mixed in 5 gallons of water. This indicates that it may be desirable, especially when combination sprays are used, to employ the larger volume of water to obtain the maximum degree of selective wetting.

Similar data for 2-methyl-4-chlorophenoxyacetic acid (MCP) and combinations of it with sodium trichloroacetate are presented in Table II. Dow MCP amine (containing 4 pounds of 2-methyl-4-chlorophenoxyacetic acid per gallon as alkanol amine salts) and sodium trichloroacetate 90% were used in preparing the solutions.

Again the mixtures at a given volume had better wetting properties than either herbicide alone. Solutions of the formulation of 2-methyl-4-chlorophenoxyacetic acid employed did not wet as well as solutions of the 2,4-D used in the tests recorded in Table I.

In the above instances, plant physiological, agronomic, and chemical investigations pointed the way toward safe use of a combination of the herbicides.

Substituted Phenols

Dinitro-o-sec-butylphenol and pentachlorophenol are two compounds in this class widely used as herbicides. These chemicals are known as contact herbicides. Translocation of the toxicant does not occur within most plants. Tissues wet with the spray are killed. Thus,

the above-ground parts of plants that are wetted and absorb the toxicant will die, but protected growing points such as underground buds which occur on many perennial plants will regrow. A coarse, low-volume spray may result in only a partial burning of the leaves. Medium to high volume is essential for satisfactory use of these compounds. Timing is also important. Both pentachlorophenol and dinitro-o-sec-butylphenol are most active when atmospheric temperatures are relatively high. When a substituted phenol is used as a salt of the parent compound, in aqueous solution for postemergence selective spraying, one must consider the stage of growth and the physiological condition of the plant. Only young weeds will be adequately controlled by such a spray at a concentration that is safe to the crop. When the plants are in a hardened condition because of slow growth, concentrations must be increased.

Methyl Bromide

This volatile compound is now widely used for killing weed seeds and vegetative organs in plant beds, particularly in connection with tobacco production. Because of the physical properties of the compound, a surface application of the spray is out of the question. Even the conventional soil-fumigant type of application is not successful because of loss of the vapors from the soil. The liquid

must be released under a gasproof plastic tarpaulin sealed with soil at the edges.

Discussion

The examples cited emphasize the many considerations that must be recognized in choosing the best method of application. The chemist must first consider physical properties and possible formulations. The plant physiologist must understand the nature of plant absorption, translocation, and response, the agronomist and the engineer must take into account many practical problems of field application, and the toxicologist must warn against any practices that might endanger human or animal life. Only by these specialists' working together can the most effective, the most efficient, and the safest application methods be developed.

Literature Cited

(1) Barrons, K. C., and Hummer, R. W., *Agr. Chemicals*, 6 (6), 48 (1951).
(2) Barrons, K. C., Thiegs, B. J., and Watson, A. J., *Down to Earth*, 7 (4), 11 (1952).
(3) Mitchell, J. W., and Brown, J. W., *Botan. Gaz.*, 107, 393 (1946).
(4) Smith, H. H., *Ibid.*, p. 544.

HERBICIDE MECHANISM

Mode of Action Other Than Aryl Oxyalkyl Acids

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The field of weed control by comparison to plant pathology and entomology is still in its infancy. Tremendous developments have accrued in the practical or applied side of this field since the advent of 2,4-dichlorophenoxyacetic acid. Fundamental knowledge regarding the action of the powerful chemicals that have been placed in the farmer's hands has not received due attention. It is only through this fundamental knowledge that further advancement of this field may be brought about.

HERBICIDE SYMPOSIUM

WITH AN INCREASING POPULATION and the concomitant increasing demand for food, we are faced with the prospect of a dwindling supply of arable land upon which to produce our food. Though man may look with covetous eyes on the vast unexplored reaches of the tropics, experts ·on tropical agriculture warn him against depending upon the nearly unmanageable raw soils of these regions coupled with a climate that seriously restricts crop production.

Reluctantly, therefore, he turns to the land resources available, in an attempt to wring from them the last possible drop of production. Great have been the achievements of plant breeders and those concerned with plant nutrition in increasing the production of our arable land, but man still faces the insidious attacks of plant diseases, insects, and weeds. The cost exacted annually by these three pests in the United States has been estimated at over $8 billion or nearly 20% of the total value of agri-

cultural production by the farms of this country.

To stem the onslaught of these rapacious destroyers of man's food supply, the chemist has been called on to provide the armaments of the arsenal. He has responded abundantly, and agriculture has become the second largest customer of the chemical industry. In spite of the present shy, mistrustful attitude of these two industries, it is safe to assert that these two giants will become yet more dependent each on the other.

As the science and technology of agriculture burgeon, there is a trend toward intensification of crop production. This means, of necessity, a concentration of crops of specific types in given areas. Such a condition, though conducive to efficient management and production, ultimately creates a monster in crop pests that threatens to destroy the crop. In order to maintain such a management procedure we are turning increasingly to the use of chemicals not alone for fertilizers, but for control of insects, plant disease, and more recently weeds.

The use of chemicals for the control of undesirable plants has gained wide acceptance. It is estimated that the use of one chemical alone, 2,4-dichlorophenoxyacetic acid, has increased cereal production in the United States by as much as 15% without expansion of crop acreage. The wide usage and acceptance of chemicals for weed control have led to a situation where knowledge of the applied aspects has far exceeded knowledge of the fundamentals.

One of the major areas of deficit in fundamental knowledge is in the realm of basic plant biochemistry. True, one can often apply the knowledge and principles of animal biochemistry to the problems, but frequently they are inadequate or do not apply to plant material.

The early discoveries in chemical weed control involved the use of inorganic compounds or relatively simple organic compounds. It was found that highly ionized solutions of certain salts would exert a differential herbicidal effect on many plants. These salt solutions may be of the plasmolytic type, such as sodium chloride, ammonium sulfate, ammonium nitrate, or calcium chloride, of the cytolytic type, which includes iron sulfate, or of the protein precipitant type such as copper sulfate. Several acids have found herbicidal use, the most practicable of these being sulfuric acid. Very little of this substance is now employed in the United States, but it still finds some use in Europe.

The vagaries of climate affect the effectiveness of all these compounds in destroying unwanted plants. As a rule high temperature, high humidity, and favorable growing conditions are conducive to maximum effectiveness. Uniform and thorough application is an absolute necessity, resulting in the requirement for high volumes of carrier, in this case water, to achieve maximum effectiveness.

Hypertonicity of the solution is essential for plasmolytic salt, which causes an irreversible change of volume of the protoplasm of the cell. On the other hand, ionic strength and ion mobility are of major importance for the effectiveness of cytolytic materials such as iron sulfate and copper sulfate.

The thickness and permeability of the cuticular membrane, which are governed by not only genotypic characteristics but climatic conditions prior to the time of application, could by reason of impenetrability impose severe restrictions upon the effectiveness of these compounds. While it was previously assumed that absorption was primarily through epidermal cells, it has now been shown that the stomata and plasmodesma are important sources of entry of these materials. Once entry has been gained into the intracellular spaces, the hypertonicity of this phase may result in irreversible spatial aberrations of the protein of the protoplasm or in the case of such heavy metals as copper may bring about outright precipitation. Patently then, death of the cell immediately follows.

Toxic doses of the material which bring about death by physical means must be of a high order of magnitude, and, therefore, only that portion of the plant intercepting a lethal dose of the material is affected. Dilution will prevent injury to the remaining portion of the plant.

Sodium Chlorate

Of the many inorganic compounds evaluated as herbicides about 1920, sodium chlorate is one of the few that are still outstandingly effective and frequently used. It is still widely employed as a temporary soil sterilant not only in agricultural land but on rights of way of highways and railroads. Sodium chlorate is highly effective against most classes of weeds when used in the appropriate manner.

Use of this compound is not without attendant dangers and difficulties, in view of the fact that it is a strong oxidant and possesses a degree of mammalian toxicity. In an attempt to overcome the fire hazard, herbicide manufacturers have resorted to admixtures of this compound with hygroscopic agents such as calcium chloride, sodium carbonate, sodium acetate, and borate. The borate mixture has been particularly popular, because the borate not only reduces flammability but also contributes to the phytotoxicity of the resultant mixture.

Various other chlorates have been tested as herbicides, including the calcium, potassium, and magnesium salts. However, for reasons of economy and other factors the sodium salt has proved the most acceptable.

Two factors are of outstanding importance in limiting the effectiveness of sodium chlorate: the solubility of the compound in water and hence its susceptibility to leaching, and soil fertility particularly as related to nitrate content and organic matter content of the soil. Because of its ease of leaching, sodium chlorate should be applied only when moisture is just sufficient to distribute it in the soil. The problem of soil fertility might be overcome through the use of additional amounts of material. In areas of extremely high pH—that is, alkalinity— the effectiveness of this compound is reduced.

Sodium chlorate may be applied as foliage spray, although it is most effective when applied to the soil and absorbed from the soil by the plant roots. When absorbed through the foliage, the material is translocated, in the xylem, whereas organic substances are translocated in the phloem tissues of the plant. Shortly after exposure to sodium chlorate, a general chlorosis of the plant results and if sublethal amounts are used the growth of the plant is retarded.

Little is known about the mechanism of action of sodium chlorate, although it has been postulated that the chlorite or hypochlorite ion is the toxic substance. If this were true, however, the substance should be most effective in a nitrate-rich soil where the chlorate would be reduced by the nitrite ion or by organic matter. It has been demonstrated that plants treated with chlorate are rapidly depleted of their carbohydrates, apparently by the increased rate of respiration, and that the enzyme catalase, which is responsible for destruction of hydrogen peroxide formed by the terminal oxidases of the plant, is severely inhibited by the presence of chlorate.

Arsenic

Arsenic salts or oxides have been used for a number of years as soil sterilants. Arsenic when used correctly has proved to be about the most long-lasting of the inorganic soil sterilants.

Many forms of arsenic have been evaluated as herbicides. As in the case of the arsenophenones, the pentavalent form has a relatively low order of toxicity, and to be effective arsenic must be reduced to the trivalent state. In this form arsenic combines readily with the sulfhydryl groups of the dehydrogenase enzymes, resulting in serious inhibition of respiration.

Arsenic is strongly adsorbed by the colloid of the soil, so that in effect the soil type becomes a limiting factor. As the colloid or clay content of the soil increases, the same dosage of the chemical becomes less and less effective. In a large measure species of plants also become a limiting factor at optimum dosage levels. Thus, plants high in sulfur, such as leguminous plants, Canada thistle, and cruciferous plants, are readily controlled by arsenic, whereas low-sulfur plants such as the grasses are much more tolerant.

Low quantities of arsenic ion can replace phosphate in glycolysis, but in the Krebs cycle slightly greater amounts bring about considerable inhibition.

Phenols

The dinitro alkyl phenols have been extensively used for a number of years as herbicides, but there is a paucity of infor-

mation on their toxic effects. It is well established, however, that the nitrophenols are toxic to a wide variety of organisms ranging from microorganisms through plants and higher animals. The nitrophenols were one of the first organic herbicides to find wide general application. They have been used for selective control of dicotyledonous plants in grain and grass crops and for pre-emergent weed control in large seed crops such as cotton and beans.

It has been known for a number of years that nitrophenols in sufficiently high concentration are protein coagulants, but only recently have the more subtle effects of these compounds on metabolism been demonstrated. Organisms or tissue exposed to the nitrophenols exhibit a high rate of respiration, sometimes as much as twice or three times as great as the untreated; but oxidative phosphorylation under these conditions is nearly inhibited. Moreover, these compounds may inhibit cellular absorption of essential organic metabolites. The nitrophenols and the chlorophenols are capable of selective inhibition of certain flavoprotein enzymes, but many of the metal-containing oxidizing enzymes and dehydrogenases are not affected by these substances.

The structural relationships of phenols to toxicity follow the usual pattern of ortho-para substitution. Thus, the introduction of a nitro group ortho or para to the phenolic group increases the toxicity. The introduction of a second nitro group to give, for example, 2,4-dinitrophenol increases the toxicity even more. A third nitration often results in a decrease in toxicity.

Substitution of an alkyl side chain of a varying number of carbon atoms frequently increases the toxicity of the phenolic molecule. The toxicity of the nitrophenols accruing to the alkyl side chain substitution may be of a specific nature. Thus, methyl substitution may enhance the activity toward one organism whereas another alkyl substituent increases the toxicity to a second organism.

While the free undissociated phenol is thought to be the principal toxicant in a system of phenol, phenylate, and water, the pH optimum, falling between 4.8 and 6.4, has been determined. This is above the pK value of dinitro-o-cresol and gives rise to the speculation as to whether absorption might be the limiting factor. Cations are of considerable importance in the activity of these compounds. Thus, the presence of the ammonium ion tends to favor the activity of the nitrophenols as selective herbicides.

Oils

Little in the way of exact information is available on the precise mode of action of the petroleum hydrocarbons, although they have been employed widely as herbicides in the past few years. Considerable work has been undertaken to relate their structure and composition to their phytotoxicity, but as yet no single index will quantitatively express this relationship. In general, the aromatic hydrocarbons exhibit a higher degree of phototoxicity than comparable alkane products.

In certain plants the hydrocarbons may materially reduce the rate of respiration, and they may also reduce transpiration but again with a differential effect, some plants recovering later.

Substituted Ureas

A recent introduction to the field of herbicides is a class of substituted ureas represented by 3-(p-chlorophenyl)-1', 1'-dimethyl urea (CMU).

CMU. This compound, introduced as a soil sterilant, has demonstrated considerable promise for the control of weedy grasses. This is the first example of an organic compound having sufficient residual effect in the soil to offer promise as a soil sterilant.

p-Chlorophenyldimethyl urea is a white crystalline asymmetrical urea having a water solubility of about 200 p.p.m. at 18° C. Although this substance has no reactive group for covalent bonding, it is strongly adsorbed on colloids. This immediately indicates a limiting factor in effectiveness with respect to soil type. Thus, the material is more effective pound for pound in light soils than in heavy clay soils high in colloids. Moreover, it exhibits a degree of specificity between certain plants, which becomes a serious weakness when it is used as a soil sterilant.

If one treats the soil with this substance and then plants a seed such as mustard or oats, the seed germinates with the subsequent development of an apparently normal seedling. After the seedling has obtained a height of 0.5 to 2 inches, marginal chlorosis develops. This chlorosis is progressive and continues until ultimate death of the seedling, in marked contrast to the action of most other soil chemicals. A similar situation of marginal necrosis and chlorosis develops if an emerged and established plant is exposed to CMU either by soil application or by leaf treatment.

The chlorotic appearance of seedling plants emerging from CMU-treated soil gave rise to the speculation that this substance was in some manner interfering with the nitrogen metabolism of the plant. Patently, it is not known whether this is an *a priori* cause of death or a secondary effect. Investigation of this phenomenon demonstrated that CMU had a marked effect on the nitrogen metabolism of treated plants. Thus, normal plants showed much higher ammonia and nitrate nitrogen than the treated plants, but treated plants showed higher protein nitrogen. Analysis of the protein nitrogen in relation to plant growth revealed that very little additional nitrogen had been laid down from the time of treatment, but growth had been prohibited, so that percentagewise the amount of protein nitrogen was higher than in untreated plants. Further studies indicated that not only was certain metabolism in the plant being interfered with by CMU but nitrate absorption was reduced to a level of less than 50% of that of the untreated plant. The carbohydrate reserve of treated plants was substantially less than that of the control, although it is not known whether this is a reflection of increased respiration or decreased growth.

Absorption of the CMU by the plant is very rapid. One-hour exposures of a single leaf of a bean plant to 30 mg. of CMU resulted in sufficient absorption to cause the death of the plant.

A number of aromatic substituted ureas are active against species of gramineae, but in all cases only the asymmetrical substituted ureas are effective. Thus, symmetrical diphenylurea is ineffective where phenylurea or 1,1-diphenylurea would be slightly active. Substitution on the aromatic nucleus also has a bearing on toxicity. Para substitution is the most active, followed by meta substitution, but ortho substitution reduces the activity to half or less than that of the comparable para substituent.

Carbamates (Aryl) Aryl substituted carbamates have certain configurations in common with the urea compounds, but the two classes of materials diverge widely in their type of activity and mode of action upon the plant. The activity of these compounds as herbicides was first noted in 1929, but it was not until 1945 that advantage was taken of this activity.

The aryl substituted carbamates are narcotic agents, acting as mitotic poisons. Cell division is stopped at the metaphase with resultant nuclear and chromosomal aberrations. Plants affected by these materials exhibit hyperplasia and are much reduced in growth. Normally they are much deeper green in color after treatment with the carbamates.

The specificity of carbamates for germinating grasses has led to their wide scale adoption for control of weedy grasses in legume crops, perennial grasses grown for seed, and more recently in cotton. They are normally used in a range from 4 to 8 pounds per acre applied prior to germination and emergence of the weed to be controlled. The low solubility of these compounds, 100 p.p.m. for isopropyl N-phenyl carbamate and about 80 p.p.m. for isopropyl N-3-chlorophenyl carbamate, imposes severe restrictions upon their use. Moreover, these compounds are highly specific in their action and the plant species on

which the isopropyl *N*-phenyl carbamate is highly effective may not respond to the isopropyl *N*-3-chlorophenyl carbamate.

The deep green color, resulting from treatment with the carbamate, is directly due to an increased amount of chlorophyll in the tissues. Treated plants will contain from 19 to 28% more chlorophyll per unit leaf area or per gram of dry weight than comparable untreated plants. Similarly, the nitrogen content of the treated plant is higher than a comparable control. Whether this is due to growth inhibition with a resultant artifact of high nitrogen content or whether it represents a true nitrogen increase is unknown. On the other hand, reserve carbohydrates of the plant are much lower than the control, although reducing sugars at any given moment will be higher. The respiration of treated seedlings follows a pattern of inhibition followed by a marked stimulation with a gradual decline in respiratory rate over a period of time. In view of the fact that the dehydrogenases of the four carbon acid cycle are nearly completely inhibited with 1×10^{-4} M concentration, this situation is not surprising.

Growth and respiratory inhibition by the carbamates can be nearly completely overcome by inositol. The reversal of growth inhibition and mitotic aberration by an inositol seems to be characteristic of narcotic agents applied to plants. Because most agents causing mitotic aberration exert their greatest effect at the metaphase of cell division, it gives rise to the speculation that the dehydrogenases might be especially important at this stage of cell division.

Aryloxy Alkanol Derivatives

Another herbicide needing considerable attention at this time is sodium 2,4-dichlorophenoxyethyl sulfate. This substance is effective not only on germinating seed but on the dicotyledonous or broad-leaved plants. Water is required to carry the material into the soil, where it is activated by the microorganisms of the soil. It is known that the substance is activated to 2,4-dichlorophenoxyethanol, but whether this is itself the active material or whether it goes through oxidative process to 2,4-dichlorophenoxyacetic acid has not been established. Preliminary work involving chromatography of soil constituents after treatment with the sodium 2,4-dichlorophenoxyethyl sulfate has given evidence that the ultimate active product may be 2,4-dichlorophenoxyacetic acid. The differential selectivity then would be dependent on the relative tolerance of a given plant to the low concentrations of this chemical.

The study of herbicides from the standpoint of use, their mode of action, and the discovery of new compounds presents a whole new array of problems to the chemist. The solubility of the compounds, the organ absorbing the compound, and the form in which the compound is absorbed and translocated are problems of importance. A knowledge of the type of gross action of the material on the plant is essential to study of its mechanism of action on the plant. Thus a contact chemical affords a slightly different problem in biochemical study than the more subtle effect exerted by 2,4-D. In this study it is necessary to consider the organism in its entirety and the manner of presentation of the material. Thus, while the chemical may exhibit Ferguson's principle of nonspecific inhibition, the cytological make-up of two different organisms may give contrasting effects. For example, the carbamates are nonspecific in their inhibition of dehydrogenases, but the location of the dehydrogenase in the cell of a grass plant in contrast to that of an alfalfa plant accounts for selectivity between the two. Such problems as this afford a real challenge in the study of mechanism of action of biologically active compounds.

Acknowledgment

Bibliography

(1) Akamine, E. K., Territory of Hawaii Agr. Expt. Station, *Circ.* 26 (1948).
(2) Albert, Adrien, *Nature*, **165,** 12 (1950).
(3) Albert, Adrien, "Selective Toxicity," London, Methuen & Co., 1951.
(4) Blackman, G. E., *Science Progr.,* **38,** No. 152, 637–51 (1950).
(5) Blackman, G. E., Holley, K., and Roberts, H. A., *Symposia Soc. Exptl. Biol.,* No. 3, 283–317 (1949).
(6) Blackman, G. E., and Roberts, H. A., *J. Agr. Science,* **40,** 62–9 (January–April 1950).
(7) Bonner, James, "Plant Biochemistry," New York, Academic Press, pp. 167–353, 468–90, 1950.
(8) Bucha, H. C., and Todd, C. W., *Science,* **114** (2967), 493–4 (1951).
(9) Carrol, R. B., *Contribs. Boyce Thompson Inst.,* **16,** 409 (1952).
(10) Crafts, A. S., *Botan. Rev.,* **17,** 203–77 (April 1951).
(11) Crafts, A. S., *Hilgardia,* **9,** 437–57 (1935).
(12) *Ibid.,* **16,** No. 10, 459–83 (1945).
(13) Crafts, A. S., *Science,* **101,** 417–18 (April 20, 1945).
(14) Crafts, A. S., and Harvey, W. A., *Proc. Twelfth Annual Western Control Conf.,* pp. 61–9 (1950).
(15) Curtis, O. F., and Clark, D. G., "Introduction to Plant Physiology," p. 752, New York, McGraw-Hill Book Co., 1950.
(16) Dunham, R. S., Crim, R. F., and Vishmeyer, V. G. Univ. Minn. Agr. Ext. Service, *Extension Pamphlet* **168** (1949).
(17) Du Pont de Nemours & Co., Inc., E. I., "80% CMU Weed Killer," Tech. Data Sheet, p. 2, 1951.
(18) Eames, A. J., *Science,* **110,** 235 (Sept. 2, 1949).
(19) Fang, F. C., Logan, A. V., Freed, V. H., Butts, J. S., and Kaworski, E. G., *Arch. Biochem. Biophys.,* **32,** 249–55 (1951).
(20) Fink, D. S., and Stark, F. L., *Crops and Soils,* **2,** 22 (April–May 1950).
(21) Frear, B. E., "Agricultural Chemistry," Vol. 1, Chap. 13, New York, D. Van Nostrand Co., 1950.
(22) Freed, V. H., "Some Factors Influencing the Effectiveness of Soil Fumigants for Weed Control," thesis, Oregon State College, 1948.
(23) Freed, V. H., unpublished data.
(24) Freed, V. H., *Weed,* **1,** No. 1, 48–59 (October 1951).
(25) Freed, V. H., and Baldwin, R. E., "Some Effects of *N(p*-Chlorophenyl) *N',N'*-Dimethylurea upon the Nitrogen Nutrition of Bean Plants," Reno, Nevada, Research Progress Report, 13th West Weed Control Conference, 1952.
(26) Gortner, R. A., "Outlines of Biochemistry," 2nd ed., New York, John Wiley & Sons, 1938.
(27) Grigsby, B. H., Churchill, B. R., Hammer, C. L., and Carlson, R. F., Michigan State College, *Bull.* **214** (1949).
(28) Hawk, P. B., Oser, B. L., and Summerson, W. H., "Practical Physiological Chemistry," 12th ed., Chap. 12, Blakiston Co., Philadelphia, 1947.
(29) Hober, Rudolph, "Physical Chemistry of Cells and Tissues," Blakiston Co., Philadelphia, Chaps. 9, 10, 11.
(30) Hurd-Karrer, A. M. U. S. Dept. Agr., *Tech. Bull.* **911** (1946).
(31) Kansas State Board of Agriculture, Noxious Weeds Division, "Kansas Weed Handbook," February 1950.
(32) Lardy, Henry, ed., "Anderson's Respiratory Enzymes," rev. ed., pp. 227–51, Minneapolis, Burgess Publishing Co., 1949.
(33) Loomis, W. E., and Schull, C. A., "Methods in Plant Physiology," pp. 301–21, New York, "McGraw-Hill Book Co., 1937.
(34) Miller, E. C., "Plant Physiology," 2nd ed., pp. 642–705, New York, McGraw-Hill Book Co., 1938.
(35) Myer, B. S., and Anderson, B. D., "Plant Physiology," 12th printing, p. 696, New York, D. Van Nostrand Co., 1939.
(36) Nightingale, Gordon, *Botan. Rev.,* **3,** 86–161 (1937).
(37) *Ibid.,* **14,** 185–210 (1948).
(38) Norman, A. G., *J. Am. Soc. Agron.,* **40,** 111–19 (1948).

(39) Oklahoma Agr. Expt. Sta., *Bull.* **B-355** (1949).

(40) Rassmussen, L. W., *Plant Physiol.*, **22**, No. 4, 377–92 (1947).

(41) Rosenfels, R. S., and Crafts, A. S., *Hilgardia*, **14**, 71–9 (1941).

(42) Schoenheimer, Rudolph, "Dynamic State of Body Constituents," Cambridge, Mass., Harvard University Press, 1942.

(43) Sexton, W. A., "Chemical Constitution and Biological Activity," Chap. 3, p. 20, London, Spon, 1949.

(44) Simon, A. W., *Nature*, **166**, 343 (1950).

(45) Simon, W. W., and Blackman, G. E., *Symposia Soc. Exptl. Biol.*, No. 3, 253–65 (1949).

(46) Sylvester, E. P., Bakke, A. L., and Staniforth, D. W., Iowa State College, Ag. Ext. Service, *Pamphlet* **140** (March 1949).

(47) Thimann, K. V., and Bonner, W. D., *Ann. Rev. Plant Physiol.*, **1**, 75–108 (1951).

(48) Turner, J. S., *Ibid.*, **2**, 145–68 (1952).

(49) Vlitos, A. J., *Contrib. Boyce Thompson Inst.*, **16**, 435 (1952).

(50) Weintraub, R. L., and Norman, R. G., *Econ. Bot.*, **3**, 289–98 (1950).

HERBICIDES

Their Absorption and Translocation

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Autographs of bean plants treated with radioactive 2,4-D prove that absorption is rapid, that the chemical migrates to the vascular tissues, and that it translocates at rates up to 100 cm. per hour through the stem and into the roots. The epicotyl of young bean plants bends, owing to the presence in it of 2,4-D. Radioactivity decreases in time in the roots and treated leaf; it accumulates up to 72 hours in hypocotyl, epicotyl, and terminal bud. An adequate water supply is required for bending of the epicotyl from 2,4-D but not for translocation through the vascular system. When radio-2,4-D is applied to spots on the bean leaf, much more 2,4-D is absorbed and translocated from spots over the midrib than from spots on the edge or tip of the leaf.

HERBICIDE SYMPOSIUM

IF A HERBICIDE is to kill the cells of leaves after application, it must penetrate the cuticle and move into the mesophyll. To kill stem and root cells at a distance from the foliage to which it is applied, it must migrate across the mesophyll into the vascular system and there move or be carried to the lower portions of the plant. Each of these processes is of both practical and theoretical interest to plant physiologists.

Cuticle

It is common knowledge that the surfaces of leaves are coated with cuticle, a fatty or waxy layer that tends to prevent rapid loss of water vapor.

Figure 1 shows a transverse section of *Photinia* or toyon, a common woody plant of the range lands of the West Coast. The upper epidermis is a distinct layer with well-developed cuticle. The lower epidermis is less strongly cutinized and is punctuated by stomata. Near the center of the section is a small vascular bundle. To enter the phloem which occurs on the lower side of the bundle, a chemical must traverse about 10 cells that constitute epidermis, palisade parenchyma, spongy parenchyma, and bundle sheath.

Figure 2 shows a pear leaf, typical of woody species encountered on the range. This section illustrates the larger veins and here, again, passage of a chemical from the upper epidermis to the phloem involves passage through living cells of several distinct types.

Figure 3 is a section of a wheat leaf, typical of many herbaceous species. Again, movement into the phloem involves passage through the cuticle, migration through cells of several types, and finally release into the phloem tissues.

The lipoid nature of the cuticle is widely recognized and it undoubtedly has played an important role in enabling plants to migrate from water to land and thence to the arctic regions, to the deserts, and to the great array of environments in which plants grow. In a sense, cutinization has enabled plants to take their aquatic environment with them into these various regions. The intercellular air within the stomatal chambers seldom attains a relative humidity much below saturation, for each 1% increment below the 100% level represents a drop of many atmospheres in diffusion pressure deficit of the air, and

mesophyll cells cannot tolerate an intercellular atmosphere below about 98% relative humidity.

Relatively impervious to all polar compounds, the cuticle also prevents the ready inward movement of herbicidal chemicals. What is known concerning its detailed structure?

Figure 4 gives two interpretations of the submicroscopic structure of cuticle as described by Frey-Wyssling (*3*). In the upper view solid lines in the horizontal and vertical directions designate cellulose; dashed lines, pectin. The diagonal grid represents the interlinked cutin chains that make up the lipoid phase. There is no attempt here to represent the actual volumetric relations of these substances.

The lower view of Figure 4 shows the intercalation of cutin wax in the cuticle layer. It is apparent that such walls are made of four distinct substances that may vary widely in composition and in distribution: cellulose, pectins, cutin waxes, and cutin.

Cellulose, fibrillar in nature, is responsible for the tensile strength of the walls. Pectins are amorphous and highly hydrophilic; they account in part for the ability of the walls to retain water.