METABOLIC AND ENVIRONMENTAL FACTORS AFFECTING ABSORPTION AND TRANSLOCATION OF 2,4,5-TRICHLOROPHENOXYACETIC ACID IN WINGED ELM

By

GENE DAVID WILLS

Bachelor of Science
Auburn University
Auburn, Alabama
1957

Master of Science
Auburn University
Auburn, Alabama
1962

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of the Oklahoma State University
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Thesis Approved:

Eddie Basler
Thesis Adviser

Dean of the Graduate College

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CHAPTER I

INTRODUCTION

A large portion of the grazing lands in the Southern Great Plains has been invaded by undesirable woody plants of which the initial infestation is predominately blackjack and post oak (Quercus marilandica and Q. stellata). Various methods are now being used successfully to control the dominant oak species. Winged elm (Ulmus alata), however, in the eastern portion of this area is a persistant understory which is released after successful clearing of these dominant species.

The herbicide 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) is becoming widely used in controlling winged elm, with aerial application often giving the most practical and economic control. The results of the 2,4,5-T treatments, however, may vary greatly throughout the growing season, possibly depending upon the degree of absorption, translocation, and chemical breakdown of the herbicide. Because of the need for obtaining greater dependability of the chemical treatments, further information is needed on the factors affecting 2,4,5-T in winged elm. This study was initiated to determine some of the metabolic and environmental factors affecting absorption, translocation, and breakdown of 2,4,5-T in winged elm. This study also was designed to determine the degree of variability of absorption and translocation within a specific tree. These data should reveal the percentage of leaves of each tree which contribute to the translocation of 2,4,5-T to the root zones where high concentrations of the herbicide are needed for adequate kill.

CHAPTER II

REVIEW OF LITERATURE

On parts of nearly all the approximately one billion acres of pasture and grazing lands in the United States woody plants present a problem. Also on recreational areas, irrigation canals, highways, railroad rights-of-way, home sites, and industrial areas undesirable brush species are of economic importance (1, 46). Various methods of brush control including cutting, burning, bulldozing, rollers, mowers, biological methods and chemicals have been used. The method of control will depend on several factors including the type and size of brush infestation, the degree of control desired, and the availability of equipment (2, 23, 74, 75).

Chemical brush control has come into extensive use since 1946 with its widespread application beginning on electric transmission lines and railroad rights-of-way. Its use rapidly extended to farmlands, pastures, and range lands (29, 54, 73, 78).

The control methods for brush species are similar to those used for other types of plants except they must be adapted to woody and heavy types of growth (46). For chemical methods to be most effective they must be absorbed by the foliage or injected into the bark and be translocated by the phloem to the actively growing root tissues in concentration high enough to cause death of the plant (21, 22, 72). The research dealing with penetration and movement in woody plants has not been very extensive. This is because woody samples are difficult to analyze and uniform samples are difficult to obtain for study (6). The available data show that absorption and translocation may vary from species to species and many factors influence response (4, 6, 15, 83). It is particularly desirable that methods be developed under field conditions for the study of translocation factors since greenhouse or growth chamber studies may not yield results comparable with field studies (6).

Methods for Tracing Herbicides

A study of individual factors which might possibly affect the translocation of a herbicide in a woody species would involve both qualitative and quantitative determinations of the movement of the herbicide into and through the plant. In qualitative studies for the determination of the areas of the plant into which a herbicide has translocated, autoradiography as described by Crafts and others (16, 48, 62, 77, 84, 85) has probably been the most important technique. In these studies radioactive herbicides have been applied to the foliage or bark and after a given time interval autoradiograms are made from distant leaves, bark, stems, and roots to determine the extent of the translocation. This method readily reveals the direction and rate of translocation. Work by Radwan, Stocking and Currier using broad bean (*Vicia faba*) showed this method of tracing could reveal the particular cells involved in translocation (63). Leonard and Crafts (48) using autoradiographs of bark samples were able to show variations of rate and direction of 2,4-D in several species of woody plants through the growing season. Yamaguchi and Crafts (84) used autoradiography to show differences in mobility of herbicides. Their work revealed that downward movement of the phenoxyacetic acids was at a peak during periods of rapid development or flush of growth. Their work also showed that the phenoxyacetic acids were equally absorbed both by inner bark tissues and outer xylem tissues in marzorita, toyon, and buckeye trees. These workers indicate that the period of optimum root kill with 2,4-D is associated with the most active movement of the assimilate stream. Some woody species appear to be more efficient than others in translocating herbicides in the phloem.

Studies using autoradiography on the seedlings of woody plants have been instrumental in determining patterns of translocation in brush species. Carvell (16) working with seedlings of hickory and privet showed the pattern of movement of ^{35}S-labeled ammate. His results indicated that upward movement was through the xylem and downward movement was through the phloem.

Walker _et_ _al_ (77) using seedlings of sweetgum (_Liquidambar styraciflua_), red maple (_Acer rubrum_), white ash (_Fraxinus americana_), and yellow poplar (_Liriodendran tuplipfera_) traced the movement of ^{14}C-labeled 2,4,5-T. The autoradiograms showed different species to exhibit different patterns of translocation for the same herbicide. They also indicated that a larger amount of movement of 2,4,5-T occurred in a downward direction than in an upward direction.

Leonard and Crafts (48) studied absorption and translocation of ^{14}C-labeled 2,4-D in several brush species by applying the herbicide to the leaves and, after one week, making autoradiographs of the bark. They showed that penetration of the leaf was through the cuticle in the absence of stomata and that the rate and direction of translocation of 2,4-D in plants varied considerably with the season of the year. They also noted the adverse effect of contact injury on absorption and translocation of 2,4-D and the direct correlation between food movement and herbicide transport in plants.

Autoradiography is an effective means for qualitatively tracing the movement of herbicides in plants, but it is of little value for quantitatively measuring the amount of material in a given tissue (32, 33, 85).

When quantitatively measuring the amount of radioactive material in a specific area of plant tissue, a method of counting radioactive disintegrations is most desirable. Among the earlier attempts to quantitatively measure the translocation of herbicides in woody species is the work of Blair and Fuller in 1952 (14). They studied the movement of the radioactive iodine-labeled herbicide, 2,4-dichloro-5-iodophenoxyacetic acid from foliage applications on eight-week-old velvet mesquite (Prosopis juliflora) seedlings. After four days, the plants were sectioned into upper stem, lower stem, hypocotyl and roots. These were dried, ground in a Wiley mill, and determined for radioactivity by Geiger counter analysis. Their results showed only three percent of the radioactive material to move downward with little increase in translocation due to added surfactants. They concluded that erratic response to the herbicides is possibly due to limited movement within the plant.

Weintraub et al (81) in 1954 studied the persistance of 2,4-D throughout the dormant season in the buds of cherry (Prunus avium) by use of a gas counting system as described by Janney and Moyer (41). Their results indicated that twenty per cent of the herbicide as applied to the buds of two year old cherry trees did not penetrate after one week at various dosage rates. The herbicide persisted throughout the dormant period in large enough quantity to cause morphological abnormalities the following year (81).

Cavel in 1954 (16) used a quantitive counting method in conjunction with autoradiography in a study of the translocation of ammonium sulfamate ^{35}S in privet. The herbicide was applied to the xylem in a frill cut through the phloem and cambium. After three days the leaves were ashed, dissolved in sulfuric acid, and the radioactivity was determined by means of a Geiger counter. Results showed the herbicide to move upward in the xylem.

Walker et al (76) in 1959 studied the absorption rates of three formulations of 2,4,5-T-1-^{14}C on water oak (Quercus nigra) and sweetgum (Liquidambar styraciflua) by using a tissue extraction technique described by Beck and Walker (11). In this procedure the unabsorbed 2,4,5-T-1-^{14}C was washed from the leaf surface with eighty per cent ethanol and the herbicide was extracted from the tissue by a series of extractions with boiling eighty per cent ethanol. Aliquotes of the extracted radioactive herbicide were then dried in planchetts and counted with a gas flow Geiger-Muller counter. They found the absorption rate to differ with the various formulations. Absorption did not increase after one day for water oak, but increased with time in the sweetgum.

Morton (56) compared the effects of various carriers on the absorption of 2,4,5-T-1-^{14}C in mesquite leaves by using a similar technique except the herbicide was extracted from the tissue in eighty per cent ethanol by homogenizing for one minute in a Waring blendor. Larger amounts were absorbed from an oil-water carrier than from an ethanol-water carrier.

Dalrymple and Basler (25) in 1963 studied the absorption and translocation of 2,4,5-T-1-^{14}C throughout the growing season as applied to the leaf surface of blackjack oak (Quercus marilandica). The absorbed 2,4,5-T-1-^{14}C was determined by washing the leaf surface with 25 ml of eighty per cent ethanol, determining the radioactivity in the wash and subtracting that from the total amount applied. The activity in the leaf was determined by homogenizing the leaf in 15 ml of eighty per cent ethanol with a high speed Virtis blendor. The ^{14}C was determined for the homogenate. Translocation was determined by subtracting the activity in the wash plus that in the leaf from the total applied. They found the absorption and translocation to be the highest in the early spring with a decrease during the last of May, June, and early July. There was an increase in both absorption and translocation during late July and continuing into September when decreases in absorption occurred. Badiei (4) in 1965 conducted absorption and translocation studies with blackjack oak using a similar assaying technique and obtained similar data.

Metabolic Factors Affecting Absorption and Translocation

Results of several workers have indicated that foliar absorption and subsequent translocation of many herbicides in woody plants vary with the age or stage of growth of the leaves (6, 28, 30, 47, 48, 70, 85).

Fisher et al (30) reported that the stage of growth at the time of treatment of mesquite leaves appeared to be one of the most important factors governing the effectiveness of 2,4,5-T. In tests with the herbicide applied at ten-day intervals from leaf initiation in the spring to mature leaf development in late summer the greatest movement of 2,4,5-T occurred from fifty to ninety days after the first leaves appeared. The effectiveness of 2,4,5-T was reduced after ninety days from leaf emergence at the same period when active growth and development slowed down.

Leonard and Crafts (48) in a study of the uptake and distribution of radioactive 2,4-D by brush species found that the optimum time for treatment may vary according to the age and nature of the plant. In many brush species they found the period for successful treatment to apparently be during a relatively brief time in the spring or early summer when the leaves are fully grown but not heavily cutinized.

Tschirley and Hull (70) found the period of maximum susceptibility of mesquite to 2,4,5-T to be approximately when fifty per cent of the leaves have reached full size but are still succulent.

Yamaguchi and Crafts (85) found the translocation characteristics of 2,4-D and 2,4,5-T to vary throughout the growing season with movement of the herbicides closely associated with downward movement of assimilates in the phloem. The peak translocation was found to be at the time of full development of the season's growth for each species observed.

Elwell (28) noted variations of the period of susceptibility of blackjack oak to 2,4,5-T throughout the growing season. He recommended the herbicide to be most effective when applied from May 15 to July 15.

Kursanov (47) applied $^{14}CO_2$ to individual leaves of plants and found that the distribution of assimilates changed as the plant aged. In mature leaves the preferential movement of assimilates is to the roots until flowering begins at which time movement predominates in the direction of fruit and seed formation. Young leaves do not yield their assimilates to other parts of the plant but will receive products from other mature leaves. Leaves near maturity will both absorb and transport assimilates. Mature leaves predominantly export products to other parts of the plant but do not exchange products between mature leaves.

Many workers have shown that the absorption of materials from the surface of leaves and translocation within the sieve tubes require several steps which utilize the metabolic energy of respiration (5, 13, 17, 18, 47, 86). Zimmerman (86) found that sieve bundle tissue which was actively conducting assimilates had a respiration rate several times higher than that of the surrounding tissue. Dalrymple and Basler (25) found that respiration rates in leaf tissue of blackjack oak closely followed the translocation rates of 2,4,5-T throughout the growing season. They postulated that energy of respiration possibly may be responsible for the translocation characteristics of this species. Kidd et al (45) determined the respiration rates for variously leaves of Helianthus annuus and found that the respiration rate of the younger leaves was about ten fold greater than that of the older leaves.

Among the limiting factors which possibly may affect the respiration rate of a plant is the iron status of the tissue (52). Iron functions in respiration of plants as part of the prosthetic groups of several respiratory enzymes in plant cells including peroxidase, cytochrome oxidase and as a constituent of the cytochromes (34).

De Kock (26) suggested that the phosphorus-iron ratio of plant tissue may serve for an evaluation of the iron status of a plant. He stated that a high phosphorus to iron content denotes a metabolic unbalance which usually is due to a deficiency of iron. This condition could ultimately result in an inadequate supply of oxidizing enzymes. Among the phosphorus-iron ratios analyzed for iron deficient versus normal leaves were: strawberry 12.1 to 7.9, Bartlett pear 53.7 to 9.1, (27), and mustard 65 to 45 (26).

Environmental Factors Affecting Absorption and Translocation

Marth and Davis (53), in a study to determine the effect of temperature on the response of weeds to 2,4-D, grew narrow leaved plantain (Plantago lanceolata) at temperature ranges of: 32 to 40°F, 50 to 60°F and 75 to 90°F. The herbicide caused rapid kill at the high temperature, moderate response at the medium temperature and little to no response at the low temperature. Plants sprayed with 2,4-D in the field while dormant at low temperatures showed no immediate response but were later killed when temperatures more favorable for growth occurred.

Kelly (43) in an experiment to determine the effect of temperature on the response of red kidney beans (Phaseolus vulgaris) to 2,4-D kept the treated plants at 5, 15, and 25°C. The plants kept at a constant temperature showed effects from 2,4-D only at 25°C. However, when the plants at 5 and 15°C were increased to the next higher temperature at the time of treatment, a response was noted from the herbicide.

Rice (64) and Pallas (59) studied the effect of temperature on the absorption and translocation of 2,4-D in red kidney bean at a range from 46 to 92°F and found an increase in absorption and translocation with increased temperature. Pallas (59) noted that the movement out of the leaves was confined to the vascular bundles which conduct the flow of assimilates into the stems, buds, and roots.

Morton (57) studied the effect of air temperature on absorption of 2,4,5-T in mesquite during a 72 hour period. No significant variations were noted between 70 and 85°F but a substantial increase was found at 100°F. Translocation was primarily downward at 70°F, both downward and upward at 85°F, and only a short distance upward at 100°F.

Currier and Dybing (24) in a review on foliar penetration of herbicides suggest that temperature affects absorption by effecting: increased rates of diffusion, lowered viscosity, an acceleration of photosynthesis, increased phloem translocation, increased protoplasmic streaming, and increased growth. Warm temperatures generally promote penetration, whereas high temperature with low humidity causes decreased absorption due to increased evaporation of herbicides from the leaf surface.

Hyder et al (40) studied the seasonal pattern of 2,4-D effectiveness of big sagebrush (Artemisia tridentata) and green rabbitbrush (Chrisothamus viscidiflorus). They found response of big sagebrush to depend essentially on the environmental conditions of soil temperature and moisture content which were satisfactory for good growth. The effect on green rabbitbrush was found to depend more on the physiological development with the greatest response when the plant developed an abundant leaf area. Cords (20) studied the effect of root temperature on the toxicity of 2,4-D to rubber rabbitbrush (Chrysothamnus nauseosus) and found the greatest effectiveness was at 75°F. He suggested that the response of plants to 2,4-D depends on an effect at an area of active growth in the plant. Temperature affects plant response to 2,4-D as it affects the growth of the plant.

Ketellapper (44) showed that reduced plant growth at low temperature could be stimulated by the addition of various essential metabolites. Muzik and Mauldin (58) found that plants normally susceptible to 2,4-D showed no response when kept at temperatures low enough to reduce their growth rate. When a metabolite, especially thiamin, was sprayed on the plant while at reduced temperature the plant became highly susceptible to 2,4-D.

Pallas (60) studied the effect of soil moisture on red kidney beans and found the plants translocated only half as much 2,4-D when growing in soil with a moisture level near the permanent wilting point as when growing in soil at field capacity. Hauser (36) found that soybean and corn plants absorbed 2,4-D more slowly as soil moisture was decreased.

Basler *et al* (10) determined the effects of moisture stress on the absorption and translocation of 2,4-D within stringless green pod bean plants. Water stress, as induced by low soil moisture, had little effect on the absorption of 2,4-D into the leaf tissue but greatly reduced translocation as leaf turgidity dropped below 80 per cent. The subsequent regain of translocation as water content was restored appeared to involve a metabolic process as indicated by a lag of several hours between regained leaf turgidity and the regain of 2,4-D translocation. Dalrymple and Basler (25) in a study of translocation in blackjack oak found no correlation between translocation and soil moisture as related to the range of soil moisture found under field conditions.

Conrad (19) found a correlation to exist between decreases in soil moisture and decreases in root growth activity. Leonard and Crafts (48) suggest that available soil moisture affects the herbicidal response of roots to 2,4-D as the response involves active root growth of the plant.

Fisher *et al* (30) found that mesquite was most effectively killed with 2,4,5-T when soil moisture was adequate to develop a uniform foliage cover with 2,4,5-T being applied after the rapid growth of new leaves.

Miller and Star (55) found that throughout the period of fully developed leaves in hardwood species, the available soil moisture is of greater consequence to the herbicidal effectiveness of 2,4,5-T than the specific period of the season for spraying.

Metabolism of Phenoxy Herbicides

The herbicidal effectiveness of a translocated phenoxy compound may be substantially affected by the ability of the plant to metabolize the herbicide (67). Audus (3), using 2,4-D with ^{14}C labeling at various positions in the molecule, found that the nature of the metabolic changes in the herbicide varies from plant to plant. Holley (38), experimenting with red kidney bean plants (Phaseolus vulgaris), found that after seven days about two-thirds of the 2,4-D ^{14}C from leaf applications had been metabolized to a water soluble material. Part of the herbicide was lost as $^{14}CO_2$. Hay and Thimann (37), using the same plant species, found a faster breakdown of free extractable 2,4-D in the light than in the dark while Jaworski et al (42), using black valentine bean plants, found no significant difference between normal and eliolated plants.

Weintraub et al (80, 82) treated terminal buds of black valentine beans separately with 2,4-D-1-^{14}C, 2-^{14}C and ring labeled ^{14}C. During culture the $^{14}CO_2$ was liberated in larger amounts from carbon 1 and in lesser amounts from carbon 2 and none from the ring. At low doses most of the ^{14}C from each position on the side chain was later found incorporated with other substances including acids, sugars, dextrins, starch, pectin, protein, and cell wall substances. Liao and Hamilton (49) treated root tip cells of Allium cernuum and Vica faba with 2,4-D-1-^{14}C for 24-hour intervals up to 120 hours. Results using autoradiographs showed labeling both in the cytoplasm and localized on the chromosomes in the nuclei of mitotic cells. They indicated that the early labeling in the plant cell may possibly be associated with RNA. Roychoudhury and Sen (65) incubated the auxin, β naphthalene acetic acid-1-^{14}C, with coconut endosperm nuclei and found the auxin to bind with nuclei and at the same time to liberate bound nuclear RNA. Bendana and Galston (12) fed IAA ^{14}C to green pea sections and found labeling confined to the 4S fraction of RNA as determined by centrifugation.

Studies relating the rate of metabolic breakdown with the herbicidal effectiveness of phenoxy compounds have shown variations from direct to no correlation between these phenomenon (7, 50, 51, 61, 67). A direct correlation with herbicidal breakdown and resistance was found by Slife et al (67) where wild cucumber was more resistant to 2,4,5-T than cultivated cucumber because of breakdown; and Pallas (61) found red maple, yellow poplar and sweetgum to be resistant to 2,4-D because of detoxification. Luckwill and Jones (50, 51) noted high rates of decarboxylation of phenoxy herbicides in the leaves of resistant varieties of currant, apple, and strawberry with low rates of decarboxylation in many susceptible varieties of the same species. Some varieties, however, showed no correlation between decarboxylation and resistance where decarboxylation was low regardless of susceptibility. Basler (7) found decarboxylation to be low in winged elm (Ulmus alata) with no apparent association with susceptibility to the herbicide.

In determining seasonal and environmental effects on the metabolism of phenoxy herbicides in blackjack oak Basler et al (8) found that 50 per cent or more of 2,4,5-T was broken down at all dates during a 24-hour treatment period with much variation throughout the season. The rate of breakdown increased during May and June, decreased during July and August and increased again in September. Morton (57) treated mesquite leaves with 2,4,5-T and found metabolic breakdown was affected by temperature with complete inhibition at 50°F, optimum between 70 and 80°F and a noticeable decrease above 100°F.

CHAPTER III

MATERIALS AND METHODS

The test plants were winged elms (Ulmus alata) growing either as mature trees in their natural habitat, as two- and three-year-old nursery stock, or as potted seedlings in the growth chamber. The studies here consisted of determinations of the effect on absorption and translocation of 2,4,5-T of 1) metabolic factors as related to leaf age (including the normal respiration rate, the effect of 2,4,5-T on respiration rates, and the phosphorus-iron ratios each in the variously aged leaves); 2) environmental and seasonal variations of factors such as temperature and rainfall, and controlled variations in soil moisture; 3) the metabolism of the 2,4,5-T herbicide within the leaves.

The experimental plan was a randomized complete block design where one leaf per plant was treated and a randomized complete block design where each leaf on one limb per tree was treated. Analyses of data were made according to methods outlined by Steel and Torrie (68) with significant differences calculated by use of Duncan's new multiple range. All data were processed at the 5 per cent level of confidence.

Absorption and Translocation of 2,4,5-T in Variously Aged Winged Elm Leaves

The effect of leaf age on absorption and translocation of 2,4,5-T was determined. The study was conducted at the Oklahoma State University agronomy farm, Stillwater Oklahoma on two-year-old winged elm seedlings which were transplanted during their first year of growth. Translocation of the variously aged leaves was determined from those of individual limbs beginning at the apex as number 1 and continuing to the consecutively older ones through number 12 near the base. The consecutive leaves are approximately four days apart in age. In preparation for each treatment the tree was held stationary from the wind by tying it to a stake. The upper surface of the leaves were held horizontally by taping the limb to a cardboard box. The treatments were conducted during the last two weeks of June and the first week in September.

Absorption and translocation of the herbicide by winged elm leaves were determined in the following manner: Twenty μg of carboxyl ^{14}C-labeled 2,4,5-T (2,4,5-T-1-^{14}C) with a specific activity of 14.1 mc/m mole was applied as the butoxyethanol ester in 0.01 ml of solution using a Hamilton micropipette with a Chaney adapter. The solution also contained 0.75 per cent of a WEEDONE base as an emulsifying agent. Applications were made to the upper surface of the leaf over the base of the midrib. The herbicide was confined on the leaf surface within a 5 mm diameter ring of stopcock grease which was applied with a blunted cork borer. After 24 hours of treatment the area of application was punched out with a 7 mm cork borer and the unabsorbed 2,4,5-T-1-^{14}C was washed into 25 ml of absolute ethyl alcohol using a volumetric pipette.

The leaves were ground separately in 10 ml of absolute ethyl alcohol with a Virtis 45 high speed homogenizer. The punches were ground separately in 5 ml of absolute ethyl alcohol with a Ten Broeck glass homogenizer. The radioactivity in the alcohol wash, the punches, and the leaves was determined by liquid scintillation counting using a Nuclear-Chicago 720 series liquid scintillation system. The samples were prepared for radioactive counting by placing 0.2 ml of each sample separately into 25 ml scintillation bottles containing 10 ml of toluene scintillation stock solution containing 0.05 grams of dimethyl POPOP-1, 4 bis-2-(4-Methyl-5-phenyloxazol)-benzene plus 4.0 grams PPO-2, 5-diphenyloxazole per liter of sulphur free toluene. The total herbicide absorbed was calculated as that part of the total applied which was not found in the alcohol leaf wash. Translocation from the treated area and from the leaves was determined as a per cent of the amount of 2,4,5-T-1-^{14}C absorbed into the leaf.

Respiration of Variously Aged Winged Elm Leaves

Respiration rate was determined for the different aged leaves of winged elm consecutively from the youngest at the growing apex as leaf number 1 to the older ones through number 12 toward the base of the limb. This study was conducted with a Warburg respirometer using the procedure described by Umbreit et al (71). One leaf from each position was placed in a separate 17 ml flask containing 0.2 ml of 20 per cent KOH in the center well and 0.2 ml of distilled water in the side arm. The temperature was held at 27$\pm$0.02°C. The results are recorded as μl O_2 per gram wet weight per hour.

Respiration of 2,4,5-T Treated Leaf Punches of Winged Elm

The effects of 0, 10^{-4}, 10^{-3}, 10^{-2} M 2,4,5-T (potassium salt) on respiration of variously aged leaves of winged elm were determined.

Leaf punches were taken using an 8-mm diameter cork borer from two adjacent leaves at three different age positions on the limb. Beginning with the youngest at the apex to the oldest near the base, the positions selected were: number 1 at leaves 1 and 2, number 2 at leaves 7 and 8, and number 3 at leaves 13 and 14. Three punches were taken per leaf from each leaf pair on each of two limbs and pooled so that each sample contained twelve punches. Punches from each position were placed separately into the specific concentrations of 2,4,5-T solution and evacuated three times with a water aspirator. Respiration was determined immediately after vacuum infiltration in a Warburg respirometer using the same procedure as described for respiration of untreated leaves. After an equilibrium period of $1\frac{1}{2}$ hours, readings were recorded for the following four-hour period. Three replications of each treatment were made. Results are recorded as $\mu l\ O_2$ per gram wet weight per hour.

Phosphorus-Iron Ratio of Various Aged Winged Elm Leaves

1. Wet-Ashing Procedure for Iron and Phosphate Determination of Winged Elm Leaves

Both iron and phosphorus content were determined on the same individual leaves from the respiration experiment taken consecutively down the limb from the youngest leaf, number 1, at the apex to the older ones through number 12 near the base. Each leaf was wet-ashed with H_2SO_4 and perchloric acid by a method described by Fiske and Subbarow (31) and modified by Guinn (35). Wet-ashing was conducted separately for each leaf. First the leaves were lyophillized for 48 hours and the dry weights were determined. Each leaf was then placed into a 10 ml Kjeldahl falsk with 2 ml of 13 N H_2SO_4, 2 ml of 1 N perchloric acid and a carborondum boiling chip. The flasks were placed on an electric variable heat controlled Kjeldahl apparatus and allowed to simmer on low heat for twelve hours. The temperature was increased until the solution cleared. Upon cooling, water was added to bring the total volume of wet-ashed leaf material to 10 ml. Separate aliquotes were used for the iron and the phosphorus determination.

2. Total Iron Determination of Winged Elm Leaves

Total iron in the wet-ashed leaf samples was determined by a modification of the o-phenanthroline method using hydroxalamine hydrochloride as described by Sandell (66). This spectrophotometric method gives good sensitivity in the range of 0.01 to 0.2 mg of iron per sample based on an orange-red complex between o-phenanthroline and ferrous iron which closely followed Beer's law. The complex was color stable for many months and had the advantage of being functional in acid solutions in which the hydroxides and phosphates of many metals are not precipated. To a 20-ml graduate test tube was added: 5 ml of the original wet-ashed leaf sample, 7 ml of 1, 10 phenanthroline (0.5 per cent aqueous solution) and enough water to make a total volume of 15 ml. The solution was allowed to stand for 30 minutes. Determinations were made using a Klett-Summerson photoelectric colorimeter with a 500 mμ (green) filter. Stock solutions of iron were prepared by dissolving 10 grams of iron wire in 250 ml of 6 N HCL and diluting to 10 μg/ml with deionized, distilled water. Two and four ml of standard containing 20 and 40 μg iron respectively were separately wet-ashed and determined concurrently with each replication of leaf samples.

3. Total Phosphorus Determination of Winged Elm Leaves

Total phosphorus in each leaf was determined by the procedure of Fiske and Subbarrow (31). This method is recommended for determination of phosphorus content between 0.1 and 1.0 μ moles per sample. Two-ml samples of the wet-ashed material from the individual leaves were placed into 10-ml graduated test tubes. To these were added 1 ml of molybdate reagent, 0.1 ml of reducing solution, and enough distilled water to make a total of 10 ml. The mixture was stirred and allowed to stand for ten minutes. Absorbance was determined at 640 mμ (red filter) on a Klett-Summerson photoelectric colorimeter. Stock solutions of phosphorus were prepared to contain 31 μg phosphorus per ml. Two ml of the phosphate standard were wet-ashed and determined simultaneously with each replication of leaf samples.

Seasonal Variation in Absorption and Translocation of 2,4,5-T in Winged Elm

The effect of season of treatment on translocation of 2,4,5-T-1-^{14}C was studied for two consecutive growing seasons. Studies during the first year (1963) were made on naturally growing winged elm trees located in Okmulgee County on the property of M. D. Thompson situated on the north side of State Highway 16, six miles east of Slick, Oklahoma.

Six winged elm trees of sizes between 15 and 20 feet in height were chosen for the experiment. A general description of the growth habits of the trees as they were numbered for the experiment is as follows.

Trees number 1 and 2 had very slow growing limbs with small leaves of 1 to 1.5 inches long and frequent branching of every 2 to 3 inches.

Trees number 3 and 5 had fast growing limbs reaching 2 to 3 feet in length with no side branches and leaves 2 to 3 inches long.

Trees number 4 and 6 had moderate growth with subsequent branching and leaves from 1 to 2 inches long.

Two limbs from each tree were treated periodically every three weeks from May 30 to October 3. During each treatment the herbicide was applied to one limb at the terminal leaf and to the other limb at the fourth leaf back from the growing tip. Fifty μg of 2,4,5-T-1-^{14}C was applied as previously described. The herbicide was confined within a $\frac{1}{4}$ inch ring of lanolin. At 24 hours after treatment, bark samples were collected and prepared for radioactive determination by autoradiography, and absorption and translocation from the leaf tissues were determined as previously described.

Bark samples were taken from the terminally treated limbs at 3, 6, and 9 inches below the treated leaf and from the laterally treated limbs at 3 inches above and 3 and 6 inches below the treated leaf. One-inch long cylinders of bark were split longitudinally down the limb, peeled away at the cambium, and stapeled out flat between small pieces of screen wire for drying. They were then glued and pressed with the phloem side out onto a sheet of 14 x 17 inch poster paper using Borden's "Elmers Glue-all" glue. Separate sheets were used for the terminal and the lateral treatments.

Autoradiographs were prepared by covering the sheets of bark samples with a single layer of "Saran Wrap" and placing each of them in contact with a 14 x 17 inch sheet of Kodak No Screen X-ray film. The film was backed on one side with a $\frac{1}{2}$ inch plywood board and pressed on the other side with a 1 inch thick foam rubber pad using the method described by Yamagauchi and Crafts (84). The autoradiographs were developed after two months in contact with the X-ray film.

Studies during the second year (1964) were conducted in Payne county on the Oklahoma State University Agronomy Research Farm at Perkins, Oklahoma. The trees for this experiment were three-year-old seedlings which were transplanted from southeastern Oklahoma and donated by Mr. Harry Elwell[1]. Six trees approximately six feet tall were chosen for treatment at three-week intervals throughout the year from May 26 to September 28.

Absorption and translocation of the herbicide by the winged elm leaves were determined in the same manner as was described for absorption and translocation of 2,4,5-T-1-^{14}C in variously aged winged elm leaves.

Autoradiographs were prepared from bark samples at 3 inches above and 3 and 6 inches below the treated leaf in the same manner as

[1]Research agronomist, U.S.D.A. Oklahoma State University Agricultural Experiment Station, Stillwater, Oklahoma.

described for the first year seasonal study.

Continuous data for temperature and rainfall at the Perkins farm during the period of this experiment was provided by Mr. Lou Morrison[2].

Effect of Soil Moisture on Absorption and Translocation of 2,4,5-T

The effects of soil moisture on absorption and translocation of 2,4,5-T-1-^{14}C in the winged elm were determined both in the field and in a controlled environment growth chamber.

1. Field Moisture Study

The field experiment was conducted at the Perkins farm in cooperation with an experiment by Mr. Harry Elwell. Three-year-old winged elm trees were subjected to controlled watering facilitated by covering the soil around the base of each separate replication of eight trees with a plastic sheet over a wooden frame to prevent watering by rainfall. Watering was accomplished with a portable water tank. Three soil moisture treatments included trees in soil of: (1) continuous drought, (2) continuous watering, and (3) increased water content at the time of treatment from prolonged drought to field capacity. The 2,4,5-T-1-^{14}C (20 μg) was applied to the upper side of a lateral leaf for 24 hours. Three trees were treated in four replications of each moisture treatment. The translocation of the ^{14}C was determined by autoradiography and liquid scintillation as was described in the second year seasonal study.

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[2]Assistant Professor, Department of Botany and Plant Pathology, Oklahoma State University, Stillwater, Oklahoma.

2. Growth Chamber Moisture Study

The growth chamber experiment was conducted on greenhouse-grown seedlings of winged elms approximately 14 cm in height contained in four-inch clay pots. Treatments were made in a growth chamber under Growlux florescent light of 2,000 ft-c with a temperature range of 82 to 86°F and a relative humidity range of 60 to 80 per cent.

Twenty-five μg of 2,4,5-T-1-^{14}C potassium salt in a 1:1 mixture of ethyl alcohol and water containing 0.5 per cent Sterox and 2.46 μc ^{14}C (1 mc ^{14}C/61.4 mg 2,4,5-T) in .01 ml was applied to the upper side of a single leaf located near the midpoint of each shoot and left for a period of 24 hours. Moisture treatments of ten trees each included plants which were: 1) watered every day, 2) watered every 2 days, and 3) watered every 3 days. The herbicide application was made at the end of each drought period and no further watering and 4) watered every 3 days with water added to field capacity immediately at the time of herbicide application. Absorption and translocation was determined into and out of the treated area and out of the entire leaf as described in the absorption and translocation of 2,4,5-T-1-^{14}C in variously aged leaves.

Translocation throughout the plant was determined by homogenizing the separate portions of the plant in 95 per cent ethyl alcohol using a Virtis homogenizer. Total volume of alcohol suspension for each portion was: 10 ml for the upper and the lower leaves, 15 ml for the upper and lower stems and 20 ml for the roots. A 1-ml aliquot of each suspension was dried and determined for ^{14}C by liquid scintillation.

Metabolism

Biochemical breakdown of 2,4,5-T-1-^{14}C by different aged leaves and leaf punches was determined by ascending paper chromatography. The study was conducted on homogenized tissues from the previous absorption and translocation studies. Samples were taken from leaf positions 1, 3, 5, 8, 12, and 15. The standard was of the same solution and concentration as used in the leaf applications.

Chromatograms were prepared on 3 x 45 cm strips of Whatman No. 1 chromatograph paper and developed in a 4: 1: 1 solution of normal butanol, 95 per cent ethanol and water plus 1 ml of concentrated NH_4OH for each 30 ml of solution. Two-tenths ml of each tissue suspension was placed in a narrow band one inch from the bottom of each strip. The chromatographs were developed for 16 hours and the radioactivity was determined by autoradiography for a period of six weeks using the same method described for determination of radioactivity in the bark samples.

CHAPTER IV

RESULTS AND DISCUSSION

Absorption and Translocation of 2,4,5-T of Variously Aged Leaves

The data for absorption and translocation of 2,4,5-T-1-^{14}C in the variously aged leaves are presented in Figure 1. The absorption value is significantly higher in the first leaf of four days old than in the remaining leaves and there was a sharp decrease at the second and third leaves of 8 and 12 days old followed by an increasing trend to leaf number 6 at $3\frac{1}{2}$ weeks old and a subsequent leveling off in the remaining leaves. Absorption was fairly uniform for all leaves except the youngest leaf at the tip of the branch. The higher amount of absorption in the youngest leaf may be explained by a lack of cutin formation in this partially developed leaf.

Translocation from the treated area did not vary in trend from leaf number 1 to leaf number 4 at two weeks old and there was a light but significant decrease to leaf number 9 at five weeks old. There was a moderately increasing trend from here through the remaining leaves. The translocation from the entire leaf followed a similar trend to that from the treated area beginning at a relatively high rate and decreasing through leaf number 7. There was a significant decrease in translocation between leaves number 1 and number 12 and leaves number 10 and number 12 at seven weeks old.

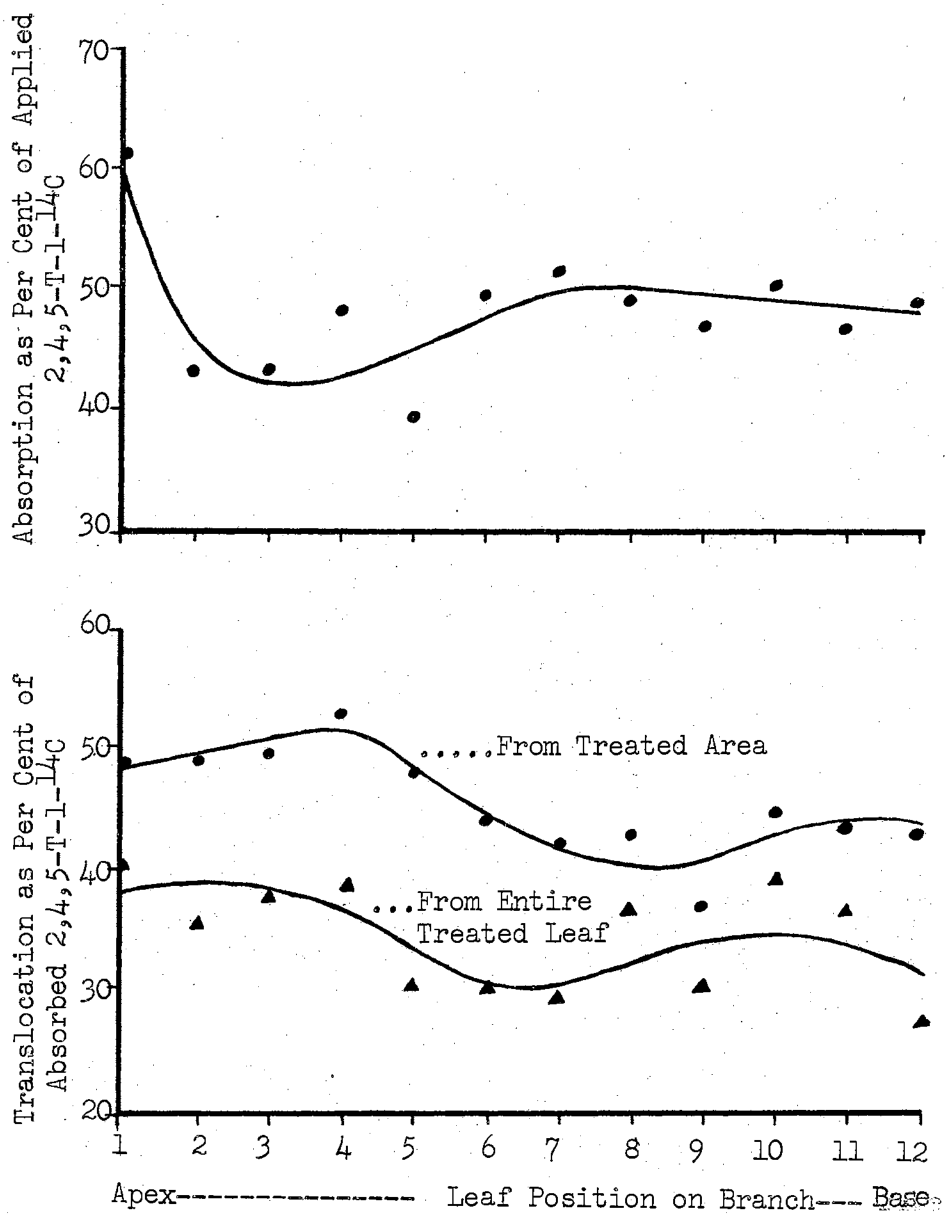

Figure 1. Absorption and Translocation by Variously Aged Winged Elm Leaves. Absorption and Translocation are Presented as a Per cent of the Total 2,4,5-T Applied and Absorbed Respectively. (30,000 cpm Applied/Leaf Treatment).

In general there was very little difference in translocation of 2,4,5-T-1-^{14}C from young and old leaves. There was a slight trend toward a decrease in translocation in older leaves. However, the differences were not extensive being much less than differences found between leaves exposed to different environmental conditions as will be shown in other experiments. Kursanov (47) showed that young leaves usually have very low rates of translocation of photosynthetic assimilates while older leaves have high rates apparently providing food materials for younger growing tissues. In the present experiment 2,4,5-T-1-^{14}C movement was higher in young tissue indicating that 2,4,5-T movement may not be strictly correlated with the movement of assimilates in winged elm.

There was a very close correlation between the amounts of 2,4,5-T-1-^{14}C translocated from the treated area and the treated leaf. These data indicate that once 2,4,5-T is moved from the treated area into to surrounding leaf tissue it is readily moved from the leaf to other parts of the plant. In these experiments the differences between translocation from the treated area and the treated leaf are less for older leaf tissue. These data suggest that older leaf tissue has a higher potential for translocation to other parts of the plant after the 2,4,5-T has moved out of the treated area. Numerical values and statistical analyses for absorption and translocation are located in appendix tables V, VI, and VII.

Respiration of Variously Aged Leaves

The respiration rate for the variously aged winged elm leaves on the individual limbs is shown in Figure 2. The respiration rate

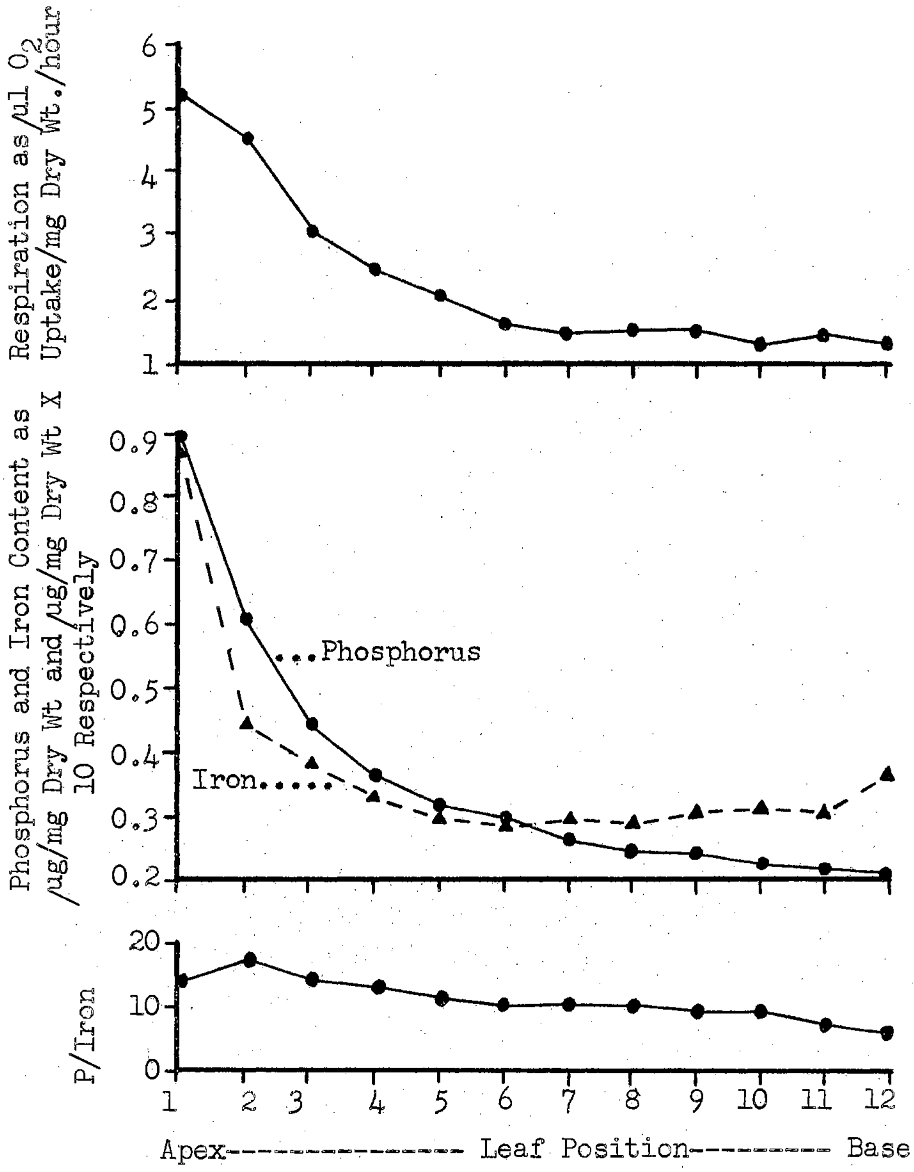

Figure 2. Relationships Among the Respiration Rates, Phosphorus Content, Iron Content, and Phosphorus-Iron Ratios in the Variously Aged Winged Elm Leaves.

is highest in the youngest leaves at the apex with a gradual decrease in rate to the seventh leaf and a leveling off of the rate in the remaining leaves toward the base of the limb. The decreasing portion of this curve generally follows the trend for translocation of ^{14}C-labeled material in these same leaves. These data correlate with the results of Kidd et al (45) and Glenister (34) where with sunflower leaves the respiration rate of the younger leaves was greater than that of the older leaves.

Steward (69) defines respiration as energy releasing reactions which involve the direct uptake of oxygen. The respiration rates as determined by measuring oxygen uptake of these different aged leaves may possibly indicate a release of energy that may be partially used in the active transport of absorbed materials. Zimmerman (86) found actively conducting sieve bundles to have increased respiration rates over that of the surrounding tissues and points out the numerous experiments showing that the metabolic release of energy is necessary for translocation. Dalrymple and Basler (25) found respiration rates in leaf tissue of blackjack oak to closely follow the translocation rate of 2,4,5-T. The numerical values and statistical analysis for these data are given in appendix table VIII.

Respiration of 2,4,5-T Treated Leaf Punches

Wedding and Black (79) have shown that high concentrations of 2,4-D uncouple oxidative phosphorylation in isolated mitochondria in a manner similar to the well known effects of 2,4-dinitrophenol. Thus, treatment with high concentrations of 2,4-D or 2,4,5-T might lead to "uncontrolled respiration" with increased oxygen uptake rates. A number of investigators have noted increased O_2 uptake rates with high rates of treatment in intact tissue. However, many tissues appear to have increased respiration rates only after treatment with low growth promoting concentrations of the auxin type herbicides while high concentrations inhibit respiration. Increased respiration rates upon treatment with high concentrations of 2,4-D have been noted by Humphreys and Dugger (39) in corn and pea stem tissue and by Basler and Nakazawa (9) in cotton cotyledon tissue. Klingman (46) showed that low 2,4-D concentrations tended to increase respiration and high concentrations inhibited respiration in many plant tissues. Either the uncoupling of oxidative phosphorylation or decreased respiration rates could possibly inhibit the translocation of 2,4,5-T in winged elm since translocation appears to be dependent on metabolic energy. High concentrations of 2,4,5-T then may impair the translocation mechanism through effects on respiration. In view of these considerations, the effects of 2,4,5-T on the respiration of winged elm leaf tissues was determined.

The effect of 2,4,5-T on respiration of variously aged leaves from three positions on the limb is shown in Figure 3. The numerical values for each replication are given in appendix table IX. There was no appreciable effect by the herbicide on the respiration rate of the leaf punches over the rate noted in the untreated check. An exception was noted in a slightly higher respiration rate with the youngest leaves treated in 10^{-3} molar 2,4,5-T. These results do not correlate with the results cited by Klingman (46) where low rates of 2,4-D

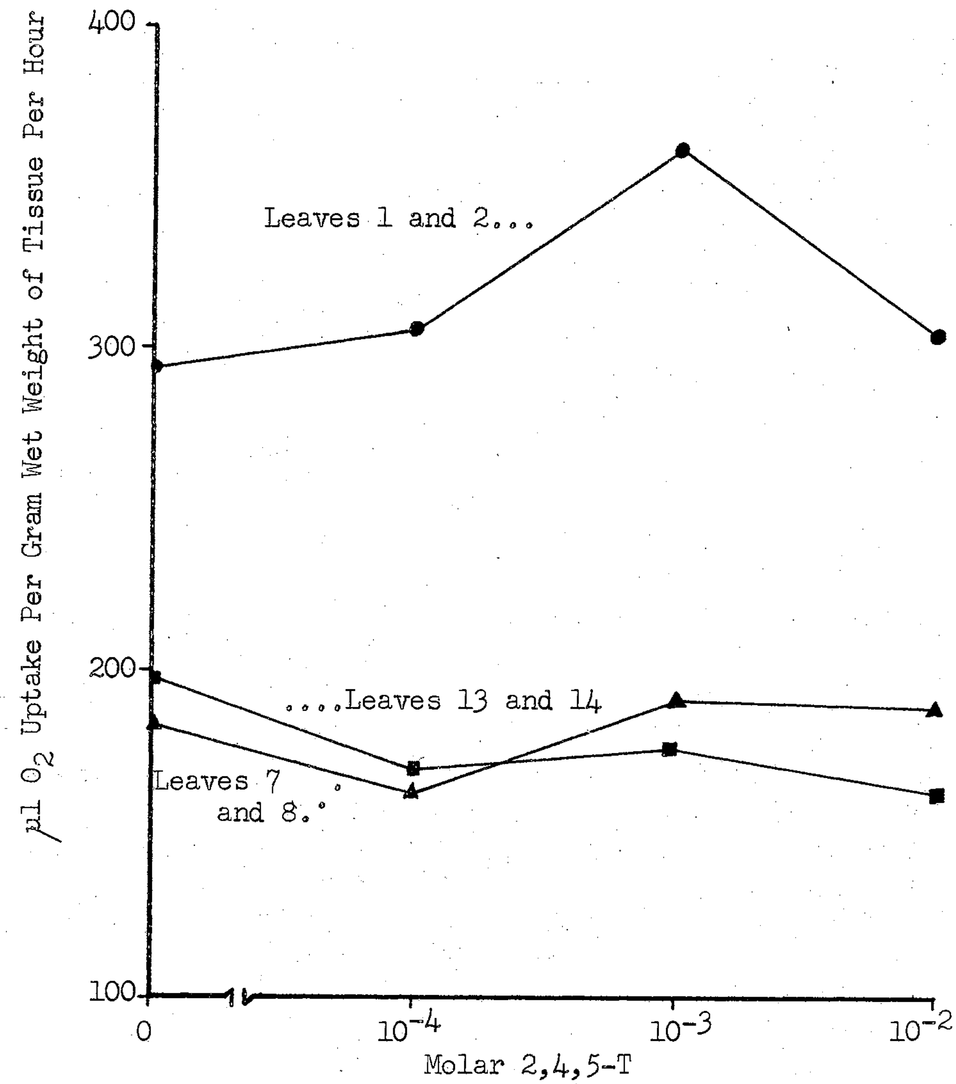

Figure 3. Effect of Three Concentrations of 2,4,5-T on Respiration of Different Aged Winged Elm Leaves Presented as Microliters of O_2 Uptake Per Gram Wet Weight of Tissue Per Hour.

tended to stimulate respiration while high rates tended to inhibit respiration. These data compare, however, with the results of Dalrymple and Basler (25) where no significant effect by 2,4-D was noted on the respiratory response of blackjack oak leaf tissue at 1.5 hours after treatment. These workers, however, noted a slight stimulation with 2,4-D at 10^{-3} molar after 21 hours.

Phosphorus-Iron Ratio of Variously Aged Leaves

The respiration data of this investigation indicate that metabolism is an important factor in translocation of the herbicide. According to DeKock (26) and DeKock and Hall (27) one measure of the metabolic potential in the tissues of many plants is the phosphorus-iron ratio where a high ratio is due to a low iron content and subsequently indicates a low metabolic potential in the tissue. Thus the iron content, phosphorus content and phosphorus-iron ratio were determined and are shown in Figure 2. The numerical values and statistical analysis are given for each in appendix tables X, XI, and XII respectively. Both phosphorus and iron are higher in the youngest leaves. Glenister (34) points out that iron is necessary as part of the prosthetic group in several respiratory enzymes including catalase, peroxidase, cytochrome oxidase, and as a constituent of the cytochromes.

In this investigation the increased iron content corresponded with the high respiration rates in the youngest leaves of the winged elm, and it appears that the iron content of the leaves can be correlated with the increased activity of the respiratory system.

Mac Donald and De Kock (26) noted that iron content affected the metabolic potential in plants in that many respiratory inhibitors were less inhibitory to oxygen uptake in iron toxic leaves than in iron deficient leaves.

The higher phosphorus-iron ratio in this study did not indicate the same lowered metabolic potential as noted in many plants by De Kock (26) and De Kock and Hall (27). In the winged elm leaves, as the iron content increased the phosphorus content also increased in even greater proportions causing increases in the phosphorus-iron ratio which corresponded with an increase in respiration rate.

Seasonal Variation in Absorption and Translocation of 2,4,5-T in Winged Elm

The 1963 data for absorption of 2,4,5-T-1-^{14}C and the subsequent translocation out of both the terminal and the lateral treated leaves of naturally-growing, mature winged elm trees throughout the growing season are given in Figure 4. The numerical data and statistical analyses are given in appendix tables XIII, XIV, XV, and XVI respectively. The absorption and translocation data show considerable variation among treatments throughout the growing season with most of the higher values being significantly different from the lower values. These large differences appear to be due to differences in environmental conditions at the time of treatment.

Comparison of the absorption and translocation values at each specific treatment date throughout the growing season shows a close correlation between the treated terminal and lateral leaves on separate limbs. These data suggests that there is much more variability

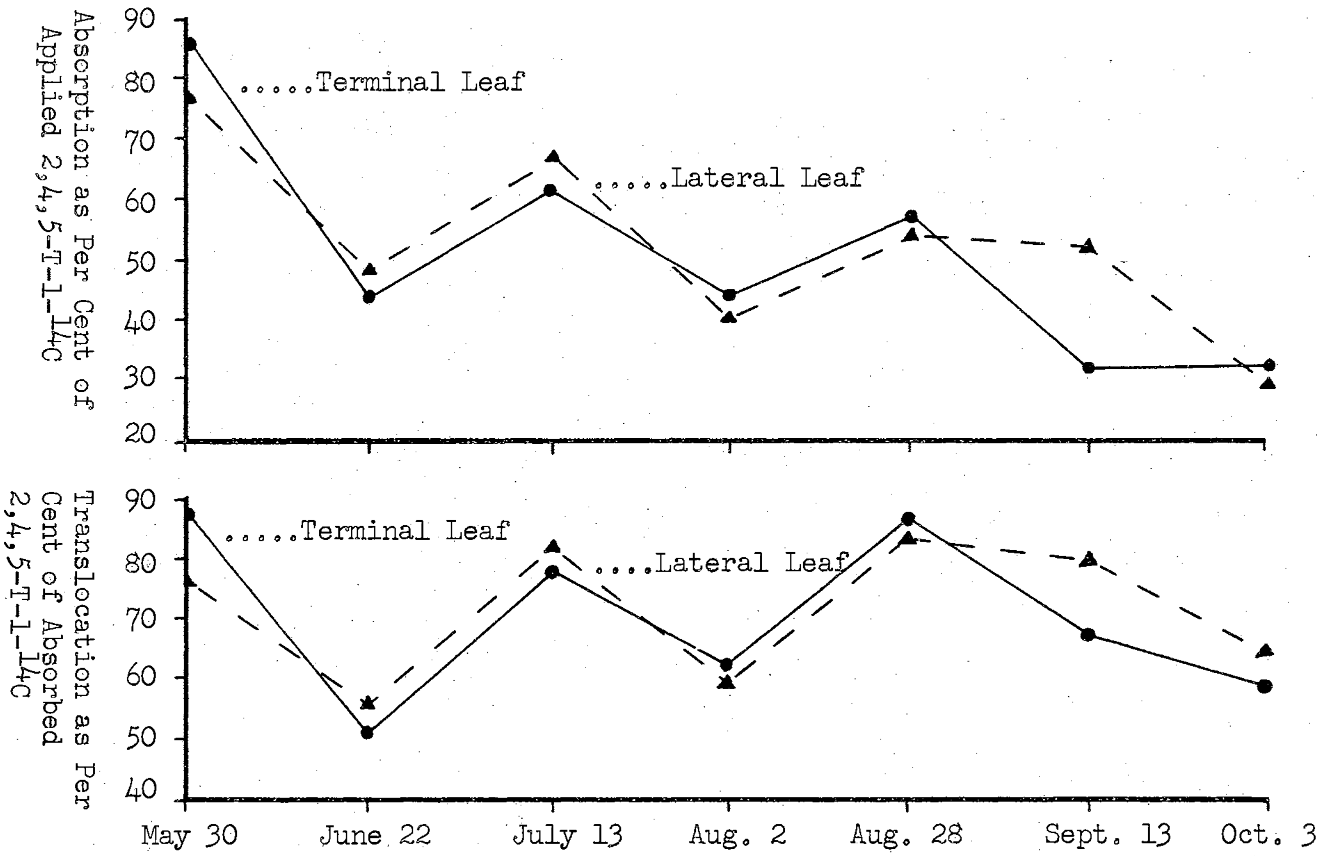

Figure 4. Absorption and Translocation of 2,4,5-T-1-^{14}C by Terminal and by Lateral Leaves on Separate Limbs of Winged Elm During the 1963 Growing Season. Absorption and Translocation Values are Presented as a Per Cent of the Total 2,4,5-T-1-^{14}C Applied and Absorbed Respectively.

in translocation due to differences in environmental conditions than the variability between leaves. The per cent of the absorbed herbicide which translocated out of the leaves follows the same pattern as the absorption into the leaves.

The absorption pattern, although variable in each case, showed a generally decreasing trend throughout the growing season; whereas, the translocation pattern showed a generally variable trend throughout the season.

Autoradiographs of the 1963 bark samples from 3, 6, and 9 inches below the treated terminal leaves and from 3 inches above and 3 and 6 inches below the treated lateral leaves of this experiment are shown in Figures 5 and 6 respectively. The seasonal translocation pattern in the bark samples of the separate terminal and lateral leaf treatments are very closely correlated. The lateral leaf treatment showed upward as well as downward movement during the same seasonal periods that the terminal treatments showed downward movement. The results of the autoradiographs throughout the season showed that the amount of ^{14}C-labeled material collecting in the first 9 inches of the limbs of the treated leaves was moderately high in samples treated on May 30, low on June 22, high on July 13, moderate on August 2, low again on August 28, moderately high again on September 13 and decreasing again on October 3.

The concentrations noted in the autoradiographs coincided with the trends of values for absorption and translocation in leaf samples in the May, June and July treatments while no correlations were evident in the August and September treatments.

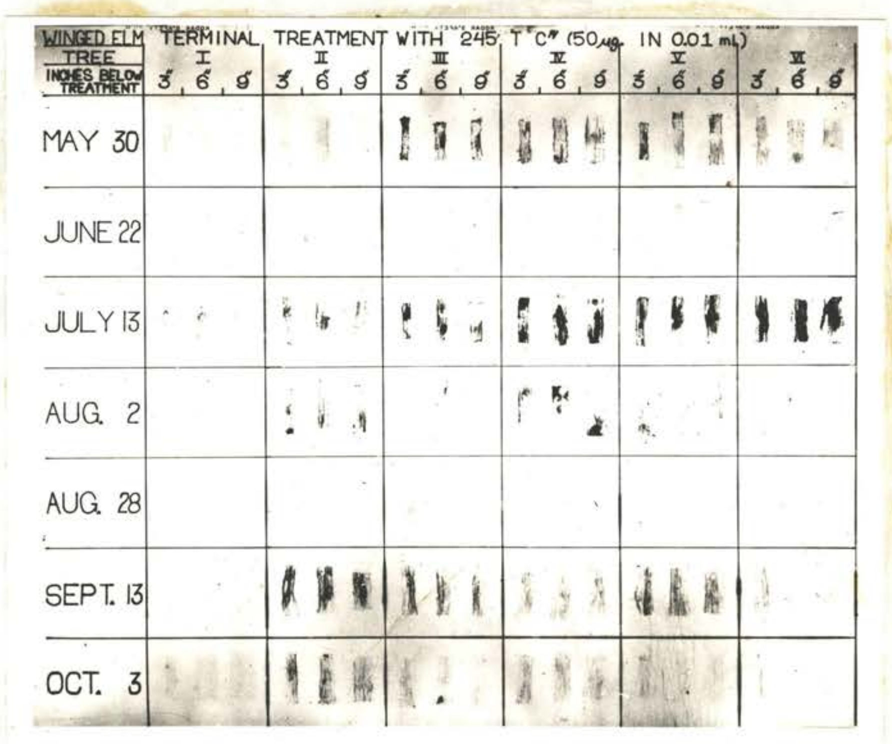

Figure 5. Translocation of 2,4,5-T-1-^{14}C From Terminal Treated Leaves to Bark Samples During the 1963 Growing Season.

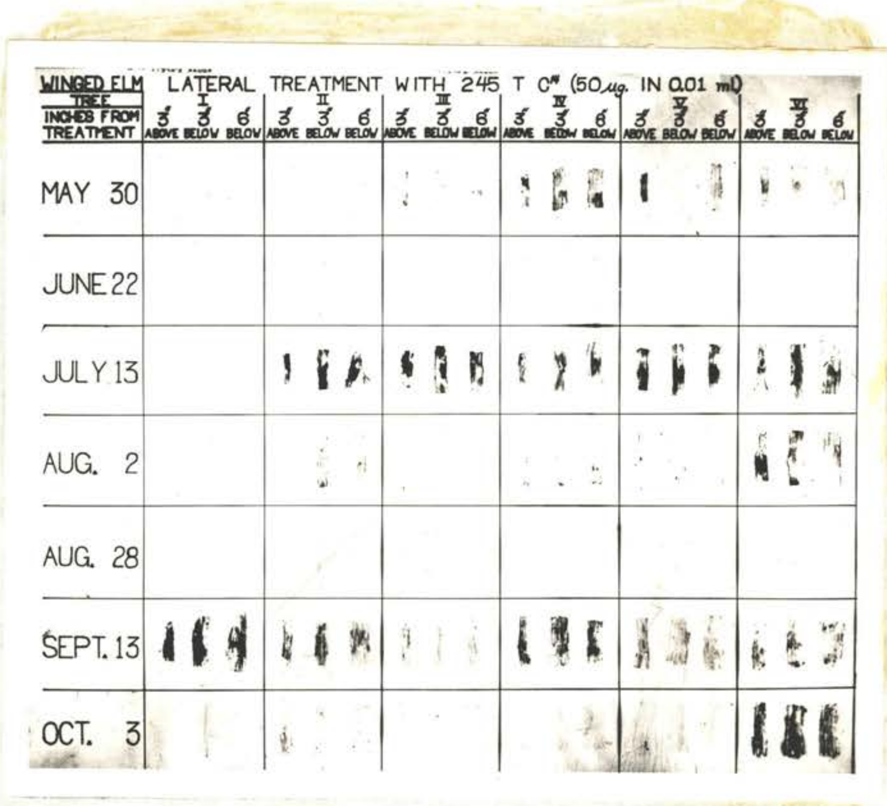

Figure 6. Translocation of 2,4,5-T-1-^{14}C From the Lateral Treated Leaves to Bark Samples During the 1963 Growing Season.

The 1964 data for absorption and subsequent translocation from the treated area and from the treated leaves of three-year-old nursery stock of winged elm are shown in Figure 7 with the numerical values and statistical analysis given in appendix tables XVII, XVIII, and XIX respectively. As was noted in the 1963 seasonal data, this translocation pattern also closely followed the absorption pattern, and the movement out of the whole leaf was closely associated with the movement out of the treated area. Both the absorption into and the translocation out of the leaves significantly increased from June 15 to July 27 and significantly decreased to August 17 with a gradually declining trend through September 7 to September 28.

Autoradiographs of the 1964 bark samples from 3 inches above and from 3 and 6 inches below each treated leaf are shown in Figure 8. This figure indicates that there was some downward movement of ^{14}C-labeled material throughout the growing season with a predominance of concentration at three inches below the treated leaf. An accelerated upward movement was noted on May 25 and to a lesser degree on June 15 while a greater downward trend was noted for June 15 and July 6. Movement was greatly decreased at July 27 and August 17 with the largest concentration at three inches below the treated leaf. There was a slight increasing trend in both upward and downward movement on September 7 and a general cessation of all movement by September 28. These dates of high translocation also roughly correspond with the dates of best translocation reported by Elwell (28) who recommended that blackjack oak was most effectively controlled with 2,4,5-T from May 15 to July 15.

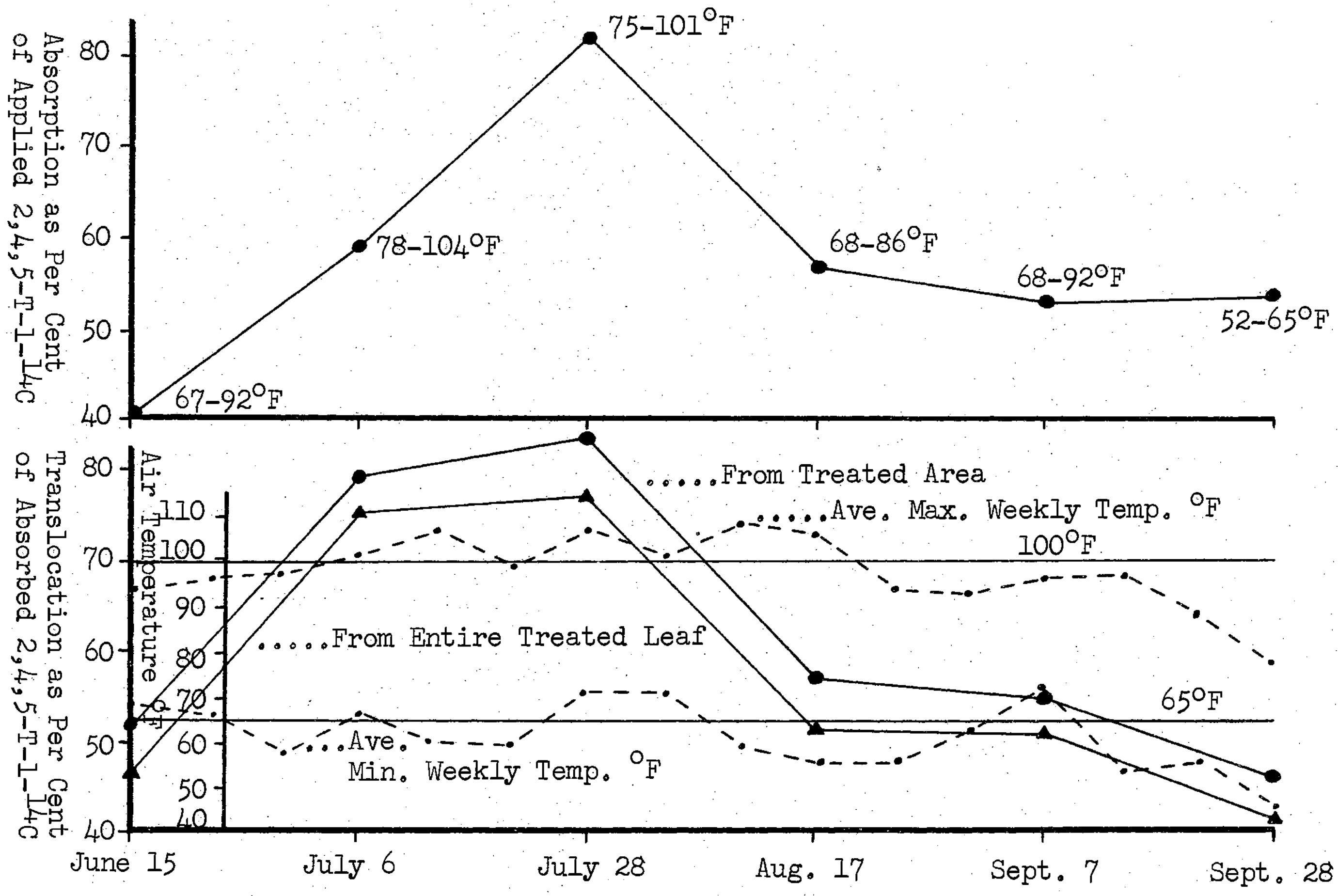

Figure 7. Absorption and Translocation of 2,4,5-T-1-^{14}C by Winged Elm During the 1964 Growing Season. Absorption and Translocation Values are Presented as a Per Cent of the Total 2,4,5-T-1-^{14}C Applied and Absorbed respectively. Also, the Temperature Range in Degrees F During the 24-Hour Treatment Period and for the Weekly Averages Throughout the Growing Season.

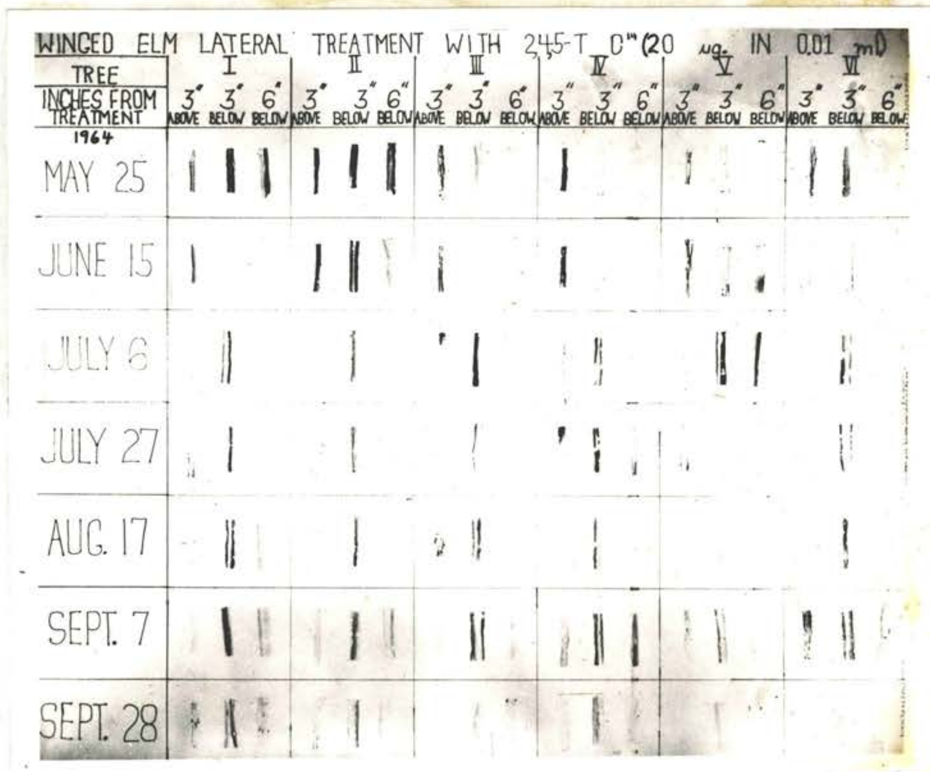

Figure 8. Translocation of 2,4,5-T-1-^{14}C From Lateral Treated Leaves to Bark Samples During the 1964 Growing Season.

In conjunction with the 1964 absorption and translocation data the air temperature in degrees Fahrenheit and the rainfall in inches throughout the growing season are showin in Tables I and II. The air temperature is presented as the weekly averages of the daily maximum and minimum temperatures and as the maximum and minimum temperatures during the time of treatment.

The absorption and translocation of 2,4,5-T-1-^{14}C appears to correlate with the maximum-minimum temperature range during the time of treatment and of the weekly average throughout the season. The cooler temperature range of low 50's to low 90's during the first two weeks of June with the low temperature range of 67-92 during the June 15th treatment corresponds to a low rate of absorption and translocation. The increasing temperature range of the mid 70's to the low 100's at the July 6 and 27 treatments correspond with increased rates of absorption and translocation. The August 17 treatment during the lowered temperature range of 68-86^{o}F was again associated with a decreased rate of absorption. The latter treatment was conducted during a short-termed cool weather condition which was associated with a weekly average maximum range of over 100 degrees. The remaining treatments were conducted in periods of gradually decreasing temperature ranges with the absorption rate leveling off while the translocation rate continued in a gradual decline through the September 28 treatment.

This correlation of the effects of temperature on absorption and translocation of 2,4,5-T in winged elm corresponds to the effects of temperature on absorption and translocation of phenoxy herbicides

TABLE I

AIR TEMPERATURE AT FOUR FEET ABOVE THE GROUND LEVEL AT THE LOCATION OF THE 1964 ABSORPTION AND TRANSLOCATION STUDIES

Week Ending	Weekly Temp. Rn. °F	Temp. Rn. During Treatment °F	Week Ending	Weekly Temp. Rn. °F	Temp. Rn. During Treatment °F
May 18	44-87		July 27	71-107	75-101
May 25	60-89	56-88	Aug. 3	71-101	
June 1	51-93		Aug. 10	60-108	
June 8	50-93		Aug. 17	56-106	68-86
June 15	70-94	67-92	Aug. 24	56-94	
June 22	67-96		Aug. 31	64-93	
June 29	58-97		Sept. 7	70-96	69-92
July 6	66-101	78-104	Sept. 14	54-96	
July 13	60-107		Sept. 21	56-88	
July 20	60-99		Sept. 28	45-79	58-65

TABLE II

RAINFALL AT THE LOCATION OF THE 1964 ABSORPTION AND TRANSLOCATION STUDIES

May	Inches	June	Inches	July	Inches	Aug.	Inches	Sept.	Inches
2	0.14	3	0.12	1	0.06	7	0.51	11	1.96
6	0.14	4	0.33	9	0.38	15	1.31	16	0.40
8	3.02	5	0.05	27	0.08	18	0.65	17	0.06
27	0.25	13	0.27	28	0.12	25	0.42	20	0.09
30	1.18	23	0.30	29	0.50	26	2.03	22	0.22
31	0.15	29	0.67			28	1.45	26	0.21

by other workers. In the studies with 2,4-D on red kidney beans Rice (64) found absorption to increase with temperature increases from 45 to 92°F and Pallas (59) found both absorption and translocation to increase with temperature increases from 20 to 30°C. Also, Morton (56) working with mesquite found absorption of 2,4,5-T to increase with increasing temperatures from 85 to 100°F.

Currier and Dybing (24) suggested that increased temperature increased foliar absorption through its effect on increased rate of difusion, lowered viscosity, acceleration of photosynthesis, increased protoplasmic streaming and increased growth.

In comparing the 1964 autoradiographs of bark samples with the temperature data throughout the growing season the greater movement of ^{14}C-labeled material to bark tissue also appears to be associated with periods of higher temperatures.

The rainfall data did not appear to correlate very closely with the absorption and translocation data. The seasonal treatments, however, were not conducted in close enough association with the occurrence of precipitation to make a valid comparison of the two.

Effect of Soil Moisture on Absorption and Translocation of 2,4,5-T

The data for the study of the effects of field soil moisture on absorption and translocation of 2,4,5-T-1-^{14}C in winged elm are presented in Table III. The per cent absorption into the leaf indicated there was no difference between the continuously high and the low to high soil moisture levels but there was a slight decrease at the continuously low soil moisture level. The translocation from the

TABLE III

EFFECT OF MOISTURE STRESS ON ABSORPTION AND TRANSLOCATION OF 2,4,5-T-1-^{14}C (FIELD TREATMENT 1964)*

Treatment	Absorbed into Leaf as Percent of That Applied	Translocated as Percent of That Absorbed	
		From Treated Area	From Leaf
Low Moisture	46.9	44.6	18.6
High Moisture	51.1	50.9	27.0
Low to High Moisture	51.2	61.5	42.8

*Average of 4 replications with 3 plants per replication.

TABLE IV

EFFECT OF MOISTURE STRESS ON TRANSLOCATION OF 2,4,5-T-1-^{14}C TO VARIOUS PARTS OF WINGED ELM SEEDLING

Section of Plant	Period From Final Watering Until Treatment			
	3 Days	2 Days	1 Day	3 Days (Water at Treatment)
Upper Lvs.	Trace	Trace	Trace	Trace
Upper Stem	2.52	3.72	3.93	2.15
Lower Lvs.	.72	Trace	.94	.54
Lower Stem	5.10	15.03	13.54	8.96
Roots	Trace	3.84	4.02	2.31
Treated Leaf	44	51	86	53
Leaf Punch	577	445	442	549
Wash	6028	5808	5956	5899

Counts/min/plant section X 100 (Average of 10 replications).

treated area and from the remainder of the leaf showed the same trend from each with the translocation being lowest at the low soil moisture and highest at the soil moisture level which was increased from low to high at the time of treatment.

The autoradiographs of bark samples from 3 and 6 inches below the treated leaf of each tree is shown in Figure 9. No appreciable difference was noted in the concentration of ^{14}C-labeled material at these locations as affected by the different soil moisture conditions.

For the growth chamber soil moisture study, the value for the translocation of 2,4,5-T-1-^{14}C to the various parts of the winged elm tree are given in Table IV. Because of the difficulties involved in homogenizing whole sections of plants in preparation for liquid scintillation counting, the variation in the radioactive counts was too great in most cases to allow valid statistical differences in the data. The general trend as noted in the average of ten replications, however, gives an indication as to the effects of different soil moisture conditions on translocation to various sections of the seedling tree. The values during the first 24 hours for translocation from a single leaf midway up the shoot showed no apparent movement into the upper leaves at the various moisture conditions. There was noticeable movement into the upper stems with the highest concentration occurring almost equally between the plants watered daily and those watered every two days. The lowest concentration occurred in the plants watered at the time of treatment after three days drought. There was slight movement into the leaves below the treated leaf with no apparent correlation between the movement to the lower leaves and

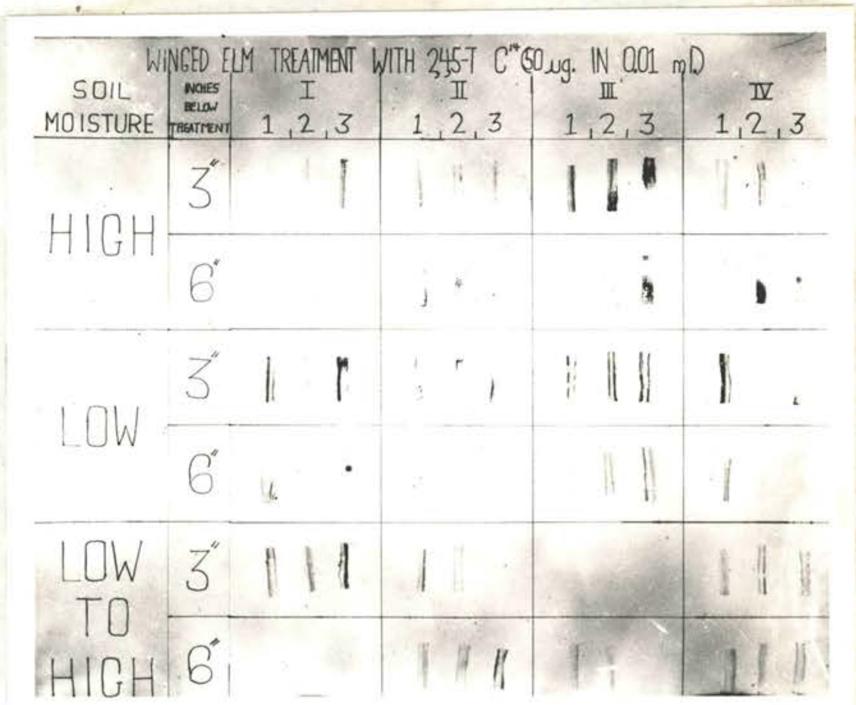

Figure 9. Translocation of 2,4,5-T-1-^{14}C From Winged Elm Leaves to Bark Samples at Various Levels of Soil Moisture Stress.

the soil moisture conditions.

Translocation to the lower stems and to the roots showed the same general pattern of movement into each with marked effects apparently due to the various soil moisture conditions. The downward movement was most pronounced in the plants which were watered daily and every two days. The plants treated after three days drought showed the least amount of downward movement with only a trace amount noted in the roots. The plants watered at the time of treatment after three days of drought showed a recovery in translocation of about one-third in the stems and about one-half in the roots as compared to the lowest movement found at three days drought and the highest movement noted at daily watering.

In a comparison of the results for the treated leaves between the field and the growth chamber soil moisture studies the leaf absorption was not appreciably affected by varying the soil moisture; whereas, the low soil moisture in each study correlated with low herbicide translocation. Basler et al (10) obtained similar results to the present study where absorption of 2,4-D in stringless green pod beans was little affected by soil moisture stress but translocation was greatly reduced during periods of water stress. They also found, as was noted in the translocation to the winged elm roots and stems, that translocation was not immediately regained in the bean plants when water content was restored. Pallas (60), in a study using red kidney beans, also found translocation of 2,4-D to be reduced during low levels of soil moisture.

The continuously high and the low to high soil moisture conditions each compared with increased translocation from the leaves. The continuously high moisture treatment resulted in the greatest translocation from the leaves in the growth chamber while the low to high soil moisture treatment resulted in the highest movement in the field. Dalrymple and Basler (25) in a study on blackjack oak, however, found no correlation between translocation and soil moisture stress under natural field conditions where the moisture range may have been less than the experimental treatments discussed above.

Metabolism of Herbicide

Chromatographs of the ^{14}C-labeled material extracted from the treated area and from the remainder of the treated leaf are shown as autoradiographs in Figures 10 and 11 respectively. Considerable breakdown of 2,4,5-T occurred during the 24-hour treatment period. The results for both the extracts of the treated area and the remainder of the leaf for each position on the limb showed similar chromatographic patterns with no apparent variations due to differences in age of the leaves. In each case the ^{14}C-labeled material divided into three separate spots with number 1 located at the solvent front, number 2 located close behind the front at an Rf of .87 and number 3 remaining at the point of origin.

The standard 2,4,5-T-1-^{14}C spot was located at the solvent front indicating that spot number 1 from the treated leaf material is unaltered 2,4,5-T. Spots number 2 and 3 are breakdown products of the original molecule. An interesting feature is that the breakdown

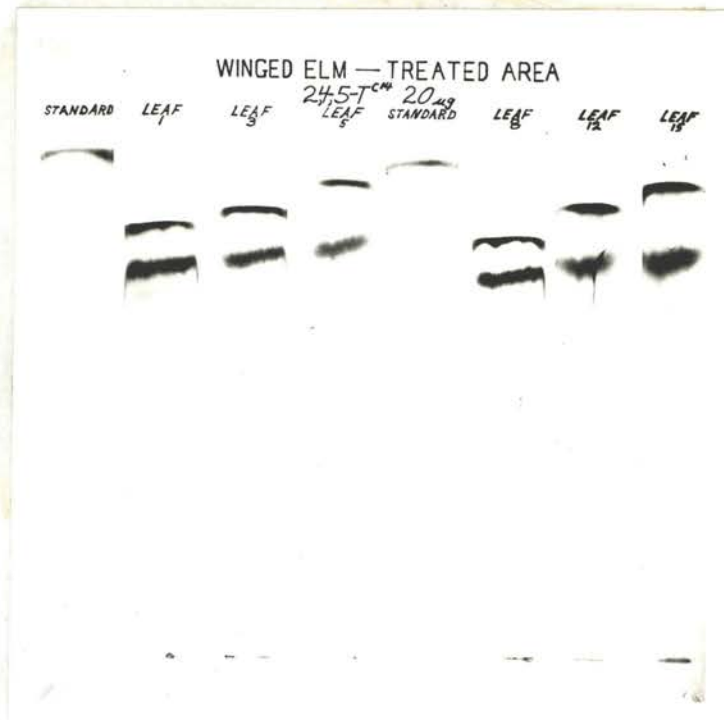

Figure 10. Chromatograph of 2,4,5-T-1-^{14}C From Extracts of Leaf Tissue from the Treated Area of Winged Elm After 24 Hours.

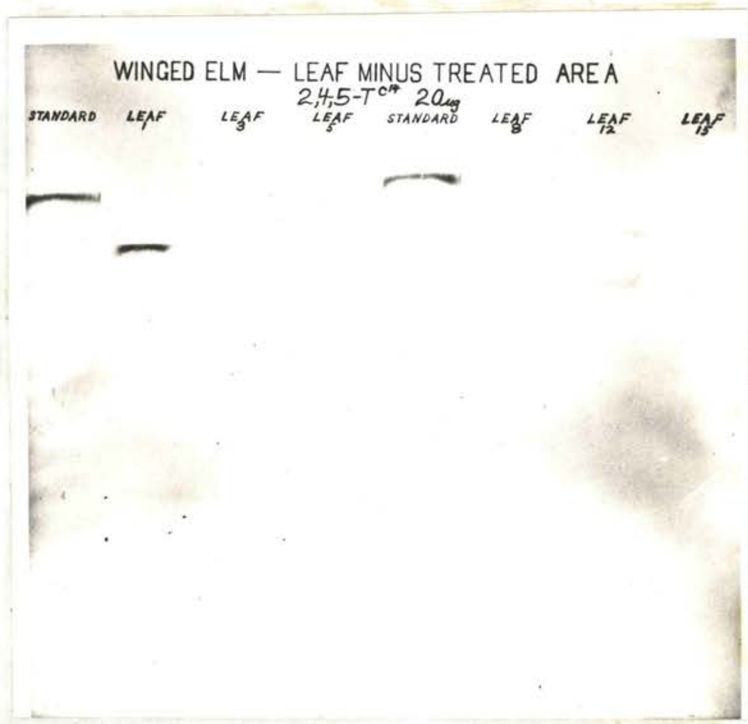

Figure 11. Chromatograph of 2,4,5-T-1-^{14}C From Extracts of Leaf Minus Treated Area in Winged Elm After 24 Hours.

product found in spot number 3 occurred only in extracts of tissue from the treated area. This may represent one mechanism whereby 2,4,5-T is immobilized in the treated area.

Holley et al (39) and Hay and Thimann (37) found 2,4-D carboxyl ^{14}C to break down to a water soluble material from leaf applications in red kidney beans. Weintraub et al (73) found 2,4-D-^{14}C as applied to terminal buds of black valentine beans to breakdown and later incorporate into many other plant substances. Liao and Hamilton (49) treated root tip cells of various plants with 2,4-D-^{14}C and indicated that 2,4-D may complex with the RNA of mitotic cells. Roychoudbury and Sen (65), using β napthalene acetic acid, and Bendana and Galston (12), using IAA ^{14}C, indicated that intact molecules of the respective auxin materials combined directly with the RNA in plant cells.

As the results of this entire study are considered in view of the causes for or lack of resistance of winged elm to 2,4,5-T, it is found that there is a small but significant decrease in translocation in the older leaves which appears to correlate with the respiration rate and the iron content of these leaves. This suggests that greater translocation and ultimate kill of the winged elm tree might be accomplished by applying 2,4,5-T primarily to the younger leaves located at the extremities of the limbs. The environmental factors of soil moisture and air temperature caused large variations of herbicidal movement in winged elm. Soil moisture at near field capacity and air temperature at the daily ranges of 70's and 100's greatly enhanced translocation of 2,4,5-T in winged elm and, thus, may have a decided effect on the kill of this species by the herbicide.

Judging from the intensity of the radioactivity on the chromatographs of the ^{14}C-labeled leaf extracts, a major portion of the 2,4,5-T was broken down during the 24-hour treatment period. Breakdown at this rate could result in detoxification of much of the herbicide and could be a major factor in determining the susceptibility of winged elm to kill by 2,4,5-T.

CHAPTER V

SUMMARY AND CONCLUSIONS

An attempt was made to determine some of the factors affecting absorption and translocation of the herbicide 2,4,5-T in winged elm. The first portion of this study was designed to determine metabolic factors affecting absorption and translocation of 2,4,5-T as related to the variously aged leaves as they were positioned consecutively on the limb from the youngest of approximately four days old at the apex to the older ones of approximately seven weeks old toward the base.

In the first experiment 2,4,5-T-1-^{14}C applied as a single droplet to each consecutive leaf was used to determine the absorption and translocation of 2,4,5-T in variously aged winged elm leaves. Radioassays were made with a liquid scintillation counting method on samples taken at 24 hours after treatment. Absorption, expressed as a percent of the total applied, began as a maximum in the four-day-old leaves and rapidly decreased to the eight- and twelve-day-old leaves. This was followed by a gradual increase to the three-week-old leaves and a subsequent leveling off for the remaining leaves. Translocation from the treated area and from the entire leaf, expressed as a per cent of the total 2,4,5-T-1-^{14}C absorbed into the leaf, began at a maximum rate in the youngest leaves from four days to two weeks old and decreased to the four-week old leaves with a high degree of variability for the remainder through the seven-week old leaves. These differences in absorption and translocation in leaves of various ages were not extensive.

Respiration of the variously aged leaves was at a maximum in the youngest leaves of four days old and steadily decreased to about 30 per cent of the maximum in the four-week old leaves. There was a subsequent leveling off in the remaining leaves.

Translocation of the absorbed ^{14}C-labeled material appeared to be closely associated with the respiration rate of the younger leaves between four days and three weeks of age and to follow the same general trend in leaves to seven weeks of age.

The phosphorus-iron ratio was determined in an attempt to relate a high ratio to a low metabolic status in the leaves. There were no correlations of phosphorus to iron ratios and possible metabolic rates but the iron content closely followed the pattern of respiration rate and is presumed to be associated with various oxidative enzymes of the plant.

The effect of 2,4,5-T on respiration of four- and eight-day-old, four-week-old, and eight-week-old winged elm leaves at 10^{-4}, 10^{-3}, and 10^{-2} molar concentration showed a slight effect only at the 10^{-3} molar concentration in the youngest leaves.

The second portion of the study involved determinations of environmental factors affecting absorption and translocation of 2,4,5-T-1-^{14}C including seasonal variations, temperature, rainfall, and varied soil moisture levels. Leaf treatments and radioassays were conducted as previously described with the addition of autoradiography for determining translocation into the bark.

A study of seasonal variations on absorption and translocation was conducted with treatments at thee-week intervals throughout the growing seasons of 1963 and 1964. The absorption pattern throughout 1963 was highly variable showing a gradual decline throughout the season. The 1964 absorption pattern began low in May with an increase to a maximum in late July and a subsequent decrease from middle August through September. Translocation from the leaf tissue followed the same general pattern as that for absorption in each leaf with translocation during 1963 following a generally level trend.

Autoradiographs of bark samples from the first nine inches of the treated limbs showed translocation to this area during 1963 to be correlated with translocation from the leaf tissue during the first half of the season but no positive correlations were noted in the latter part of the season. During the 1964 season translocation into the bark was roughly proportional to the translocation from the leaves.

Data for air temperature at the location of the 1964 seasonal study indicated that temperature may affect translocation from the leaf tissues. Movement into and out of the leaf tissues was greatest during the higher daily temperature ranges of 70's to 100's. This was probably due to an increased rate of diffusion for the herbicide plus a lowered viscosity of the protoplasm in the plant cells.

Both field and growth chamber studies of the effect of soil moisture on absorption and translocation of 2,4,5-T in winged elm showed absorption to be very little affected by soil moisture stress; whereas, translocation from the leaf tissue and downward into the stems and roots was adversely affected by decreased moisture. Soil moisture stress appeared to have more than a mechanical effect on the leaf tissue as translocation was not immediately restored to the plants which were under water stress and watered at the time of treatment.

Metabolism of 2,4,5-T-1-^{14}C in tissues of the treated area and of the entire leaf was qualitatively determined for variously aged leaves by paper chromatography. Breakdown to two products was observed and the rate of breakdown was very extensive.

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APPENDIX

TABLE V

ABSORPTION OF 2,4,5-T-1-^{14}C IN VARIOUSLY AGED WINGED ELM LEAVES AS PERCENT OF THAT APPLIED

Rep #	Leaf 1	Leaf 2	Leaf 3	Leaf 4	Leaf 5	Leaf 6	Leaf 7	Leaf 8	Leaf 9	Leaf 10	Leaf 11	Leaf 12
I	73.6	63.3	65.0	86.1	69.3	83.9	80.8	43.4	-	46.0	47.3	53.4
II	85.0	50.0	34.2	21.4	32.7	35.0	52.6	-	44.7	43.2	57.9	53.4
III	50.4	24.4	30.1	26.7	33.9	27.5	31.6	56.4	43.6	47.7	42.1	42.5
IV	-	41.7	39.1	56.0	51.9	53.0	66.5	60.5	-	56.8	49.6	44.4
V	49.7	50.4	66.6	58.2	-	60.0	58.9	50.4	52.3	67.8	68.2	67.1
VI	-	30.2	30.7	33.2	22.9	-	35.4	40.2	-	52.8	30.6	30.8
VII	-	34.8	36.2	57.1	20.2	40.8	41.0	33.2	40.3	47.4	22.2	43.9
VIII	57.1	46.9	40.7	45.9	33.4	47.3	49.9	55.0	41.1	32.3	45.6	49.0
IX	51.8	43.7	43.8	49.7	48.7	-	47.1	54.1	59.7	59.0	58.9	55.8
Ave.	61.2 a*	42.8 bc	42.9 bc	48.3 c	39.1 bc	49.6 b	51.5 b	49.1 bc	47.0 bc	50.3 b	46.9 bc	48.9 bc

*Any two averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variance	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	9	8,912.62	990.3	9.71**
Blocks	8	2,371.97	296.5	
Error	78	7,953.51	102.0	
Total	97	19,238.10		

**The required F at the 5% level of probability is 2.48

TABLE VI

TRANSLOCATION OF 2,4,5-T-1-^{14}C FROM THE TREATED AREA OF VARIOUSLY AGED WINGED ELM LEAVES AS PERCENT OF THAT ABSORBED

Rep #	Leaf 1	Leaf 2	Leaf 3	Leaf 4	Leaf 5	Leaf 6	Leaf 7	Leaf 8	Leaf 9	Leaf 10	Leaf 11	Leaf 12
I	58.8	62.0	63.2	88.3	71.7	89.5	88.1	47.6	-	54.1	69.1	66.4
II	63.7	23.6	28.6	17.7	41.2	30.5	25.8	4	35.3	45.1	34.5	17.7
III	43.6	36.8	48.1	50.9	40.4	35.2	32.2	52.8	26.6	35.2	42.9	39.7
IV	-	42.9	29.1	35.1	27.3	20.1	19.8	23.1	-	31.8	24.1	92.0
V	39.2	50.5	56.1	41.0	-	34.3	41.5	51.1	51.6	47.9	51.3	49.6
VI	-	53.9	65.7	56.1	43.6	-	53.1	47.7	-	59.0	22.8	3.8
VII	-	53.4	48.6	79.3	51.9	40.9	29.5	51.5	36.2	50.4	51.3	25.0
VIII	50.2	58.8	60.9	58.8	52.9	60.8	45.2	32.0	29.4	38.6	39.0	51.0
IX	38.0	61.3	45.8	47.8	55.4	-	43.0	39.5	39.8	37.4	56.8	40.6
Ave.	48.9 ab*	49.2 ab	49.6 ab	52.7 a	48.0 ab	44.5 ab	42.0 ab	43.2 ab	36.4 b	44.4 ab	43.5 ab	42.9 ab

*Any two Avarages followed by the same letter are not significantly different at the 5% level pf probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variance	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	11	9,415.93	855.99	4.53**
Blocks	8	1,627.89	203.48	
Error	78	14,723.30	188.76	
Total	97	25,767.12		

**The required F at the 5% level of prebility is 2.48

TABLE VII

TRANSLOCATION OF 2,4,5-T-1-^{14}C FROM VARIOUSLY AGED WINGED ELM LEAVES AS PERCENT OF THAT ABSORBED

Rep #	Leaf 1	Leaf 2	Leaf 3	Leaf 4	Leaf 5	Leaf 6	Leaf 7	Leaf 8	Leaf 9	Leaf 10	Leaf 11	Leaf 12
I	45.2	34.9	39.0	37.0	30.4	42.9	41.3	36.6	-	41.9	63.6	60.4
II	45.7	6.6	17.8	0.0	27.2	21.7	15.7	-	22.5	36.5	23.8	6.1
III	32.5	21.3	39.5	39.7	29.4	18.9	19.9	45.0	17.2	24.5	33.9	32.4
IV	-	18.9	16.8	33.9	17.5	11.1	11.7	14.5	-	21.1	15.9	0.0
V	39.2	50.5	56.1	41.0	-	34.3	41.5	51.1	51.6	47.9	51.3	49.6
VI	-	42.3	51.1	45.4	27.9	-	49.7	44.2	-	56.4	19.2	0.0
VII	-	40.2	38.3	73.3	43.0	36.0	23.1	46.0	31.5	47.6	44.5	19.8
VIII	43.6	53.0	46.9	39.6	35.6	45.4	22.8	25.8	24.3	45.2	32.8	44.8
IX	33.5	54.0	36.3	35.0	28.5	-	37.1	35.3	35.5	33.7	52.2	29.0
Ave	40.0 a*	35.7 ab	37.9 ab	38.3 ab	30.0 ab	30.0 ab	29.2 ab	37.3 ab	30.4 ab	39.4 a	37.4 ab	26.9 b

*Any two numbers followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIENCE OF THE ABOVE DATA

Source of Varience	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	11	9,026.68	820.60	7.12**
Blocks	8	2,352.11	294.01	
Error	78	8,987.07	115.22	
Total	97	20.365.80		

**The required F at the 5% level of probability is 2.48

TABLE VIII

RESPIRATION OF VARIOUSLY AGED WINGED ELM LEAVES AS MICROLITERS OF OXYGEN UPTAKE PER GRAM WET WEIGHT OF TISSUE PER HOUR

Rep #	Leaf 1	Leaf 2	Leaf 3	Leaf 4	Leaf 5	Leaf 6	Leaf 7	Leaf 8	Leaf 9	Leaf 10	Leaf 11	Leaf 12
I	274.76	173.22	-	94.45	94.21	80.70	71.27	80.83	98.15	76.63	95.76	87.08
II	133.88	118.49	98.45	74.42	58.56	52.13	40.79	49.08	54.26	40.81	54.30	45.41
III	107.60	130.50	96.46	79.79	70.88	49.06	49.48	49.02	50.91	38.37	55.50	56.23
IV	126.85	141.71	100.75	81.28	78.40	61.92	46.18	45.65	52.80	33.78	56.96	53.48
V	155.71	110.65	93.92	73.41	67.08	53.28	54.35	51.66	54.47	60.27	49.46	50.69
VI	-	88.21	88.68	82.24	84.14	56.29	57.67	62.01	54.64	51.44	52.83	53.27
VII	155.09	106.89	75.84	75.76	73.08	57.41	55.98	62.15	64.88	50.82	54.80	42.27
VIII	122.32	91.25	86.40	89.50	80.75	68.08	59.66	74.09	60.84	52.94	59.28	67.47
IX	83.27	97.33	89.16	85.80	86.69	67.61	62.32	61.77	61.50	55.48	61.85	56.17
X	135.30	121.86	113.89	88.41	88.12	68.36	64.44	69.80	62.73	59.04	57.58	65.95
Ave.	143.86	118.01	93.73	82.51	78.19	61.48	56.21	60.51	61.52	51.96	59.83	57.80
	a*	a	b	bc	c	d	d	d	d	d	d	d

*Any two Averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIENCE OF THE ABOVE DATA

Source of Variation	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatments	11	84,511.52	7,688.32	31.77
blocks	9	17,122.24	1,902.47	
Experimental Error	97	23,542.00	242.70	
Total	117	125,235.75		

**The required F at the 5% level of probability is 2.47

TABLE IX

RESPIRATION OF WINGED ELM LEAF PUNCHES AFTER
TREATMENT WITH VARIOUS CONCENTRATIONS OF 2,4,5-T

Molar 2,4,5-T	Rep. No.	µl O_2 uptake/gm fr wt/hr		
		Leaf 1 + 2	Leaf 7 + 8	Leaf 13 + 14
0	I	322	180	212
	II	349	193	233
	III	209	181	152
	Ave	293	184	199
10^{-4}	I	244	200	126
	II	390	134	197
	III	280	153	190
	Ave	304	162	171
10^{-3}	I	423	180	174
	II	352	203	199
	III	316	195	161
	Ave	364	193	178
10^{-2}	I	371	216	137
	II	306	175	178
	III	241	181	173
	Ave	306	191	163

Table X

IRON CONTENT OF WINGED ELM LEAVES AS MICROGRAMS OF IRON PER MILLIGRAM DRY WEIGHT OF LEAF TISSUE

Rep #	Leaf 1	Leaf 2	Leaf 3	Leaf 4	Leaf 5	Leaf 6	Leaf 7	Leaf 8	Leaf 9	Leaf 10	Leaf 11	Leaf 12
I	.057	.028	.029	.028	.029	.037	.044	.036	.054	.042	.035	.053
II	.081	.047	.067	.038	.028	-	.030	.028	.037	-	.035	.030
III	.064	.027	.026	.022	.023	.028	.029	.028	.036	.023	.028	.031
IV	.153	.087	.036	.072	.030	.022	.016	.020	.019	.025	023	.026
V	.024	.017	.019	.016	.019	.016	.019	.019	.021	.024	.033	.023
VII	.205	.038	.029	.020	.022	.019	.023	.022	.026	.032	.026	.029
VIII	.088	.045	.092	.029	.043	.029	.034	.031	.025	.026	.025	.031
IX	.049	.066	.039	.047	.043	.042	.039	.037	.029	.039	.038	.042
X	.059	.035	.018	.019	.023	.027	.026	.029	.027	.037	.028	.058
Ave	.087 a*	.043 b	.039 b	.032 b	.029 b	.028 b	.029 b	.028 b	.030 b	.027 b	.030 b	.036 b

*Any two averages followed by the same letter are not significantly different at the 5% level of probability

ANALYSIS OF VARIENCE OF THE ABOVE DATA

Source of Variation	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatments	11	.029283	.002662	6.81**
Blocks	8	.008341	.001043	
Error	86	.033591	.000391	
Total	105	.071215		

** The required F at the 5% level of probability is 2.48

TABLE XI

PHOSPHORUS CONTENT OF WINGED ELM LEAVES AS MICROGRAMS OF PHOSPHORUS PER MILLIGRAM DRY WEIGHT OF LEAF TISSUE

Rep #	Leaf 1	Leaf 2	Leaf 3	Leaf 4	Leaf 5	Leaf 6	Leaf 7	Leaf 8	Leaf 9	Leaf 10	Leaf 11	Leaf 12
I	.884	.696	.495	.396	.345	.315	.279	.254	.263	.225	.214	.225
II	1.330	.781	.567	.416	.363	.333	.293	.270	.264	-	.236	.219
III	.850	.673	.380	.276	.252	.281	.233	.231	.205	.202	.201	.203
IV	.905	.439	.454	.326	.298	.257	.266	.215	.263	.265	.213	.187
V	.904	.681	.530	.394	.354	.299	.268	.245	.244	.241	.213	.237
VII	.700	.461	.372	.319	.246	.223	.235	.225	.240	.188	.198	.201
VIII	.784	.616	.463	.417	.342	.343	.280	.271	.245	.254	.234	.208
IX	.722	.543	.331	.397	.336	.340	.298	-	-	-	.221	.249
X	.943	.544	.386	.312	.284	.284	.278	.244	.209	.197	.179	.180
Ave.	.891 a*	.604 b	.442 c	.361 cd	.313 cd	.297 cd	.270 d	.244 d	.241 d	.225 d	.212 d	.212 d

*Any two numbers followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIENCE OF THE ABOVE DATA

Source of Variation	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatments	11	2.273925	.206720	8.60**
Blocks	8	.189975	.023747	
Error	85	2.044279	.024050	
Total	104	4.508179		

**The required F at the 5% level of probability is 2.47

TABLE XII

PHOSPHORUS IRON RATIO OF WINGED ELM LEAVES

Rep #	Leaf 1	Leaf 2	Leaf 3	Leaf 4	Leaf 5	Leaf 6	Leaf 7	Leaf 8	Leaf 9	Leaf 10	Leaf 11	Leaf 12
I	15.5	24.9	17.1	14.1	11.9	8.5	6.3	7.1	4.9	5.3	6.1	4.2
II	16.4	16.6	8.5	10.7	13.0	-	9.8	9.6	7.1	-	6.7	7.3
III	13.3	24.9	14.6	12.5	10.9	10.0	8.0	8.2	5.7	8.8	7.2	6.5
IV	5.9	5.0	12.6	4.5	9.9	11.7	16.6	10.7	13.8	10.6	9.3	7.2
V	37.7	36.3	27.9	24.6	18.6	18.7	14.1	12.9	11.6	10.0	6.5	10.3
VII	3.4	12.1	12.8	16.0	11.2	11.7	10.2	10.2	9.2	5.9	7.6	6.9
VIII	8.9	13.7	5.0	14.4	7.9	11.8	8.2	8.7	9.8	9.7	9.4	6.7
IX	14.7	8.2	8.5	8.4	7.8	8.1	7.6	-	-	-	5.8	5.9
X	16.0	15.5	21.4	16.4	12.3	10.5	10.6	8.4	7.7	5.3	6.4	3.1
Ave	14.64 ab*	17.46 a	14.26 ab	13.51 abc	11.50 bcd	11.37 bcd	10.15 cde	9.47 de	8.72 de	7.94 de	7.22 e	6.45 e

*Any two averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIENCE OF THE ABOVE DATA

Source of Variation	Degree of Freedom	Sum of Squares	Mean Squares	
Treatments	11	1691.09	153.73	11.73**
Blocks	8	1510.97	188.87	
Error	83	1087.09	13.10	
Total	102	4289.15		

**The required F at the 5% level of probability is 2.47

TABLE XIII

ABSORPTION OF 2,4,5-T-1-^{14}C BY THE TERMINAL LEAF THROUGHOUT THE 1963 GROWING SEASON AS PER CENT OF THAT APPLIED

Rep	May 30	June 22	July 13	Aug. 2	Aug. 28	Sept. 13	Oct. 3
I	78.5	45.4	52.5	19.6	61.9	19.6	18.0
II	60.6	40.0	45.3	73.3	51.8	26.0	43.1
III	96.3	37.7	60.1	25.0	59.6	22.8	17.5
IV	86.6	61.7	67.7	31.0	70.0	18.0	24.0
V	90.0	34.3	70.3	72.1	44.8	64.6	26.4
VI	90.1	45.5	66.2	32.7	49.9	31.4	53.5
Ave	83.7 a*	44.1 cd	62.2 b	42.3 cd	56.3 bc	30.4 d	30.4 d

Any two averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variance	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	6	13,110.50	2,185.08	10.25**
Blocks	5	1,020.00	204.00	
Error	30	6,397.91	213.26	
Total	41	20,528.41		

**The required F at the 5% level of probability is 2.53.

TABLE XIV

TRANSLOCATION OF 2,4,5-T-1-^{14}C FROM THE TERMINAL LEAF THROUGHOUT THE 1963 GROWING SEASON AS PER CENT OF THAT ABSORBED

Rep	May 30	June 22	July 13	Aug. 2	Aug. 28	Sept. 13	Oct. 3
I	89.7	72.2	46.8	43.5	75.5	63.7	53.4
II	70.3	48.3	82.2	90.5	96.6	59.6	87.4
III	88.4	39.0	92.1	60.9	91.1	53.1	25.9
IV	81.4	45.2	75.9	36.5	86.9	51.9	23.2
V	96.1	62.2	88.7	97.0	93.0	96.0	79.5
VI	96.0	39.6	87.7	43.6	82.5	88.0	90.3
Ave	87.0 a*	51.1 c	78.9 ab	62.0 bc	87.6 a	68.7 abc	60.0 bc

*Any two average followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variation	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	6	7,187.9	1,198.0	4.21**
Blocks	5	4,257.6	851.5	
Error	30	8,539.2	284.6	
Total	41	19,984.66		

**The required F at the 5% level of probability is 2.53.

TABLE XV

ABSORPTION OF 2,4,5-T-1-^{14}C BY A LATERAL LEAF THROUGHOUT THE 1963 GROWING SEASON AS PER CENT OF THAT APPLIED

Rep	May 30	June 22	July 13	Aug. 2	Aug. 27	Sept. 13	Oct. 3
I	37.7	41.1	66.5	28.8	57.2	79.6	15.9
II	80.7	54.5	76.7	32.7	57.2	16.5	15.9
III	92.1	32.2	79.0	27.7	56.1	16.5	14.2
IV	83.7	57.8	51.0	49.1	56.6	58.3	23.1
V	85.6	43.7	74.5	18.9	46.7	78.4	25.6
VI	84.7	64.7	56.0	84.3	60.3	62.2	77.5
Ave	77.4 a*	49.0 bcd	67.3 ab	40.3 cd	55.7 abc	52.0 bcd	28.7 d

*Any two averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variation	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	6	9,465.2	1,577.5	4.52**
Blocks	5	2,900.6	580.1	
Error	30	10,471.7	349.1	
Total	41	22,837.5		

**The required F at the 5% level of probability is 2.53.

TABLE XVI

TRANSLOCATION OF 2,4,5-T-1-^{14}C FROM A LATERAL LEAF THROUGHOUT THE 1963 GROWING SEASON AS PER CENT OF THAT ABSORBED

Rep	May 30	June 22	July 13	Aug. 2	Aug. 28	Sept. 14	Oct. 3
I	2.9	33.6	89.7	52.1	92.2	88.0	31.9
II	95.1	71.3	94.0	48.3	86.8	61.5	74.8
III	94.3	70.0	96.1	76.4	92.7	66.2	91.5
IV	84.4	35.7	57.7	23.6	82.8	88.4	13.4
V	93.0	55.0	90.8	65.4	92.1	93.4	79.7
VI	86.6	71.8	68.5	98.4	80.4	92.6	94.3
Ave	76.1 b*	56.2 c	82.8 ab	60.7 c	87.8 a	81.7 ab	64.3 c

*Any two averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variance	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	6	5,485.5	914.2	2.15**
Blocks	5	6,637.9	1,327.6	
Error	30	12,742.4	424.7	
Total	41	24,865.8		

**The required F at the 5% level of probability is 2.53.

TABLE XVII

ABSORPTION OF 2,4,5-T-1-^{14}C BY LATERAL LEAVES THROUGHOUT THE 1964 GROWING SEASON AS PER CENT OF THAT APPLIED

Rep	June 15	July 6	July 27	Aug. 17	Sept. 7	Sept. 28
I	31.0	55.8	77.3	61.3	40.3	65.4
II	70.8	57.3	79.3	58.7	38.3	50.6
III	34.4	54.9	81.9	54.1	65.4	52.7
IV	30.3	51.2	81.1	59.1	54.5	53.2
V	33.5	77.9	80.0	47.7	60.2	52.1
VI	33.9	61.2	91.9	57.6	60.7	49.9
Ave	39.9 a*	59.7 b	81.9 c	56.4 b	53.2 b	53.9 b

*Any two averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variance	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	5	22,783.4	4,556.68	63.88**
Blocks	5	954.9	190.9	
Error	25	1,783.3	77.33	
Total	35	25,521.1		

*The required F at the 5% level of probability is 2.60.

TABLE XVIII

TRANSLOCATION OF 2,4,5-T-1-^{14}C FROM THE TREATED AREA OF LATERAL LEAVES THROUGHOUT THE GROWING SEASON AS PER CENT OF THAT ABSORBED

Rep	June 15	July 6	July 27	Aug. 17	Sept. 7	Sept. 28
I	52.6	77.4	83.7	52.4	53.3	66.5
II	34.6	78.2	86.9	69.7	57.7	41.3
III	49.1	76.1	81.2	47.9	36.6	48.1
IV	68.6	78.5	82.5	59.7	62.0	45.6
V	51.6	91.4	79.0	59.5	68.7	51.4
VI	56.9	77.8	87.4	49.7	45.9	54.7
Ave	52.2 b*	79.9 a	83.4 a	56.5 b	54.0 b	51.3 b

*Any two averages followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variance	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	5	26,824.9	5,364.98	71.70**
Blocks	5	374.1	74.82	
Error	25	1,870.6	74.82	
Total	35	29,069.6		

**The required F at the 5% level of probability is 2.60.

TABLE XIX

TRANSLOCATION OF 2,4,5-T-1-^{14}C FROM THE LATERAL LEAVES THROUGHOUT THE 1964 GROWING SEASON AS PER CENT OF THAT ABSORBED

Rep	June 15	July 6	July 27	Aug. 17	Sept. 7	Sept. 28
I	49.0	75.4	78.6	42.6	47.3	36.2
II	33.5	76.6	84.8	65.8	52.4	33.0
III	38.7	74.5	79.5	45.1	28.4	40.6
IV	64.4	76.6	79.4	53.3	53.9	39.0
V	48.9	75.4	74.9	53.8	53.4	46.4
VI	51.3	73.2	64.8	47.2	41.5	49.4
Ave	47.6 b*	75.3 a	77.0 a	51.3 b	46.1 b	40.8 b

*Any two average followed by the same letter are not significantly different at the 5% level of probability.

ANALYSIS OF VARIANCE OF THE ABOVE DATA

Source of Variance	Degree of Freedom	Sum of Squares	Mean Squares	F
Treatment	5	23,733.0	4,746.60	78.94**
Blocks	5	323.9	64.8	
Error	25	1,522.5	60.90	
Total	35	25,579.4		

**The required F at the 5% level of probability is 2.60.

VITA

GENE DAVID WILLS

Candidate for the degree of

Doctor of Philosophy

Thesis: METABOLIC AND ENVIRONMENTAL FACTORS AFFECTING ABSORPTION AND TRANSLOCATION OF 2,4,5-TRICHLOROPHENOXYACETIC ACID IN WINGED ELM

Major Field: Botany and Plant Pathology

Biographical:

Personal Data: Born at Birmingham, Alabama, April 11, 1934. Son of Leonard A. and Jewel (Love) Wills.

Education: Attended grade school at Palmerdale, Alabama; graduated from Tarrant High School, Tarrant, Alabama in 1952; received the Bachelor of Science degree and a commission in the U. S. Army from Auburn University with a major in Agricultural Science in June 1957; received the Master of Science degree from Auburn University with a major in Botany and Plant Pathology in June 1962; completed requirements for the Doctor of Philosophy degree in May 1967.

Experience: Captain in the U. S. Army Reserve serving with Reserve components 1952-1967; active military duty 1957-1959, Platoon leader with the First Guided Missile Brigade at Ft. Bliss, Texas; graduate research assistant in the Department of Botany and Plant Pathology and Counselor for men's dormitory at Auburn University, 1959-1962; Graduate research assistant in the Department of Botany and Plant Pathology at Oklahoma State University, 1962-1966.

Member of: Phi Kappa Phi, Gamma Sigma Delta, Sigma Xi, Phi Sigma, Alpha Zeta, and Scabbard and Blade.