cides with selective effect by applying them in such a way that they do not come in contact with the plant organs where beneficial insects occur. To realize the most value from these new opportunities of utilizing both pesticides and natural enemies, more extensive research will be necessary. More information is required in order to ascertain which beneficial species will be of most value in maintaining low population densities under conditions as modified by the treatment.

As the absorption, translocation, ultimate distribution, and degradation of the systemic insecticides largely take place within the plant system rather than on the surface, the entomologist will be more dependent on plant physiologists, biochemists, and other plant scientists for most effective use of systemic insecticides. The result should be closer coordination between entomologists and research workers in other plant sciences.

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SYSTEMIC INSECTICIDES

Plant Physiological Aspects of the Use of Systemic Insecticides

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The development of effective methods for the use of systemic insecticides requires consideration of the physiology, biochemistry, and anatomy of the plants on which they are to be used. Permeability, translocation and accumulation, and activation and inactivation are problems in the field of plant physiology in which research work on systemics may be useful to entomologists. As examples of this type of work, investigations are reported in which radioactive tracer–labeled Systox and OMPA have been used. When Systox is applied to the stem or leaves of citrus plants it is translocated both up and down in the phloem at first, but gradually diffuses into the xylem and moves past girdles in the stem. The rate of movement in the phloem was determined to be from 2.5 to 10 cm. per hour.

THE DEVELOPMENT OF SYSTEMIC INSECTICIDES has brought into sharp focus the need for effective cooperation between entomologists and research workers in other fields of biological sciences. The active participation of the plant in the distribution and in some cases in the activity of these materials as insecticides makes it possible for a plant physiologist to contribute to both basic and applied research in the use of systemics.

Permeability of Plant to Insecticide

In the development of materials for use as systemic insecticides consideration should always be given to the physiology and biochemistry of the plants on which they will be used. The first point at which the plant must be taken into account in the selection and development of a systemic insecticide is the permeability of the plant to the material in question, or the rate at which it will pass into the plant tissue. As the insecticide must be present in or pass through living cells before the physical and chemical reactions which make it systemic can occur, the cuticle, the cell wall, and the plasma membrane must be penetrated.

The cuticle is usually highly lipoidal in nature, and thus nonpolar substances may penetrate more rapidly than ones that are strongly polar. However, the cuticle of most plants is interrupted by a variety of openings, such as lenticels, hydathodes, and stomata, as well as cracks and wounds, which may serve as points of entrance for compounds that are not readily soluble in the cuticle. The cell wall usually does not present much of a barrier to the penetration of any substance, being composed of cellulose fibers and pectic materials. The plasma membrane, however, possesses the property of differential permeability, selectively preventing the entrance of certain compounds, while permitting rapid entry of others. This differential permeability may be altered by a variety of external conditions and by the presence of certain foreign substances. In general, the two factors which largely control the rate of penetration of organic molecules into living plant cells are the polarity of the compound and its molecular size (*1*). Highly nonpolar substances usually pass through the plasma membrane more rapidly than polar ones; thus the undissociated form of a compound usually will penetrate more rapidly than its constituent ions. However, small molecules which possess the same oil-water partition coefficients will enter more rapidly than larger ones.

Under some conditions, however, highly polar compounds may penetrate readily, particularly into the roots, where they may be passed into the xylem and be distributed throughout the plant in the water streams moving through xylem vessels. From these vessels, they will diffuse out of the woody tissue into living cells of the leaf or steam and there afford protection against insects. Perhaps the best known example of this type of systemic insecticide is selenium, although many organic compounds may act more or less in the same manner, depending largely on their relative water solubility.

The more nonpolar or oil-soluble compounds which penetrate rapidly into the waxy cuticle of leaves usually will pass through the plasma membrane more readily than polar compounds. Materials of this type may be more effectively used by spraying on part of the leaves, by painting on the trunk, or by bark injection, although they may also be effective by soil application or injection into the xylem of the plant. This type of material, when applied to leaves or bark, is translocated primarily in the phloem, the living cells of the plant, as opposed to the xylem transport, where movement occurs mainly in the nonliving woody cells of the plant.

Another aspect of plant permeability to insecticides is the difference between various tissues and organs of the plant with regard to the ease with which the compound may be taken up. The portion of the plant to which a given insecticide should be applied is probably best determined by experiment. The cultural practices used with the crop and to a certain extent the value of the crop will probably determine the choice of a method of application.

Translocation

A second question is the method by which the compound is translocated within the plant. If a material penetrates into the cells near the site of application, but remains localized in these cells, it is of little value as a systemic insecticide. After it has been determined that a material may be applied to one portion of a plant and be toxic to insects feeding on other portions of the plant, it is desirable to know which tissue is primarily concerned with its transport. The compound which moves readily in the phloem is usually most effective when applied by spraying or by application to the stem. Compounds which move most readily in the xylem, on the other hand, are probably best utilized by application to the soil, if they are not too strongly adsorbed by the soil particles, or by injection directly into the xylem.

It is also desirable to know approximately how rapidly the material is transported in the plant. The rate of passive transport in the transpiration stream in the xylem will depend on the rate of water movement through the plant. Many environmental factors such as light intensity, temperature of the surrounding air, humidity of the air, and amount of soil water available are involved in this transport rate. The active transport in the phloem system will probably be somewhat slower than xylem movement, at least in the early stages. A variety of factors affect the transport of organic molecules in the phloem, temperature probably being one of the most important. As the temperature approaches 0° C., translocation in most plants becomes very slow or ceases altogether (*2, 6*). An interesting factor which has recently been brought out as affecting the translocation of plant growth regulators, but has not yet been extensively studied with systemic insecticides, is the necessity of a carbohydrate reserve. If 2,4-D, for example, is applied to plants held in darkness, no outward movement takes place until the plant is either placed in light or supplied with carbohydrates (*8*). If the same relationship occurs in the use of systemic insecticides, it might be necessary to avoid the application of a systemic during cold, dark weather, if rapid protection were desired.

Many materials, when applied to plants, are distributed throughout the plant, but accumulate preferentially in certain tissues or organs. Thus certain highly fat-soluble compounds tend to reach their greatest concentration in tissues containing the greatest amount of fatty materials. Other compounds, which may be actively concerned with cell division or growth, tend to accumulate in the young, actively metabolizing cells of the stem and flower primordia. Information of this type for a systemic insecticide is necessary for the development of its most effective uses. The optimum situation from the pest-control standpoint is to obtain the greatest concentration in the tissues preferred by the insects which it is desired to control. On the other hand, high concentrations of toxic materials in the portion of the plant which is consumed as food may be very undesirable, particularly if the tissue does not have a system for rapid detoxification of the material.

The effect of accumulation on the plant itself may be important. While the sensitivity of the plant to the compound may be low, if it accumulates in large quantities in certain tissues, the threshold for response may be exceeded and the insecticide may become locally phytotoxic.

Activation of Compound by Plant

The last aspect of the insecticide-plant relationship, and perhaps the most important, is the activation or inactivation of the compound by the plant. Inactivation, which is probably most frequent, will depend on detoxification of the compound by spontaneous reactions with plant materials or by enzyme systems of the plant. A highly effective detoxification system in the plant will reduce the effectiveness of a systemic insecticide very considerably, but the compound must eventually be changed to reduce its toxicity to animals, if the crop is to be used for animal feeding. Therefore, dosage must be worked out for individual varieties of plants, to give the desired protection against insects but still permit the use of the plant for food within the time available.

Activation, where a relatively nontoxic substance becomes highly effective as an insecticide after passage through a plant, is a very interesting problem to the plant biochemist, and the mechanism is probably similar to that in animals. However, this problem is in a very fluid state; no two workers in the field agree exactly as to what happens, or even whether such activation occurs (*4*).

Tracer-Labeled Insecticides

Some of the problems mentioned are being investigated in this laboratory with the use of radioactive tracer–labeled systemic insecticides. It was found (*7*) that P^{32}-labeled octamethyl pyrophosphoramide (OMPA) tended to accumulate more rapidly in young leaf and stem tissues of Black Valentine bean plants than in older ones. After uptake from the soil, this compound moved upward through the stem of bean plants at a rate of about 20 cm. per hour. The application of OMPA to the soil did not appear to be economical, as only 1% of the $OMP^{32}A$ was recovered from the above-ground portions of the plants 120 hours after the solution was applied to pots containing the bean plants. Bioassay of the treated plants showed that

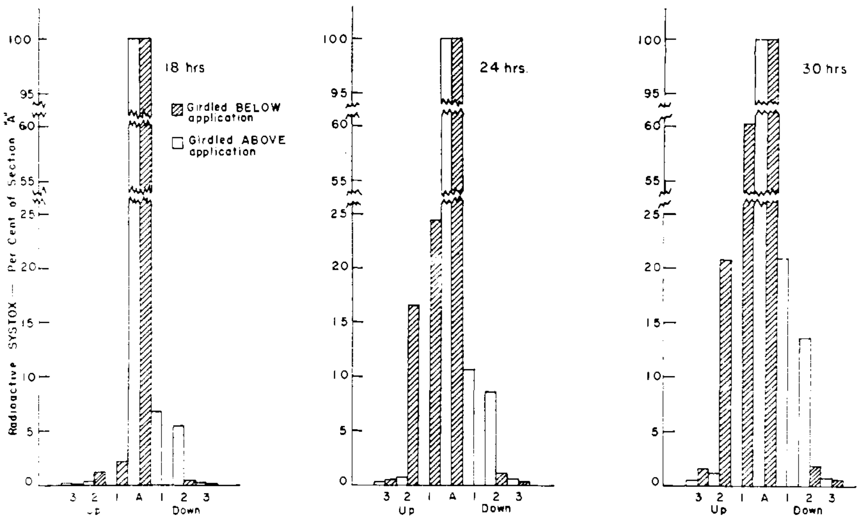

Figure 1. Distribution of S^{35}-labeled Systox in rooted lemon cuttings

Bars represent activities of 1-cm. sections above and below the point of application of radioactive material. White bars, plants girdled above application; shaded bars, plants girdled below application. Activities are expressed as percentages of section A, the one to which Systox was applied.

toxicity to insects was correlated with concentration of active phosphorus-containing materials, and insecticidally inactive breakdown products of the OMPA did not appear until 8 days after the plants were treated. These findings are in general agreement with those of other workers in the field (*3, 5*).

The question of the tissue concerned with translocation of *O,O*-diethyl-*O*-mercaptoethyl thiophosphate (Systox) has recently been studied by means of S^{35}-labeled Systox (provided through the courtesy of Farbenfabriken Bayer, Leverkusen, Germany).

The radioactive Systox was applied to rooted lemon cuttings about 12 inches in height. Plants were selected so as to have a section of stem at least 10 cm. in length which was free of leaves. Girdles were made by removing the bark for a distance of 1 cm. at a point near the center of this 10-cm. section. Half of the plants had 10 μl. of radioactive Systox applied in a band around the stem about 5 mm. above the upper edge of the girdle. The other half had the Systox applied 5 mm. below the lower edge of the excised bark section. Thus the distribution of radioactivity in the plants would show the effect of removing the phloem, both below and above the application point, on the movement of Systox applied to the bark.

After 18, 24, and 30 hours duplicate plants of each treatment were harvested and the stem was cut into 1-cm. sections. The girdled portion of the stem was not used; thus each plant yielded six sections, the one to which the Systox had been applied, *A* in Figure 1, and in the case of plants girdled below the application (represented by shaded bars) three sections on the upper side of section *A* and two below the girdle. The plants that were girdled above the point of application (white bars) had three sections below section *A* and two sections above the girdle. These tissues were homogenized in water with a Potter homogenizer and the active Systox was then taken into a layer of ethyl ether. An aliquot of this layer was dried on a planchet for determination of activity.

The results of this experiment are summarized in Figure 1. On the left is pictured the concentration of Systox in the plants which were harvested 18 hours after application. The activity of section *A* is taken as 100% and the others are calculated as a percentage of this value. The white bars, representing the plant girdled above the Systox application, show that very little activity has moved upward past the girdle, but appreciable quantities have already moved downward. The shaded bars show that only a small quantity of Systox has moved downward past the girdle, while more has moved upward, when unimpeded by an interruption in the phloem. If the girdle is disregarded, there has been a greater movement downward during the first 18 hours of exposure, which included approximately 12 hours of darkness, than in an upward direction. This tendency is reversed after 24 hours, when appreciably more activity has moved upward from the application than has moved downward. The 24-hour data (center), however, still show that very little Systox moves past the girdle, regardless of whether it is located above or below the point of application. The graph on the right shows that after 30 hours the trend is the same; more Systox moves upward from the *A* section than downward, but only a small amount moves past the girdles. The quantity of Systox which has passed the girdle has increased over that found in earlier harvests, and it appears that some of the material must be moving in both directions past the portion of the stem which had the bark removed.

These data indicate that the movement of Systox in lemon plants is primarily in the phloem after its application to the bark. After 24 hours, however, the presence of appreciable amounts of radioactive material in tissues separated from the point of application by a girdle indicates that some must diffuse into the xylem and be transported in this tissue.

Results similar to those reported here have been obtained with the application of S^{35}-labeled Systox to leaves of lemon plants, and P^{32}-labeled OMPA to the leaves of bean plants. In these cases also the first movement is in the phloem, although it may tend to be more rapid in either direction. After longer exposures, some labeled material is found to have passed the girdle, although in experiments continued for 5 days, the movement past the girdle has never equaled the rate of movement in the same direction in an intact plant.

Calculations of the rate of movement of Systox under the conditions of this experiment gave values of 2.5 cm. per hour downward and about 10 cm. per hour upward. This is appreciably lower than the upward rate found in beans with OMPA applied to the soil, but is of the general order of magnitude which has been established for many materials moving in the phloem (*2*).

The experiments with Systox movement reported here, as well as other similar trials, indicate a marked diurnal effect on both direction and rate of translocation. The possibility that this is due to an effect of light is being investigated, and there may be some relationship between the movement of these systemic insecticides and supply of carbohydrate.

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