ABSORPTION AND TRANSLOCATION OF 2,4-DICHLOROPHENOXYACETIC ACID AND P^{32} BY LEAVES[1, 2]

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Foliar applications of nutrient minerals and the increasing use of systemic pesticides have served to reemphasize the importance of absorption and translocation in plant physiology. Studies of the movement of these materials have an immediate application value; at the same time they can aid in the solution of basic problems in plant behavior.

A number of workers (5, 12, 14, 24, 30) have stressed the importance of surfactants in increasing the effects of herbicides applied to leaves. Bryan et al (5) and Hauser (12) showed that the rate of absorption of 2,4-D as well as the total qualtity absorbed was increased by lowering the surface tension of sprays. Some of this effect is due to the better wetting leaves (12, 21) by solutions of low surface tension. However, leaves without surface wax deposits (23) show greater absorption of herbicides when surfactants are added, and additions far beyond those giving minimum surface tension give continued increases in toxicity (24). Weintraub et al (30), for example, found that surfactants increased 2,4-D absorption from alcoholic solutions, even though surface tension was not affected.

Bryan et al (5) and Hauser (12) showed that absorption of 2,4-D was accelerated by rising temperatures, indicating that chemical reactions are limiting the process at some point. The work of Bennett (2) suggests types of membrane changes that might be concerned in this response. Biddulph (3) and Swanson and Whitney (25) showed that P^{32} could be absorbed through leaf surfaces. The latter workers found, however, that this absorption was reduced by the single surfactant tried in their work.

The older work on translocation is reviewed by Curtis (8). More recent work, particularly as it applies to the mass-flow hypothesis, is reviewed by Crafts (6). Translocation of organic molecules, up or down, is normally limited to the phloem, while inorganic substances may move either in the xylem or phloem (17). Many workers find that translocation in the phloem is accelerated by temperature (4, 13, 25, 26), although complicating factors of respiration, fixation, etc., enter the picture at temperatures above about 25° C. Leonard (15) and others (18, 29) have shown that sugars may be exported from leaves against steep concentration gradients.

In the present research we have rechecked earlier experiments on the absorption of 2,4-D and have added experiments on the absorption of P^{32} by leaves and on the translation of 2,4-D and P^{32}. The radioactive element has been used as a check on the results with the herbicide.

MATERIALS AND METHODS

Soybean seedlings were the main experimental material. Uniform plants growing in pots were used when the unifoliolate leaves were mature but before expansion of the trifoliolate leaves had begun. Treatment with 2,4-D usually consisted of wetting 2/3 of one unifoliolate leaf on each plant with a solution containing 750 ppm of Na-2,4-D and 0.1 % of Triton B-1956. Penetration periods were controlled by washing the treated leaves thoroughly after a specified penetration time, typically two hours. The method of washing with a series of water and detergent solutions has been shown (12) to reduce residual 2,4-D on the leaf below that required for a significant effect on the plant. Translocation time was controlled by removing the treated leaf and its petiole after a specified time. Since significant penetration was obtained in two hours while significant translocation from the treated leaves required more than four hours (cf table II), it was possible to separate the effects of temperature, for example, on penetration and on translocation.

The effect of the 2,4-D absorbed (and subsequently translocated) before the treated leaves were washed, or absorbed and translocated before the treated leaves were removed, was measured as a reduction in the growth of the plant parts above the unifoliolate leaves. An experimental unit consisted of two, uniform, treated seedling plants in one four-inch pot. Ten replications, or 20 plants, were commonly used for each treatment. The minimum number of replications was six in a few experiments when a larger number of suitable plants was not available. All data were treated by analysis of variance. Values for least significant differences at the 5 and the 1 % levels ($LSD_{0.05}$ and $LSD_{0.01}$) are given in the tables whenever these values aid in the interpretation of the data. Plumule growth of soybean seedlings is variable under the best conditions and this variability is shown in the relatively large values required for least significant differences.

The P^{32} was obtained as a high specific activity solution (approximately 5 mc/ml) of the phosphate ion in a weak HCl solution at a pH of about 4.5. In general, 1 μc of P^{32} was dissolved in 10 μl of solution and applied with a micropipette to the central area of one unifoliolate leaf on each treated plants. Treated leaves were washed or removed at specified periods after applying the P^{32}, as for experiments with 2,4-D. P^{32} was measured in dried plant briquets by the counting method of Mackenzie and Dean (20). When

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TABLE I

EFFECTS OF 0.1 PERCENT WETTING AGENT ON THE ABSORPTION OF P^{32} WHEN APPLIED IN 20 μL OF SOLUTION

WETTING AGENT	ABSORPTION OF P^{32}	
	EXPT 1	EXPT 2
	cpm	*cpm*
None	7,968	6,421
B-1956	1,112	984
Tween 20	10,073	8,144
Dreft	2,592	2,028
Dodecyl alcohol	4,727	4,870
X-100	8,849	7,489

Expt. 1: LSD$_{0.05}$ = 3,961; LSD$_{0.01}$ = 5,403. Expt. 2: LSD$_{0.05}$ = 3,321; LSD$_{0.01}$ = 4,529.

the quantity of radioactive material of a specific tissue was small, or when the radioactivity was inconveniently high, the radioactive tissue was mixed in known proportions with non-active tissue before forming the briquets. Activity is reported for most experiments in counts per minute for comparable tissues receiving varying treatment. Variations in total activity with treatment, rather than specific activity, gave the information desired in these experiments.

RESULTS

Many workers have shown important effects of surfactants on the absorption of 2,4-D (cf 12 and 30). Swanson and Whitney (25) found no comparable effect on the absorption of P^{32} in an inorganic form. The results in table I show the variable effects of different wetting agents on P^{32} absorption. Some agents, as Triton B-1956, greatly reduced absorption, probably because of the formation of insoluble phosphorus compounds. None of the surfactants tested significantly increased the absorption of P^{32} by soybean leaves. If absorption had been through stomates (11) more effect from some of the wetting agents would have been expected.

TABLE II

ABSORPTION AND TRANSLOCATION OF 2,4-D BY SOYBEAN LEAVES

2,4-D, PPM	EXPOSURE, HRS	FATE OF LEAF AT END OF EXPOSURE	WT NEW GROWTH, GM
None	4	Washed	1.44
None	4	Removed	1.52
500	1	Washed	1.28
500	2	Washed	0.91
500	4	Washed	0.62
500	1	Removed	1.47
500	2	Removed	1.71
500	4	Removed	1.63
1000	1	Washed	1.22
1000	2	Washed	0.62
1000	4	Washed	0.94
1000	1	Removed	1.43
1000	2	Removed	1.60
1000	4	Remived	1.69

LSD$_{0.05}$ = 0.42; LSD$_{0.01}$ = 0.55.

TABLE III

EFFECT OF TEMPERATURE ON ABSORPTION OF 2,4-D DURING A 2-HR EXPOSURE

TREATMENT	TEMP, °C	WT NEW GROWTH, GM
None	15	3.86
None	30	4.35
2,4-D, 750 ppm	15	1.09
2,4-D, 750 ppm	30	0.60

LSD$_{0.05}$ = 0.72; LSD$_{0.01}$ = 1.09.

The general pattern of the absorption and translocation of 2,4-D is shown in table II. When the leaves were washed 1 hr after treatment to remove unabsorbed chemical, the total growth reduction 12 days later was not statistically significant. Reduction was apparent if the 2,4-D was left on the leaves for 2 hrs before washing. These figures indicate rates of penetration into leaves which subsequently remained on the plants so that translocation was limited only by absorption. When the treated leaves were removed at the end of the treatment period, none of the growth figures was lowered significantly, even with 4 hrs and 1000 ppm 2,4-D. Translocation of 2,4-D from these leaves was a slow process, and was not significant 2 hrs after toxic levels of the herbicide had penetrated into the leaves. In subsequent experiments with 2,4-D, 2 hrs was allowed for the absorption of 2,4-D and 24 hrs for translocation from the leaves.

A composite picture of the movement of P^{32} in a soybean plant somewhat larger than those generally used is given by figure 1. One μc of P^{32} was applied to one unifoliolate leaf after the first trifoliolate was partly unfolded. The treated leaf was washed after 2 hrs and the plant was allowed to grow for 1 week, then pressed, dried and radioautographed. The treated leaf was removed before making the exposure to avoid streaking the plate. P^{32} was abundant in the stem, roots and new leaves. It was nearly absent from the untreated unifoliolate leaf and also from the trifoliolate which was partly unfolded at time of treatment. Accumulation was most marked in the bud and in the root tips and branch rot primordia. The reduced movement into older leaves is an indication

TABLE IV

EFFECT OF TEMPERATURE ON ABSORPTION OF P^{32} DURING A 2-HR EXPOSURE

TEMP	ABSORPTION OF P^{32}	
	EXPT 1	EXPT 2
°*C*	*cpm*	*cpm*
15	6,023	2,905
30	5,856	3,275

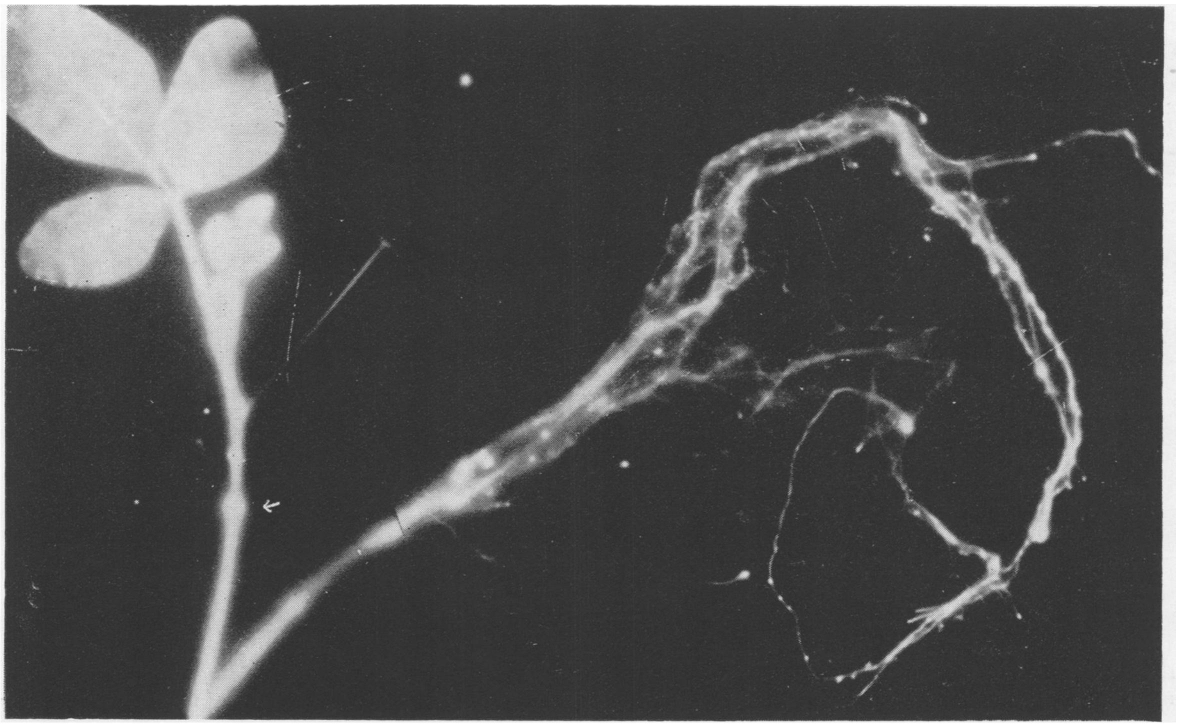

FIG. 1. One μc P^{32} was applied to one unifoliate leaf of a soybean seedling. The treated leaf was washed 2 hrs later, the plant allowed to grow for 1 wk, then pressed dried and radioautographed.

The treated leaf, containing 66 % of the absorbed P^{32}, was removed before autographing. Note near absence of translocation into leaves that were mature (unifoliolate) or partly expanded (first trifoliolate) at time of treatment.

TABLE V

EFFECT OF SUCROSE ON ABSORPTION OF 2,4-D BY CARBOHYDRATE DEPLETED PLANTS

TREATMENT	WT NEW GROWTH, GM
None	1.25
Sucrose, 5 %	1.31
2,4-D, 750 ppm	0.77
2,4-D + sucrose	0.88

that the phosphorus was largely changed to and remained in an organic form, hence did not rise from the roots in the transpiration stream. Exclusion from older leaves agrees with the findings of Leonard (15) and Loomis (18) that translocation of organic materials is polarly outward from older leaves.

The positive effect of temperature on absorption of 2,4-D is shown in table III. The *reduction* in growth at 15° C was 2.77 gm compared to 3.75 gm at 30° C. A temperature differential was maintained only during the 2-hr period immediately after treatment. The treated leaves were then washed thoroughly to remove unabsorbed chemical and the plants were grown together in the greenhouse for 12 days. This result agrees with those obtianed by Bryan et al (5) and Hauser (12), although the response was less striking in this experiment.

The absorption of P^{32} showed no temperature effect (table IV). The absorption of inorganic P^{32} thus differs from the absorption of an organic molecule in being unaffected by both wetting agents and temperature.

Added sucrose had no effect on the absorption of 2,4-D, table V. Light before, but not after, treatment increased absorption of P^{32}. It is not clear whether opening of stomates or electrcial charge of leaves (27) was involved in this effect on P^{32} absorption.

In contrast to the experiments on absorption, the addition of sucrose to carbohydrate depleted leaves increased the translocation of both 2,4-D and P^{32}

TABLE VI

EFFECT OF SUCROSE ON TRANSLOCATION OF 2,4-D FROM CARBOHYDRATE DEPLETED LEAVES

FATE OF TREATED LEAF AT END 24-HR DARK PERIOD	TREATMENT		WT NEW GROWTH
	2,4-D	SUCROSE	
	ppm	*%*	*gm*
Leaf attached	0	5	1.11
Removed	0	5	0.99
Removed	750	5	0.79
Removed	750	0	1.16

$\text{LSD}_{0.05} = 0.24$; $\text{LSD}_{0.01} = 0.33$.

TABLE VII

EFFECTS OF SUCROSE ON THE TRANSLOCATION OF P^{32} FROM CARBOHYDRATE DEPLETED LEAVES OF SOYBEANS

TREATMENT DURING EXPOSURE	SUCROSE	P^{32}
	%	*cpm*
Dark	0	749
Dark	5	4,791
Light	0	15,701

$LSD_{0.05} = 3{,}340$; $LSD_{0.01} = 4{,}683$.

All plants received 1 μc P^{32} in 10 μl of solution. All treated leaves removed after a 24-hr exposure.

(tables VI and VII). For 2,4-D the comparison between plants receiving 2,4-D, with and without added sucrose, was particularly striking. In the experiment with P^{32}, the effect of sucrose was just short of the 1 % level of significance. Light before and after application of the phosphorus gave an even larger effect, presumably because it resulted in a better carbohydrate supply within the leaf. Our results add P^{32} to the list of 2,4-D (9, 16, 22) and Co^{60} (11) the translocation of which appears to depend upon the sugar supply in the leaf. This effect of sugars on translocation has been claimed by Day (9) to indicate mass flow in the translocatoin of 2,4-D, with the herbicide swept along in a translocation stream of sugars. Work by Currier et al (7) raises a serious question of the mechancial feasibility of mass flow. It seems at least equally probable that a high level of carbohydrates may be required to supply energy or materials for some step in the loading (19) or movement of the chemicals. It is significant in this connection that a period of hours was required for the export of measurable quantities of 2,4-D or P^{32} from treated leaves. In contrast, Vernon and Aronoff (26) obtained export of radioactive sugars from soybean leaves within 5 minutes after supplying $C^{14}O_2$ in light.

A separation of the organic and inorganic fractions of P^{32} was made by the trichloroacetic acid method. Analyses showed that inorganic P^{32} applied to leaves was largely transformed to organic compounds within the leaf. Fang and Butts (10) have shown that 2,4-D may form organic combinations within the plant. If translocation is limited or essentially limited to some such combination, sugars could have a controlling effect without the introduction of the mass-flow hypothesis. The work of Wanner (28) suggests, however, that the translocated form of P^{32} is not a sugar phosphate.

TABLE VIII

EFFECT OF TEMPERATURE ON TRANSLOCATION OF 2,4-D DURING A 24-HR PERIOD

TREATMENT	TEMP, °C	WT NEW GROWTH, GM
Check	15	1.89
Check	30	1.86
2,4-D, 750 ppm	15	1.62
2,4-D, 750 ppm	30	1.22

$LSD_{0.05} = 0.23$; $LSD_{0.01} = 0.31$. $Q_{10} = 1.79$.

TABLE IX

EFFECTS OF TEMPERATURE ON TRANSLOCATION OF P^{32} DURING A 24-HR PERIOD

TREATMENT	TEMP	P^{32}	
		EXPT 1	EXPT 2
	°*C*	*cpm*	*cpm*
Treated leaves left on	..	2,878	2,133
Treated leaves removed at end of 24 hrs	15	450	353
" "	30	1,614	1,037

Expt. 1: $LSD_{0.05} = 1{,}004$. Expt. 2: $LSD_{0.05} = 507$. $Q_{10} = 2.21$ (av).

The effects of temperature on the rate of translocation from leaves are shown in tables VIII and IX. The Q_{10} for translocation of 2,4-D, calculated on the reduction of growth of plants treated at 15 and 30° C, was 1.79. This coefficient is in the range of processes limited by chemical reactions, and considerably larger than the value of 1.31 for the change in the viscosity of a 20 % sucrose solution over the same temperature

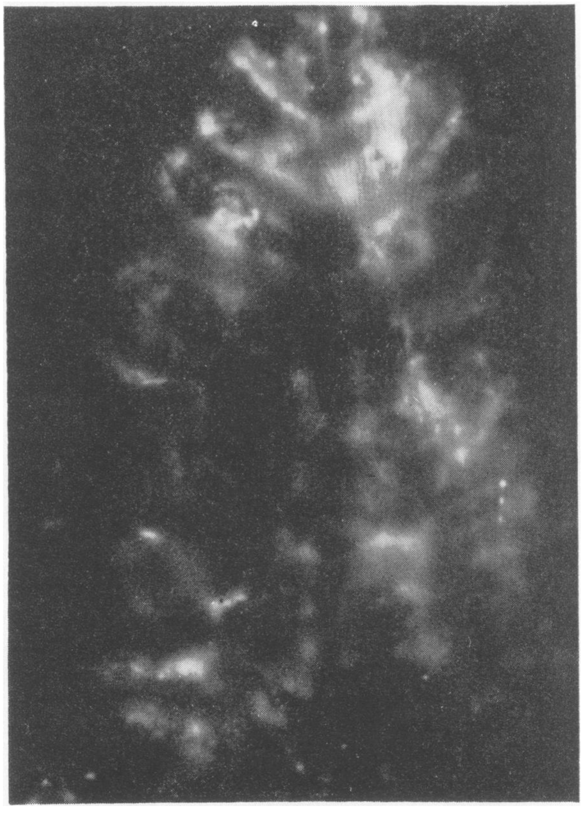

FIG. 2. Radioautograph of excised beet leaf blade washed and frozen 1.5 hrs after painting with P^{32} solution. Irregular penetration and little accumulation of P^{32} in veins.

FIG. 3. Radioautograph of beet leaf blade washed and frozen 6 hrs after painting with P^{32} solution. Heavier penetration than in figure 2 and marked loading of the radioactive phosphorus into the main veins.

range. In the experiments with P^{32} the temperature coefficients, Q_{10}, averaged 2.21, a typical coefficient for an enzymatically controlled chemical reaction. These responses and similar results obtained by others seem to establish the presence of some chemical reaction as the slow step in translocation from leaves. They do not distinguish between reactions changing the form of the translocated materials and respiratory reactions supplying energy for some step in the process.

For a comparison of absorption by leaves and roots, soybeans were grown in culture solutions until the unifoliolate leaves were mature. The culture jars were placed in water baths at 13 and 23° C and the solutions allowed to come to the bath temperatures. 2,4-D at 45 ppm was then added to the solutions and left for 24 hrs. The temperature coefficient for absorption of 2,4-D by roots was just over 1, as measured by subsequent growth of the plants, indicating basic differences in the absorption of 2,4-D by roots and leaves.

The work of Leonard (15) showing the extreme polarization of movement of sugars from sugar beet leaves suggested an experiment with P^{32} on this material. Solutions of P^{32} were painted uniformly over the detached blades of sugar beet leaves (approximately 100 μc per leaf). The blades were then held in moist chambers with the base of the cut midrib dipping in water. After varying periods the leaves were removed, scrubbed to remove surface P^{32} as thoroughly as possible, and radioautographs made of the fresh, frozen leaves at a temperatures of $-20°$ F. Experiments with dried leaves showed a pronounced tendency for equalization of P^{32} throughout the leaves as they dried.

The results of these tests are shown in figures 2 to 5. Figure 2 shows the radioautograph of a blade washed 1.5 hrs after applying the P^{32}, frozen, and radioautographed. Penetration was spotted, and the veins were generally low in radioactivity. The leaf in figure 3 was washed and radioautographed after 6 hrs and shows a very different condition. Penetration had been considerably greater, but, of greatest importance, practically all of the P^{32} in the effectively washed areas of the blade was collected in the main veins. Since these were detached blades, no translocation was involved, and the phenomenon is clearly that which we have called loading (19).

The accumulation of scattered P^{32} molecules into the veins of the leaf requires work, and we assume that respiratory energy is used. Figure 4 shows the accumulation of phosphorus in the veins of a blade normally supplied with carbohydrates and kept in diffuse light for 24 hrs after treating and before washing. Accumulation in all main veins was marked. A

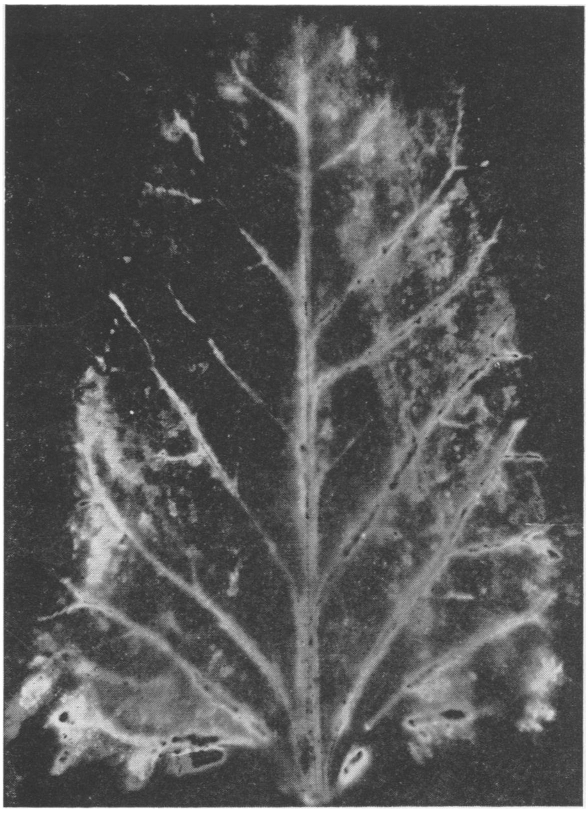

FIG. 4. Loading in a beet leaf blade after 24 hrs. Most of the P^{32} was accumulated in the veins, even though no translocation occurred in this excised blade.

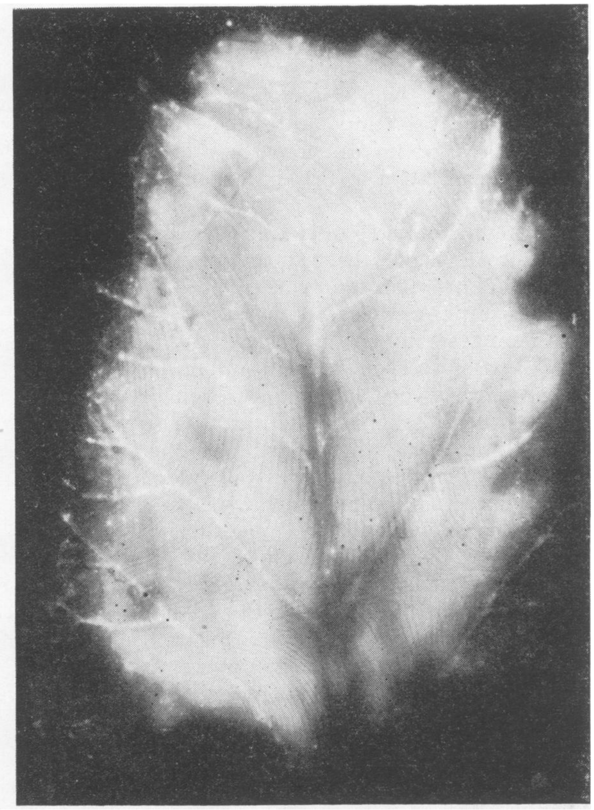

FIG. 5. General absence of loading in a blade low in available carbohydrates. Otherwise the same as figure 4.

paired leaf blade which was covered to exclude light before and after applying P^{32}, and thus to bring about carbohydrate depletion in the leaf, is shown in figure 5. Loading was greatly reduced, particularly in the midrib.

Loading, or some comparable reaction, has been indicated by experiments on polarization of transport from leaves. Leonard (15), Loomis (18) and Wanner (29) have shown that sugars may move out of leaves against diffusion gradients. Wanner found the sugar concentration of the phloem to be 20 × that of the blade and to consist entirely of sucrose, whereas blade sugars were mixed sucrose and reducing sugars. Loading seems clearly to be a concept to be added to our knowledge of translocation, and is an additional complication in an already complicated situation.

SUMMARY AND CONCLUSIONS

The absorption of 2,4-D by leaves is increased by surface active chemicals and by increased temperature. The absorption of inorganic phosphorus showed neither of these responses. The results suggest differences in the mechanism of absorption of an organic molecule and an inorganic ion. Absorption of 2,4-D by roots of soybean plants was not accelerated by a temperature rise of 13 to 23° C.

Radioactive phosphorus pipetted onto one trifoliolate leaf was translocated throughout the plant. Sixteen percent of the P^{32} applied to a leaf had been absorbed in 2 hrs and could not be removed by washing. Of the absorbed P^{32}, 66 % remained in the treated leaf. The remainder was concentrated in the bud and young growing leaves, in the stem above the point of application, and in the roots. Leaves which were mature or considerably expanded at the time of treatment received relatively small quantities of the phosphorus.

Absorption of 2,4-D and P^{32} was not reduced by depletion of leaf carbohydrates. Translocation from the leaves, in contrast, was slowed or stopped. Translocation of both substances showed the temperature coefficients of a chemical reaction, with Q_{10} values on the order of 2. Absorption and movement of either 2,4-D or P^{32} from leaves in significant quantities required more than 2 hrs. Absorption alone required less than 2 hrs. Radioactive photosynthate may move out of soybean leaves within minutes after supplying $C^{14}O_2$ (26). This difference suggests that chemical or physical transformations are required before 2,4-D and P^{32} can be translocated through the phloem of soybean plants. Analyses of leaves treated with P^{32} showed that 80 % of the radioactive phosphorus was present in organic compounds after 24 hrs.

Six hours after painting detached beet leaf blades with P^{32} solution, a large percentage of the phosphorus was concentrated in the veins. Considerable areas of mesophyll were nearly free of radioactive material. This loading of the veins occurred in the absence of translocation from the blade but required a supply of available carbohydrate. Various observations on polar transport from leaves suggest that this loading reaction is a normal and important part of the translocation mechanism.

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GROWTH IN VITRO OF MARIGOLD AND TOBACCO TISSUE WITH NUCLEIC ACIDS AND RELATED COMPOUNDS[1,2]

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With increased recognition of the importance of nucleic acids for growth, the roles of certain acids, of their individual component parts, and of some analogs have needed clarification both for normal and diseased growth.

Concerning normal growth, this interesting viewpoint may be mentioned. As a dicot stem matured, many cells as they differentiated might be in a "straight jacket" so that they could no longer divide unless released. In any case, the encouragement or inhibition of growth by common metabolic chemicals might be approached with tissue cultures.

Concerning diseased situations, tolerances shown by tissues might be critical. This is so whether abnormal amounts of metabolites have occurred through abnormal physiology or because of parasitism. Cellular responses have varied from the normal between such extremes as abnormal cell growth, injury, and necrosis. The encouragement or inhibition of growth by various common sources of nitrogen, carbohydrates, alcohols and organic acids, as well as tolerances for them, have been reported earlier (16).

Some relationships of the nucleic acids in the crown gall disease of plants were reviewed by Braun (1) and by Klein and Link (10). Certain correlations of these materials to cell enlargement, cell division and differentiation in isolated tissues of normal origin were analyzed recently by Skoog (18). Plant tissue that grew in vitro under controlled chemical and physical conditions provided excellent experimental material to examine the metabolic roles of some of these compounds.

Certain of the nucleic acid components added to

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