tissue.

The plants used in the metabolic studies were each treated with 50 µg of 2,4,5-T applied to three leaves. Treated leaves were harvested at designated time intervals after treatment, rinsed in 80% ethanol, homogenized in a blender, and the homogenate filtered. The filtrates were evaporated under vacuum to a volume of 5 ml, streaked on Whatman No. 1 paper, and developed ascendingly in an isopropanol-ammonium hydroxide-water (10:1:1 v/v/v) solvent system. Identification of 2,4,5-T was accomplished by co-chromatography of the filtrates with standard 2,4,5-T. Radioactive areas on the chromatograms were located by passing them under the D-47 Geiger-Müller detector connected to a count-rate meter and recorder. Rf values were computed from the peaks produced by the recorder and the relative amounts of C¹⁴ were calculated by finding the areas under the curves (1). The C¹⁴ present at each site on the chromatogram then was expressed as a percentage of the total activity on the chromatogram.

RESULTS AND DISCUSSION

Rate and amount of absorption. Seedlings were treated with 5 µg of 2,4,5-T applied to one leaf attached to the stem approximately equidistant between the base and the apex. After treatment, one group of seedlings was kept in the greenhouse and the treated leaves were harvested 1, 2, 4, 8, 16, and 24 hr after treatment. A second group

was subjected to an environment of 85 F and a 75 to 80% humidity level. Treated leaves were harvested 1, 2, 4, 24, and 72 hr after treatment. A third group was treated with 2,4,5-T at 5, 10, 20, 25, 50, and 100 µg and kept in the greenhouse where the temperature fluctuated from 80 to 95 F and the humidity from 80 to 100%. The treated leaves were harvested 24 hr after treatment.

Absorption of 2,4,5-T took place throughout the 72-hr treatment period in the cabinet (Table 1). Absorption

Table 1. Absorption of 2,4,5-T by leaves of mesquite seedlings treated with 5 µg of carboxyl-labeled 2,4,5-T.

Time period hr	Greenhouse µg	Cabinet at 85 F µg
1.....	1.4	0.3
2.....	1.1	0.4
4.....	1.5	0.9
8.....	2.1	—
16.....	2.5	—
24.....	3.1	1.5
72.....	—	2.6
L.S.D. ₀₅	0.7	1.3

during the first 4 and after 24 hr was greater in the greenhouse than in the cabinet. When 2,4,5-T was applied at rates of 5, 10, 20, 25, 50, and 100 µg per leaf, absorption was 2.5, 5.3, 8.3, 12.2, 24.9, and 52.7 µg per leaf, respectively. This rate of 2,4,5-T absorption by leaves of mesquite seedlings compares favorably with foliar absorption of 2,4-D in soybeans (2) and red kidney beans (4). Walker *et al.* (22) and Fang (10) indicate that there is considerable difference in the period during which absorption of 2,4-D and 2,4,5-T takes place in different plant species. Since 2,4,5-T is taken up over a relatively long period of time, its absorption pattern is undoubtedly a factor contributing to the susceptibility of this plant to the lethal action of 2,4,5-T. While peas do not absorb 2,4-D after the first day, tomatoes absorb 2,4-D for at least 7 days (10). Although mesquite and pea both are legumes and susceptible to the lethal action of substituted phenoxy acids, there seems to be no correlation between taxonomic classification of plants and their absorption of organic compounds.

Influence of temperature on absorption and translocation. Absorption of 2,4,5-T was determined while treated seedlings were subjected to temperatures of 70, 85, and 100 F for 72 hr. The treatment consisted of 5 µg of 2,4,5-T deposited on the upper surface of one centrally located leaf. Translocation from the treated leaf into six untreated tissue fractions was determined by separating each plant into six parts: growing tip, upper leaves, upper stem, lower leaves, lower stem, and roots.

The influence of temperature on translocation and accumulation of soluble sugars was investigated by placing seedlings which had been grown in the greenhouse in two growth cabinets maintained at 70 and 100 F and humidity level of 60 to 65%. Other seedlings were kept in the greenhouse at temperatures which varied from 72 to 93 F and humidity levels of 75 to 100%. Ten seedlings were harvested from each of these three environments 44 and 140 hr after the experiment was initiated. Soluble sugars were extracted from leaf, stem, and root tissues with 80% ethanol; following clarification, deleading and hydrolysis reducing sugars were determined by the semi-micro method of Wildman and Hansen (24).

³Surfactant contained alkylaryl polyoxyethylene glycols, free fatty acids, and isopropanol.

No differences in 2,4,5-T absorption were detected at 70 and 85 F, but an increase occurred at 100 F (Table

Table 2. 2,4,5-T absorbed by treated leaves and accumulation of C¹⁴ in untreated tissues of mesquite seedlings exposed to three temperatures for 72 hr after treatment.

Amount absorbed, ^a µg	70 F	85 F	100 F
		1.68	1.70
Tissue fraction ^b	Counts/min 0.1 g fresh wt tissue		
Growing tip.....	0	198	0
Upper leaves.....	0	22	0
Upper stems.....	0	76	134
Lower leaves.....	0	0	0
Lower stems.....	116	46	0
Roots.....	65	48	0

^aTreatment consisted of 5 µg of carboxyl-labeled 2,4,5-T.

^bLocation of tissue fractions relative to treated leaf.

2). Translocation was primarily basipetal from the point of application at 70 and both basipetal and acropetal at 85 F. Carbon-14 was detected only in stems above the treated leaves at 100 F. The percentages of absorbed 2,4,5-T recovered from all untreated tissues were 12, 13, and 3 at 70, 85, and 100 F, respectively.

From the data in Tables 2 and 3, it is evident that the basipetal movement of 2,4,5-T at 70 F was correlated

Table 3. Percentages of soluble sugars in mesquite seedlings exposed to three environments.

Tissue fraction	Exposed 44 hr			Exposed 140 hr		
	Greenhouse 72 to 93 F	70 F	100 F	Greenhouse 72 to 93 F	70 F	100 F
Leaves.....	2.5	4.1	5.1	0.5	14.6	4.7
Stems.....	1.3	9.4	3.7	3.6	8.8	4.6
Roots.....	9.4	16.2	6.6	10.7	19.3	7.9

with the accumulation of soluble sugars in the stems and roots. The lower soluble sugar levels found at the 100 F temperature would be expected due to the high rate of transpiration. The lack of detectable C¹⁴ in the lower stems and roots at 100 F suggests that translocation of 2,4,5-T is inhibited when the readily available energy source is depleted. Contact injury of the vascular tissue as was found by Hull (12) and Leonard and Crafts (15) also may have contributed to reduced translocation at the 100 F temperature.

These data showed that temperature has a profound influence upon translocation. Likewise, they seem to refute the concept of translocation of substituted phenoxy acids toward sinks as described by Clor *et al.* (5, 6). However, this seeming anomaly is readily explained when it is recognized that when mesquite seedlings are changed from a temperature of approximately 90 to 70 F, they do not elongate rapidly if at all. Transpiration and other metabolic processes are reduced markedly; however, photosynthesis continues. Deprived of a sink at the growing tip, the plant accumulates photosynthetic products in the storage tissues; and simultaneously it translocates foliar applied 2,4,5-T to the lower stems and roots.

Influence of relative humidity on absorption and translocation. Mesquite seedlings were treated with 10 µg of 2,4,5-T and kept in the greenhouse or subjected to humidity levels of 35 to 40, 55 to 60, 70 to 80, or 95 to 100%

and to a constant temperature of 85 F. The seedlings were harvested 24 and 96 hr after treatment, and absorption by the treated leaves and translocation into five untreated tissue fractions were measured.

Table 4 contains data which are averages of data obtained from plants harvested 24 and 96 hr after treat-

Table 4. 2,4,5-T absorbed by treated leaves and accumulation of C¹⁴ in untreated tissues of mesquite seedlings exposed in cabinets to four humidity levels or kept in greenhouse.^a

Amount absorbed, ^b µg	Humidity level at 85 F, %				Greenhouse
	35-40	55-60	75-80	95-100	
	3.62	3.58	3.33	3.84	3.67
Tissue fraction ^c	counts/min per 0.1 g green wt tissue				
Upper leaves.....	11	75	0	47	0
Upper stems.....	20	23	52	92	80
Lower leaves.....	75	90	10	0	45
Lower stems.....	77	108	203	292	180
Roots.....	266	324	355	462	347

^aData are averages from plants harvested 24 and 96 hr after treatment.

^bTreatment consisted of 10 µg of carboxyl-labeled 2,4,5-T.

^cLocation of tissue relative to treated leaf.

ment. No increased absorption was found at the higher relative humidity levels; and, although absorption was higher after 96 hr than after 24, there were no changes in the relative rates of absorption or translocation patterns at the different humidity levels. The total amounts of C¹⁴ detected in the untreated tissues of the seedlings tended to increase, particularly in the roots and stems, with increasing humidity. The percentages of absorbed 2,4,5-T recovered from untreated tissues were 12 at 35 to 40%, 17 at 55 to 60%, 27 at 75 to 80%, 23 at 95 to 100%, and 21% from the greenhouse seedlings. Likewise, there was better distribution of C¹⁴ in the mesquite seedlings at humidity levels from 35 to 60% than at 75 to 100%.

These data are in disagreement with the findings of Clor *et al.* (5, 6) who used cotton and oats and Pallas (19) who used beans. These investigators not only found greater absorption of 2,4-D at high humidity levels but increased translocation. Mesquite is the most xerophilic of these plants and its ability to adapt to changes in humidity levels which alter physiological processes in more mesophyllic plants may account for the same rates of absorption at all humidity levels. It is of interest to note that the tissues which do not contain C¹⁴ at the higher humidity levels are in all cases leaf tissues. Movement of C¹⁴ from one mature leaf to another is usually not expected.

Crafts and Yamaguchi (8) discussed evidence which indicates that compounds applied to leaves will be translocated into the roots and are often excreted into the external medium or transferred into the xylem and transported to the leaves. If this is the route by which C¹⁴ entered the untreated foliage of the mesquite seedlings, the higher transpiration rates of the seedlings at lower humidity levels would have aided the translocation of C¹⁴ to the leaves and its uniform distribution in the shoot tissues. This also may explain why the total amounts of C¹⁴ detected in the untreated tissues of the seedlings tended to increase, particularly in the roots and lower stems, with increasing humidity.

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Rate of metabolism. Twenty mesquite seedlings were each treated with 50 µg of 2,4,5-T and retained in the greenhouse. The treated leaves from each of five seedlings were harvested 24, 48, 72, and 168 hr after treatment and metabolites determined by paper chromatography as described above.

After 24 hr, unknown compounds which had Rf values ranging from 0.10 to 0.27 were present (Table 5). Rf values with greatest radioactivity were 0.26 after 24 hr, 0.35 after 48, 0.24 after 72, and 0.32 after 168.

Table 5. Rf values of radioactive compounds and percent unaltered 2,4,5-T in ethanolic extracts of mesquite leaves after treatment with 50 µg of carboxyl-labeled 2,4,5-T.

Time after treatment hr	Rf		% unaltered 2,4,5-T
	Unknowns	2,4,5-T	
24.....	0.10-0.27	0.71	20
48.....	0.18-0.39	0.73	25
72.....	0.12-0.28	0.71	34
168.....	0.06-0.37	0.71	26
2,4,5-T standard.....	—	0.77	100

Only 20% of the detected C¹⁴ was contained in unaltered 2,4,5-T 24 hr after treatment; however, 34 and 26% of the radioactivity was unaltered 2,4,5-T 72 and 168 hr after treatment, respectively. This conversion rate was much more rapid than that found by Jaworski and Butts (13) and Fites *et al.* (11) for 2,4-D in bean and jimsonweed but was comparable to that found by Slife *et al.* (21) for 2,4-D in wild and domesticated cucumbers. The increase in relative amount of 2,4,5-T in the ethanol extracts of treated leaves of mesquite after 72 hr may have been due to a release of 2,4,5-T from the unidentified compounds, similar to that found by Jaworski and Butts (13) in ethanol extracts of bean tissues. Another reason for the increase in relative amounts of 2,4,5-T at 72 hr above that found at 24 hr may be the continued uptake of 2,4,5-T by the leaves and an inhibition or lowered rate of its conversion. Data in Table 1 show that 2,4,5-T was absorbed by mesquite leaves over at least a 3-day period. It is possible that the processes which are responsible for the metabolism of 2,4,5-T are inhibited after 24 hr but absorption continues.

Influence of temperature on metabolism. Twenty-five mesquite seedlings were each treated with 50 µg of 2,4,5-T. Five then were placed in each of three cabinets, five were kept in the greenhouse, and five were placed in a cold room at 50 F. The cabinets were kept at constant temperatures of 70, 85, and 100 F and a relative humidity of 75 to 80%. Temperatures in the greenhouse fluctuated from 80 to 100 F and the humidity fluctuated from 80 to 100%. Seedlings in the cold room were illuminated with two 150-Watt incandescent lamps. All treated leaves were harvested 48 hr after treatment and metabolites of 2,4,5-T were determined by paper chromatography.

At 50 F, only 2,4,5-T was found in the treated leaves (Table 6). Carbon-14 extracted from leaves in the growth cabinets and the greenhouse was found in two areas on the chromatograms: those with Rf values ranging from 0.08 to 0.13 and those with Rf values of 0.74 to 0.75. Under all conditions, from 50 to 70% of the unidentified C¹⁴ was found at Rf 0.12. The radioactive compound with Rf 0.75 was identified as 2,4,5-T. The percentages of

Table 6. Rf values of radioactive compounds and percent unaltered 2,4,5-T in ethanolic extracts of mesquite leaves exposed to four temperatures or kept in the greenhouse. Leaves harvested 48 hr after treatment with 50 µg of carboxyl-labeled 2,4,5-T.

Temperature	Rf		% unaltered 2,4,5-T
	Unknowns	2,4,5-T	
F			
50.....	—	0.68	100
70.....	0.08-0.13	0.74	26
85.....	0.10-0.12	0.75	26
100.....	0.10-0.12	0.75	42
Greenhouse.....	0.08-0.12	0.74	36
2,4,5-T standard.....	—	0.75	100

unaltered 2,4,5-T in the ethanolic extracts were 26% at both 70 and 85, 42% at 100 F, and 36% in the greenhouse.

It would appear from these data that 2,4,5-T metabolism was stimulated at the 70 and 85 F temperatures in the cabinets and inhibited at 100 F, as compared with the greenhouse; however, data in Table 5 show that when the treated seedlings were left in the greenhouse, 25% of the 2,4,5-T remained unaltered after 48 hr. This value is almost identical to the 26% found in the cabinets at the two lower temperatures and 11% below the 36% found in this experiment.

This variability in data from the greenhouse was found in all experiments of this study. Conditions in the greenhouse were not as rigidly controlled as they were in the growth cabinets; and while hygromographs were used to record temperature and humidity levels at all times, changes in other conditions such as light intensity and quality were not recorded. Therefore, comparisons between experiments are not always valid.

Influence of pretreatment environment on metabolism. Mesquite seedlings were grown in the greenhouse at temperatures ranging from 76 to 95 F and relative humidity levels of 80 to 100%. Five groups of five seedlings were introduced into a growth cabinet 0, 1, 2, 5, or 7 days before treatment with 50 µg of 2,4,5-T and one group was treated and kept in the greenhouse. The cabinet was kept at 85 F and a relative humidity of 75 to 80%. The treated leaves were harvested 48 hr after treatment and metabolites of 2,4,5-T in the treated leaves were determined by paper chromatography.

Again, C¹⁴ was found in two areas on the chromatograms. The area with Rf values ranging from 0.00 to 0.37 contained unknown compounds; and the other, with Rf values ranging from 0.73 to 0.76, was identified as 2,4,5-T. When the plants were treated at the time they were moved from the greenhouse to the cabinets, the unknown compounds had Rf values ranging from 0.10 to 0.12. However, when the plants were placed in the cabinet and treated the next day, the Rf values of unknown compounds ranged from 0.08 to 0.24 with most of the C¹⁴ occurring at Rf 0.20 (Figure 1B). At least two unknown compounds were present when the period of exposure in the cabinet before treatment was lengthened to two days, with the greatest amount of C¹⁴ occurring at Rf 0.16 (Figure 1C). When the pretreatment exposure was further lengthened to 5 days, nearly all the C¹⁴ was present at Rf 0.33 (Figure 1D). With 7 days of pretreatment exposure, the greatest amount of C¹⁴ was found at Rf 0.10 and only small quantities of C¹⁴ were detected at the higher Rf values (Figure 1E). The percentages of

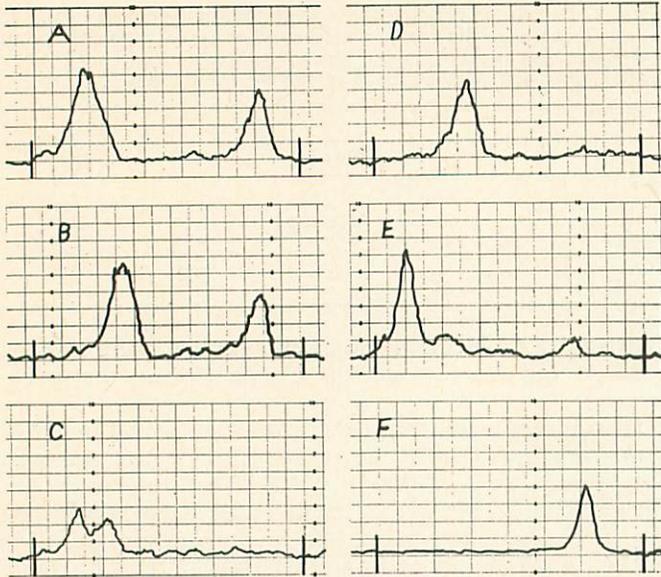


Figure 1. Curves traced during scanning of unidimensional chromatograms. A through E: Ethanolic extracts from mesquite leaves treated with 2,4,5-T. All treated leaves harvested 48 hr after treatment. Origin on left, solvent front on right. A, Extract from leaves of plants retained in greenhouse; B, Extract from leaves of plants placed in cabinet 1 day before treatment; C, Same, 2 days before treatment; D, Same, 5 days before treatment; E, Same, 7 days before treatment. F, Standard 2,4,5-T.

unaltered 2,4,5-T were 26, 20, 13, 7, and 13 when the pre-treatment exposure periods were 0, 1, 2, 5, and 7 days, respectively.

Influence of humidity on metabolism. Twenty mesquite seedlings were each treated with 2,4,5-T and 5 were placed in each of four cabinets maintained at a constant temperature of 85 F and relative humidity levels of 35 to 40, 55 to 60, 75 to 80, and 95 to 100%. Treated leaves were harvested 24 hr after treatment and metabolites of 2,4,5-T in the treated leaves were determined by paper chromatography.

At all humidity levels, most of the unidentified C^{14} was found at Rf 0.12; however, compounds which had Rf values as high as 0.29 were present. Humidity level did not influence the rate of 2,4,5-T metabolism as the percentages of unaltered 2,4,5-T in the extracts were 23, 20, 24, and 18% at the 35 to 40, 55 to 60, 75 to 80, and 95 to 100% humidity levels, respectively.

Since no striking differences in the metabolites of 2,4,5-T formed in leaves of mesquite exposed to the four humidity levels were found, it is probable that the formation of these metabolites is not related to the lethal action of the herbicide. While 2,4,5-T is more effective in killing mesquite at high humidity than at low humidity⁴, the metabolic products formed at both levels were the same and the rates of metabolism were essentially unchanged. It is probable that other significant changes took place at the different humidity levels, but they were not detected by the methods used in this study.

The significance of the metabolites detected and the role they play are not completely understood. These data

⁴Morton, H. L. Unpublished Ph.D. Dissertation, Texas A & M University, 1961.

indicate that mesquite leaves metabolize 2,4,5-T rapidly and this rate of metabolism increases when mesquite seedlings are adjusting to a new environment. Rapid alteration of the 2,4,5-T molecule, such as the formation of 2,4,5-T-protein complexes as reported by Butts and Fang (4), would very likely reduce its mobility. Crafts' (7) data, which indicate that 2,4-D is translocated as either the free acid or a salt of the acid, support the reasoning that this metabolite formation in mesquite leaves is responsible for the relatively small amounts of 2,4,5-T found in untreated tissues in the translocation experiments.

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