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CURRENT PROBLEMS IN RESEARCH

Translocation of Particles within Plants

The translocation systems of plants can move particles that vary in size from the ionic to the macromolecular.

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Many kinds of chemicals are absorbed when they are applied to the roots or to the above-ground parts of plants. Once inside, some of these substances are readily translocated from one part of the plant to another. An understanding of these two processes, absorption and translocation, aids in the development of effective and safe methods of using chemicals in crop production. The subject of translocation is of particular interest to food technologists, plant pathologists, physiologists, entomologists, weed research scientists, and those engaged in the commercial production of chemicals that are applied to crop plants.

The present article sets forth some background information about translocation and presents some typical problems that confront investigators engaged in this type of research. Translocation of externally applied substances is viewed here mainly from the standpoint of the ability of plants to translocate particles that vary widely in size, ranging from ions through the relatively large particles exemplified by viruses. It should be emphasized, however, that factors other than size influence the translocation of a compound—for example, the chemical characteristics of a substance or the environment under which the plant exists.

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Ions

Ions, such as potassium and magnesium, usually enter the plant via the roots, but they may also be supplied as a nutrient spray to the above-ground parts, leaves and stems. Movement of ions within the plant may involve different tissues, depending on whether they entered the roots or the leaves.

In considering, first, the movement of ions from the root, it is necessary to consider how the ions entered the root and where they are located. The cell wall, composed primarily of cellulose, may be easily permeated by most substances, and thus ions can readily enter as far as the cytoplasm which lines the inside of the root cells (*1*). At the juncture of the cytoplasm and the cell wall there exists a special structure of the cytoplasm, "plasmolemma," which constitutes a differentially permeable membrane. This three-layered membrane is thought to be a lipoid layer about 50 angstroms thick with layers (each about 70 angstroms thick) of protein on each side which stablize the lipoid layer (*2*). For ions to enter the cytoplasm they must traverse this membrane except where fine strands of cytoplasm, plasmodesmata, extend through the walls of adjoining cells (*1*). The omnipresence of plasmodesmata has not been established, but plasmodesmata have often been found to connect the cytoplasm of contiguous plant cells.

Ions may move into the cytoplasm by diffusion or exchange for ions in the cytoplasm. In most parts of the cytoplasm the ions are considered to be in the "free space"—that part of the tissue or cell that is in free diffusion communication with the environment and without major permeation barriers (*3*, *4*). Ions in this portion of the cell can return readily to the environment or be translocated to the tops of the plants after movement to the xylem (wood) vessels (*5*). Ions enter this area by means of one or more physical processes and do not directly require metabolic energy in order to accumulate.

Lining the vacuole or cell sap, however, is another differentially permeable membrane called the "tonoplast." Movement of ions through the tonoplast apparently depends on the action of "carrier molecules," and accumulation in the vacuole appears to depend on metabolic energy from aerobic respiration (*5*). Metabolic energy is required for the production and maintenance of the carriers, as well as for the "active" accumulation of ions by the vacuole (*5*). Current evidence indicates, however, that ions make essentially a one-way trip when they pass into the vacuole and hence are not free to move to the tops of the plant. It has, therefore, been postulated that the ions which move to the top of the plant are the ones which "escape being absorbed [into the vacuoles] by the roots!"

In the movement of ions upward through the plant, one may therefore be concerned with ions outside the vacuoles—that is, those in the "ap-

parent free space" of the cell. It is generally agreed that the main pathway for the upward movement of ions is the xylem, but there is only speculation as to how and why the ions move across the intervening cells of the root and finally are deposited into the xylem vessels (*1*, *5–7*). It has been suggested that the inner, living cells near the xylem produce a volatile, endogenous inhibitor which prevents accumulation of ions by those cells and actually permits the movement of ions into the xylem vessels (*4*). This hypothesis is in contrast to the older theory which proposed, as an explanation for transfer of ions to the xylem, decreasing oxygen or increasing carbon dioxide concentrations in the innermost cells next to the xylem as compared with the concentrations in the surface cells of the root. Once the ions are in the xylem vessels, they appear to be carried along with water in the "water stream." There are not, however, equal rates of upward movement of ions and of water, and hence it is clearly indicated that water and salt absorption and water and salt movement are independent processes. Under most conditions upward movement of ions in the xylem is rapid, as indicated by the fact that radiophosphorus applied to the roots of tomato plants 6 feet tall appeared at the tips within 40 minutes (*8*). Movement of ten different ions from the roots to the tops of tomato, soybean, and tobacco plants was independent of aerobic mechanisms in the root (*9*).

In the upward movement of ions in the xylem there appears to be relatively little lateral movement. Ions supplied to a given root tend to appear in a branch or branches located directly above that root.

Downward Transport of Ions

Downward movement of ions may occur after the application of nitrogen, phosphorus, iron, magnesium, and some other elements to the foliage. "Foliar nutrition" is currently attracting considerable attention. Ions may also move out of a given leaf if a deficiency of a given element develops elsewhere in the plant or if the leaf becomes senescent. Current evidence, much of it being obtained with radioactive elements or with compounds containing radioactive elements, indicates that movement of ions from leaves is via the phloem. When an ion reaches the stem, it may continue in an upward or downward direction in the phloem (*6*, *10*, *11*). Interestingly enough, if two or more ions are supplied to a leaf, their movements in the phloem of the stem may be in different directions simultaneously or in the same direction, but at different rates (*12*). Such observations immediately raise a question concerning the nature of movement of ions in the phloem, since such phenomena are quite different from the unidirectional "sweeping along" of ions in an upward direction in the xylem. The rate of movement of ions in the phloem is much too rapid to be explained on the basis of simple diffusion (*1*, *13*). Radiophosphorus and photosynthate have been observed to move downward in the phloem at rates of 21 and 100 centimeters per hour, respectively (*13*, *14*).

One of the most plausible explanations for the rapid and even bidirectional movement of ions in phloem is the rapid movement of ions along interfaces. Rates of 20 centimeters per second (almost 0.5 mile per hour) have been observed along liquid-liquid interfaces, and there are many liquid-liquid interfaces and one liquid-solid interface for such movement in each sieve tube of the phloem (*15*). The addition or withdrawal of an ion or any other constituent at any one point immediately sets in motion a redistribution of that ion or constituent throughout the interfaces. Simultaneous, bidirectional movement of two substances, for example, is possible with this type of mechanism (*2*). Bidirectional movement need not necessarily occur in a single sieve tube, since various sieve tubes in a strand of phloem could carry materials in opposite directions (*11*). In cucurbits, where "inner" and "outer" phloem occur, there is evidence that the inner phloem may conduct in one direction while the outer phloem is conducting in the opposite direction (*16*). Seemingly, this movement over interfaces might be involved, although some researchers feel that the entire mechanism of translocation in the phloem is still obscure (*17*).

Admittedly, there are certain observations which are difficult to explain solely on the physical basis of movement over interfaces (*16*). Inasmuch as the sieve tubes of the phloem are living, active metabolism is occurring. Phloem is functional only when alive, and substrate, such as sugar, is essential for these cells. The "integrity" of the protoplasm is undoubtedly altered when phloem cells are killed, and the natural organization of the protoplasm is apparently required for the type of translocation under consideration. It is difficult, however, to rule out a direct relation between translocation of ions and sugar movement. Radiophosphorus and $Co^{60}Cl_2$ move out of leaves only when "sugar" is simultaneously moving out of the same leaf (*18*, *19*). There must remain for the time being, therefore, the possibility that there is more to the mechanism of translocation in the phloem than simple movement of ions and other substances over interfaces.

Ion Movement Related to Translocation of Molecules

One of the newest leads in the problem of translocation of ions in plants is evidence that there may be an interdependence between the movements of certain ions and certain molecular constituents of the plant.

First, there is evidence that the element boron, in the form of the borate ion, facilitates or is required for the movement of sugar in the plant (*20*, *21*). The borate ion forms complexes with hydroxyl-rich compounds such as sugars. Boron increases the respiration rate of carbohydrate-depleted root tips receiving sugar, presumably by increasing the entrance and translocation of sugar to the respiring cells of the root tips (*20*). Particularly for plants in an incipient stage of boron deficiency, the addition of boron to C^{14}-labeled sucrose increases the translocation of the sucrose or C^{14}-labeled photosynthate (*20*, *22*). Boron also enhances translocation of the growth-regulating chemical 2,4-dichlorophenoxyacetic acid from leaves to other parts of plants (Fig. 1) (*23*, *24*). From several corroborative lines of research there is evidence for an effect of the inorganic ion borate on the translocation of an organic molecule, sugar. The explanations for the effect of the borate ion on the movement of sugar molecules are of interest in connection with this discussion of translocation. One explanation for the enhancement of sugar translocation by boron revolves around the fact that when the borate ion complexes with sugar, the complex behaves as a negatively charged "ion" (*21*). Possibly negatively charged sugar "ions" may pass through membranes with greater facility than neutral sugar molecules.

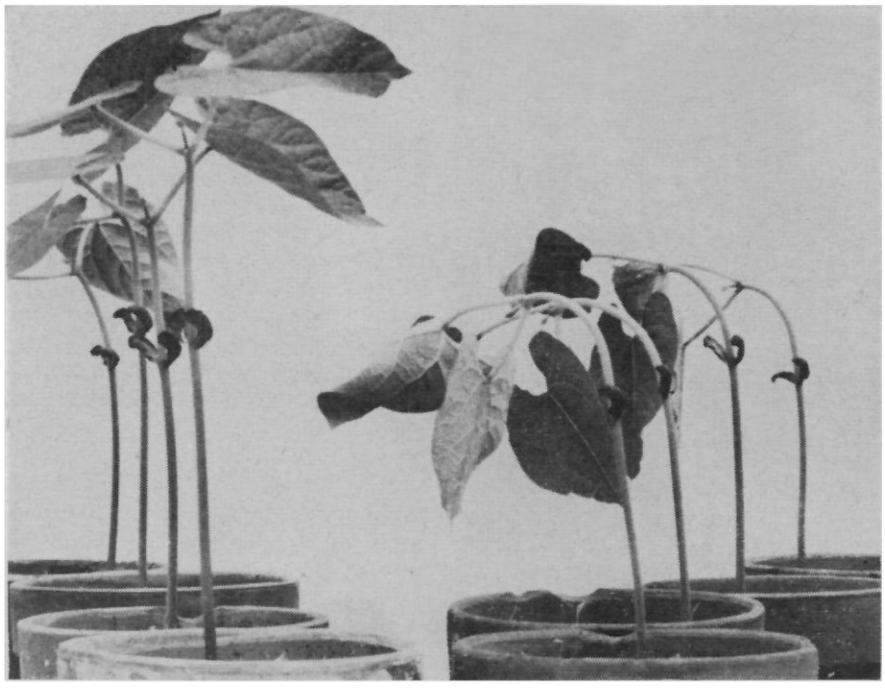


Fig. 1. Stem curvatures of carbohydrate-deficient bean plants due to application of a plant-growth-regulating chemical, sugar and boron, to the right leaf of each plant (right row) compared with curvature induced by the application of the regulator and sugar without boron (left row). The curvature indicates that translocation of the regulator, which is associated with sugar transport, was accelerated by the addition of boron.

The second explanation is that the borate ion is affixed to the differentially permeable membranes of the cell and that sugar molecules pass through the membranes over these "boron sites," with these loci or sites acting essentially as "carriers" or "assisting carriers" already present in the membrane (*21*).

Secondly, there is evidence that the interdependence between an inorganic ion and an organic molecule may be in the opposite direction, in that sugar molecules may affect the movement of foliarly applied radioactive $Co^{60}Cl_2$ (*19*). This relationship was demonstrated with carbohydrate-starved plants in the dark, and hence the effect of sugar on movement of Co^{60} may suggest only that respiratory energy is directly or indirectly required for translocation by the phloem rather than that the more specific types of action postulated for the effect of the borate ion on sugar movement occur.

Molecules

Molecules, some many times the size of inorganic ions, are sometimes readily absorbed when applied to the roots or the aerial parts of plants, then translocated in amounts that can affect either the plants themselves or insects and pathogenic organisms as these attack the plants. That aerial parts of plants can absorb effective amounts of various organic substances is evident when we realize that the usefulness of growth-regulating compounds, herbicides, and some insecticides depends on the ability of stems and leaves to absorb and translocate these chemicals. Several hundred organic compounds are known which have growth-regulating properties when applied to the above-ground parts of plants. Activity of these substances depends on the ability of plants to absorb and translocate the molecules (possibly as ions) of these substances, which are many times the size of the inorganic ions considered above. An understanding of the absorption and translocation of particles of this size is therefore important.

Inorganic substances, such as those considered above, usually dissolve readily in water, and when these substances contact the plant they are generally in relatively dilute aqueous solutions. It is thought, therefore, that these inorganic substances are for the most part subjected to the plant in the form of ions or individual molecules.

A somewhat different situation exists when organic compounds other than salts are applied to the above-ground parts of plants for crop protection or growth regulation. Many of these substances are relatively insoluble in water. Mixed with water, organic compounds such as these are probably dispersed in the water mainly as molecules or as larger particles composed of groups of molecules. Experimental evidence indicates that greatest absorption and translocation of these regulating compounds occur when these substances contact the aerial parts of plants in a nonpolar form and when the molecules are dispersed rather than clumped together (*25, 26*). It is, therefore, assumed that these relatively insoluble organic compounds enter the plant mainly as molecules.

Once within the cytoplasm of cells on the surface of the plant, molecules of the applied substance are apparently translocated through the cells rapidly. The speed is apparent when indoleacetic acid, for example, is placed on the surface of the stem of a young bean or cucumber plant. Curvature will often develop in the stem some distance from the treated area within an hour or two, indicating that movement of the compound even through cells outside the main translocation systems must have been relatively rapid. In roots and leaves, however, the actual distance traveled by the compound in passing through nonvascular tissue before it reaches a vascular system is relatively short. Movement of the substance through these nonvascular cells may be aided by cytoplasmic streaming (*27, 28*) and perhaps by the protoplasmic structures that afford interfaces over which the molecules may move rapidly (*27, 29*).

As far as the whole plant is concerned, lateral movement of molecules (from one side of a stem to the opposite side) of most organic substances absorbed by the plant is relatively limited. For example, many growth-regulating substances induce curvature when applied unilaterally to the stems of plants. The reason is that relatively slow movement of the regulator from the treated side of the stem allows cells on that side to respond to the chemical and to elongate more rapidly than those on the opposite side of the stem, farther from the site of application. One regulating substance, gibberellic acid, is an exception, however, since many kinds of plants are apparently capable of translocating this substance laterally in their stems so rapidly that the compound induces the entire stem to elongate more or less uniformly and without pronounced curvature (*30*).

Both the phloem and the xylem are involved in the vertical translocation

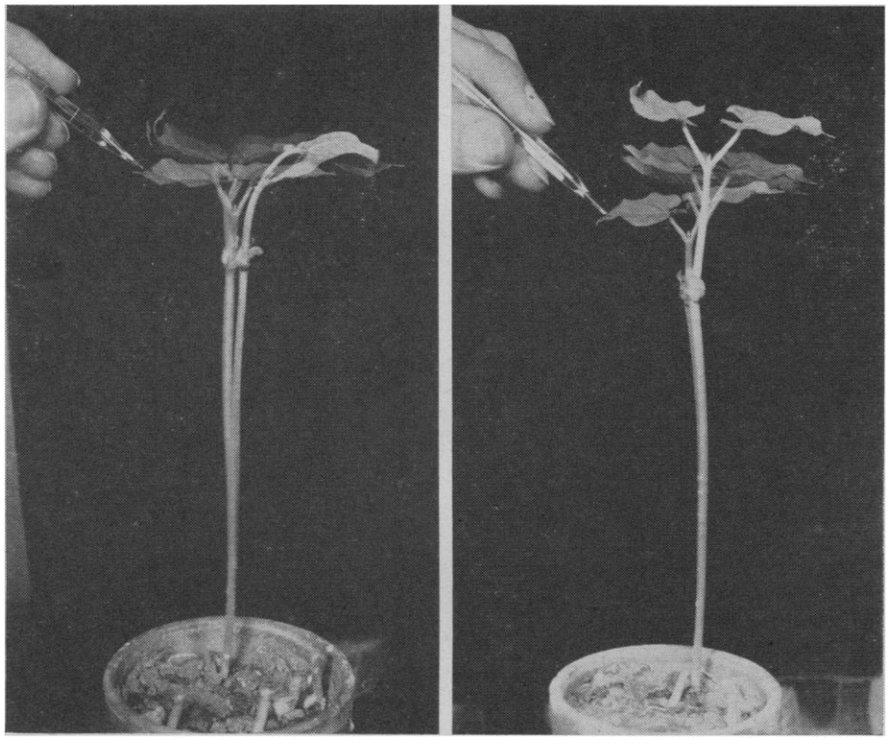


Fig. 2. Stem curvature due to the application of a plant-growth-regulating chemical to one leaf of a carbohydrate-deficient bean plant that was placed in the light (left) as compared with the lack of curvature in a comparably treated plant placed in darkness (right). The response illustrates the importance of light and of the resultant photosynthate in the translocation of regulating chemicals. The multiple photographic exposures of the same two plants were made 4, 8, and 22 hours after treatment to record progressive development of the curvature.

of some kinds of externally applied organic compounds. Many growth-regulating substances, for example, are readily transported downward in plants through phloem. These same substances are also readily translocated upward through the water-conducting tissues (*31*).

Movement of these molecular-size particles vertically in the phloem is thought to be due, on the one hand, to a mass flow somewhat similar to that which exists when a solution flows through a tube (*32, 33*). A second theory holds that movement through phloem involves living protoplasm, as discussed above—a process sometimes referred to as "active transport." In this case the molecules are thought to move through the sieve elements partly, at least, by cytoplasmic streaming. They may also move rapidly over the interfaces that exist within the protoplasm (*28*). It has also been postulated that some molecules can move vertically in the highly hydrated walls of the phloem elements, the activating force in this case being thermal activity of the molecules (*32*).

Some externally applied organic substances move readily upward through the water-conduction system of plants but less readily, or not at all, downward through the phloem. Most antibiotics and some insecticides behave in this way (*34, 35*). For this reason, these substances do not move from leaves to stems of plants as readily as do growth-regulating compounds such as 2,4-dichlorophenoxyacetic acid (2,4-D) and some chlorinated benzoic acids which are readily translocated in phloem. Molecules of all these substances are, however, apparently capable of entering the water-conducting tissue in stems or roots, where, like ions, they are carried upward through the plant in the water stream in biologically effective amounts.

Molecules of an organic compound that enter the stem may move upward fairly rapidly through the plant in the water stream. Radioactively tagged regulating substances have, for example, moved at the rate of 1 foot per minute when traveling upward in the water stream of a a bean stem (*36*). Traveling in this manner, the substance apparently can become rather uniformly distributed within the leaves of a plant. When placed directly in the water stream of a stem, the substance may build up in detectable amounts in the nearby leaves within a few minutes or, if placed on the outside of the stem, within a few hours (*24, 35*). The speed and direction of movement of externally applied organic compounds that enter the plant as molecules of moderate size are, therefore, governed partly by the ability of the plant to translocate the substance in the xylem, in the phloem, or in both tissues.

The downward transport of organic molecules of moderate size in the phloem is a somewhat more complex process than is their upward translocation in the water stream. There is first the requirement that the plant be capable of translocating that particular type of molecule in the phloem, for, as mentioned above, not all organic compounds can move in the phloem of plants in measurable amounts, even under the most ideal conditions. Secondly, translocation of externally applied organic substances from leaves of broad-leaved plants is thought to be associated with the translocation of photosynthate from the leaves (*37*). This relation between movement of photosynthate and movement of absorbed compounds can be easily illustrated by first placing a young bean plant in darkness for about 15 hours to reduce the readily available carbohydrates in its leaves. Application of 2,4-D to a leaf of such a plant will not induce curvature in the stem as long as the treated leaf is kept in darkness, where photosynthesis cannot take place (Fig. 2). Photosynthesis can be prevented, and the same result can be obtained, by illuminating the entire plant but at the same time subjecting the treated leaf to air free of carbon dioxide. When the treated leaf is illuminated and fed air containing carbon dioxide, 2,4-D is then translocated to the stem along with photosynthate and stem curvature develops. The exact nature of the relation between the regulator and the photosynthate is not known.

Mobilization of Absorbed Organic Substances

As molecules of externally applied organic compounds are absorbed and translocated from the site of application, they form a pattern of distribution within the plant. This pattern of distribution is sometimes characteristic of the particular compound. For ex-

Table 1. Distribution of radioactivity (as percentage) after application of 2-iodo^{131}-3-nitrobenzoic acid (INBA) or 2,4-dichloro-5-iodo^{131}-phenoxyacetic acid (2,4-DI) to one primary leaf of each bean plant.

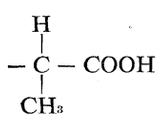
Plant part	INBA	2,4-DI
Terminal bud	60	3
First internode	12	37
Hypocotyl	28	56
Roots	0	4

ample, among those compounds that have growth-regulating properties, 2-iodo-3-nitrobenzoic acid or its metabolites accumulate in greatest amounts in the terminal buds of bean plants after application to the leaves. In contrast, 2,4-dichloro-5-iodo-phenoxyacetic acid or its metabolites accumulate in greatest amounts in the lower stems when applied in a similar manner, and relatively little is found in terminal buds of treated plants (Table 1).

Since the movement of absorbed organic compounds from leaves of broad-leaved plants seems to be closely associated with the movement of photosynthate from the leaves, it might be expected that the mobilization of photosynthate into regions of high metabolic activity in stems might also bring about accumulation of regulating substances in the same place. In fact, regions of high metabolic activity have been artificially created in stems through the application of the appropriate chemical "mobilizer," which stimulates metabolic activity. As a result, a second regulating chemical applied to the leaves was mobilized in the stems at these sites of induced metabolic activity (*26*). Thus, the distribution of 2,4-D, or its metabolites, in the stems of plants was controlled to some extent through chemically induced metabolic activity brought about by use of a second growth regulator, indoleacetic acid. Distribution of the 2,4-D was shifted from the upper part toward the lower part of the plant (Table 2). These results support the concept that the direction of transport of externally applied organic substances, such as growth regulators, is governed to some extent by the location of regions of high metabolic activity and the mobilization and utilization of photosynthate in these areas.

Metabolic activity of the type involved in the storage of carbohydrates and other plant constituents may in some instances also govern the distribution of some organic compounds absorbed by the plant. For example, when a small amount of Amo-1618—a growth-inhibiting regulator that is chemically known as (4-hydroxy-5-isopropyl-2-methylphenyl) trimethylammonium chloride, 1-piperidine carboxylate—is placed on the stem of a young bean plant, the compound is absorbed and apparently translocated very widely throughout the plant. As the plant matures, a sufficient amount of the regulator is translocated into the seeds that develop to alter very noticeably the growth of the generation of plants obtained by planting these seeds (*38*).

The ability of a plant to absorb and translocate molecules of an organic compound applied to its surface is partly, at least, related to the molecular structure of the chemical. Effort has recently been directed toward the identification of some molecular configurations that enhance intake and translocation of certain regulators. It was first learned that α-methoxyphenylacetic acid was somewhat more readily translocated in the stems of bean plants than was a closely related compound, phenylacetic acid. This pointed to the methoxy group, or possibly to a methyl group associated with an alpha carbon, as accounting for the enhanced translocatability. 3-Chloro-isopropyl-N-phenylcarbamate and isopropyl-N-phenylcarbamate were used to test the hypothesis, since these compounds are not readily absorbed and translocated downward by leaves of such plants as barley and oats. Substitution of a "lactic acid" group



for the isopropyl group in each of these compounds resulted in regulators that were apparently very readily absorbed and translocated by leaves of these plants (*39*). The "lactic acid" group is therefore of interest as one possible means of enhancing absorption and translocation of some exogenous compounds that are translocated downward in plants.

Research with α-methoxyphenylacetic acid led to the discovery that the growth regulator and several related compounds are translocated into the roots of plants and then exuded in sufficient amounts to be absorbed by the roots of nearby plants. These substances are then translocated upward by the receptor plant, which may be of the same or of a different species. The receptor plant then responds to the regulator, provided it is sensitive to the compound. Methoxy compounds that behave in this way include *m*-chloro-, *m*-fluoro-, and *p*-fluoro-α-methoxyphenylacetic acids (*40*).

Table 2. Distribution of radioactivity after application of C^{14}-tagged 2,4-dichlorophenoxyacetic acid with and without the use of indoleacetic acid. Results expressed as counts per unit of ground plant tissue.

Plant part	Without indoleacetic acid	With indoleacetic acid
Terminal bud	85	34
First internode	1060	848
Hypocotyl	2384	3289
Roots	410	509

More recently it was discovered that a different family of growth-regulating substances, the chlorinated benzoic acids, also includes compounds that are absorbed by leaves of some herbaceous plants, translocated to the roots, and then exuded in easily detectable amounts (*41*). These substances include 2,3,6-trichloro- and 2,3,5,6-tetrachlorobenzoic acids. The question as to why these methoxy and benzoic acids are exuded from roots while their structural isomers are not provides an interesting problem for future research.

Larger Particles

Plants not only translocate the small inorganic ions and organic molecules just considered but they also readily translocate much larger particles. In this section we shall concern ourselves with viruses exclusively, since translocation of these very large particles has been studied to some extent while essentially nothing is known about the translocation of nonviral particles of comparable size.

The extensive and rapid translocation of viruses within some plants contributes greatly to the severity of the diseases they cause. In many plants, however, some viruses are not translocated very far from the place where they are introduced. Although, in agricultural practice, such plants are considered resistant to these viruses, in reality the plants are highly susceptible. The failure of these "apparently resistant" plants to translocate viruses is thus very often a factor in limiting the damage the viruses cause to crop plants.

Unlike the smaller particles considered above, plant viruses are unable to enter the unbroken surfaces of the plant (*42*). Viruses are, in general, spherical or rodlike. The spherical type

range from about 130 to 1300 angstroms in diameter; the rodlike viruses may have diameters as small as 100 angstroms and are occasionally as long as 50,000 angstroms (*43*). The relatively large size of virus particles appears to explain why they enter plants only through wounds.

The size of virus particles may also have a profound influence on their translocatability. Infectious virus particles, when isolated from the plant, are typically a combination of nucleic acid and protein known as nucleoprotein. Some scientists believe, however, that only a part of this so-called "complete form" is actually translocated from cell to cell. One basis for this view is that virus particles in their "complete form" may be too large to pass readily from cell to cell (*44*). Hypothetically, the translocated forms suggested include relatively small precursory particles which become "complete virus" after transport. These particles may be infectious nucleic acid (*44, 45*). Particles composed of nucleic acid, possibly together with a small amount of protein, cause virus infections at the site of introduction (*46*). It has not been shown, however, that nucleic acid particles after translocation by the plant can cause infection.

As for the detection of virus translocation, it is the "complete virus" particle that is detected. This fact brings up an interesting contrast in the detection of translocation of virus particles and translocation of ions and molecules. When molecules of a substance are applied to leaves, for example, some of these are absorbed and then translocated to other parts of the plant, where they accumulate in concentration to a detectable level. The very same molecules originally absorbed by the leaf are therefore detected when they accumulate in other parts of the plant. On the other hand, when virus particles are introduced into a leaf, these introduced particles are immediately involved in the production of new virus particles. The detection of virus transport is in reality, then, the detection of newly formed virus particles after translocation, infection, and multiplication have occurred.

This indirect measurement of virus transport does not indicate the amount, or the exact rate at which virus is translocated. The method is, however, a very sensitive one. Infection by a single translocated particle, which by itself is not detectable, can presumably result in the production of easily detectable amounts of virus.

There are pitfalls, however, connected with the interpretation of results obtained through this indirect method of detecting virus translocation. For example, the absence of infection after virus transport will generally prevent the detection of any virus movement. Furthermore, the rate of multiplication before, after, or during translocation affects the time required for the detection of transport without affecting necessarily the rate of movement of individual particles.

Pathways Followed by Viruses

In considering the pathways of virus transport, three major interconnected routes are available. Epidermal and parenchymatous cells, interconnected by means of plasmodesmata, provide one pathway (*42*). These cells provide for the translocation of virus particles to vascular tissue in the leaf. In the stem, such cells can provide vertical transport and also lateral transport, which may finally carry the virus to vascular tissue. Movement or spread of virus via this first pathway alone is very slow, even though virus increase occurs concurrently. Virus spread by this means in a leaf may be no more than 2 millimeters per day (*42*). Although higher rates of spread may occur, this pathway is insufficient in itself to provide for the rapid transport of virus throughout the plant.

In the second pathway of transport, the phloem, individual virus particles are transported much greater distances and much more rapidly than in parenchymatous cells (*42*). Particles can move out of a leaf, upward and downward through the stem, and then back into other leaves via the phloem. Virus may pass through long sections of stem without being detectable. Movement of a relatively few particles without intervening infections and virus increase probably explains these results. It has even been suggested that virus may not multiply in sieve tubes, where the rapid long-distance transport is presumed to occur (*47*). In support of this idea, virus *x* of potato was readily transmitted downward through an intermediate section, considered immune from the virus (*48*). The virus could not subsequently be recovered from the intermediate scion.

Phloem provides for the rapid long-distance transport of many plant viruses. Some data indicate that tobacco mosaic virus can move at least 7 inches per hour in tomato stems, and curly top virus at least 60 inches per hour in the phloem of beet leaves (*42*).

Although viruses may be translocated upward or downward in the phloem, there is considerable evidence indicating a correlation between directional translocation of carbohydrates and viruses in the phloem (*42*). As with particles discussed in other sections of this article, the bidirectional and independent movement of some viruses through phloem is suggested (*49*).

A third pathway of transport is the xylem, presumably the water-conducting cells of the xylem; but the xylem has generally been considered unimportant as a pathway involved in the rapid systemic invasion of plants by viruses. There is, to be sure, considerable evidence against the upward translocation of one virus—namely, tobacco mosaic virus—by this route (*50*). On the other hand, Pierce's disease virus moved upward in the xylem of alfalfa at the rate of about 10 inches per hour, and southern bean mosaic virus moved upward in bean plants by this route at the rate of 12 inches per minute (*51, 52*). Other evidence indicates that bean plants do translocate southern bean mosaic virus upward in the dead xylem elements (Fig. 3) (*52*). It is known, then, that at least two viruses are translocated rapidly upward in the xylem. There is also evidence that viruses may differ in their translocatability even after being directly introduced into the water stream (*53*). Whether the size, and perhaps the shape, of different virus particles, as well as other factors, influence their ability to move with the water stream is not known.

The biological interactions between viruses and their hosts influence significantly the distribution of virus. For example, viruses may be more or less restricted to the phloem (curly top virus), more or less restricted to the xylem (Pierce's disease virus), or able to invade most living cells of all plant tissues, including the phloem and the xylem (mosaic viruses) (*42*). Restriction of some viruses to certain tissues does not necessarily indicate the inability of the plant to translocate virus particles to other portions of the plant by the various pathways indicated. Restriction to certain tissues may only indicate the inability of the virus to "survive," infect, or multiply in detectable amounts

in the "noninvaded tissues." Virus distribution may also depend on where the virus is placed, and insect vectors play a role, since different ones feed in different tissues (*54*).

Efforts have recently been made to learn more about the translocation pathways available to virus particles as affected by the site of introduction of the virus. To start with, this study of translocation pathways was carried out by using southern bean mosaic virus and a "local-lesion-responding host" (pinto bean) in which the virus does not ordinarily move far from the inoculated area. With conventional inoculation of southern bean mosaic virus into superficial leaf cells, necrotic lesions a few millimeters in diameter result. The virus multiplies and spreads to some extent, but most of it remains localized in these affected areas. After the inoculated plant grows to maturity, the entire plant (except the inoculated leaf) remains free of detectable virus (*55*). Presumably, under these conditions virus particles do not reach vascular tissues.

The stem is another portion of the pinto bean plant in which superficial cells can be infected with southern bean mosaic virus without extensive translocation of the virus (*56*). Although the spread of this virus after superficial stem inoculation is somewhat more extensive and sometimes more rapid than that after leaf inoculation, the major portion of a mature plant remains free of detectable virus. With the superficial stem inoculation, the virus moves only a few inches from the area where it is introduced (*52*).

When southern bean mosaic virus is introduced deeply rather than superficially into the lower portion of a stem, very rapid translocation of virus occurs (*53*). Infectious particles are then carried several feet upward to the top of the plant, and thus they reach parts not ordinarily invaded as the result of superficial inoculation of the lower stem (*57*). Dead xylem elements are the cells in which this extremely rapid upward translocation occurs. Just how these translocated virus particles finally leave the dead xylem elements and enter living cells is not known. It is evident that a pathway between the dead and the living cells exists, however, since new infections occur in relatively young leaves located in the uppermost part of the plant. No infections occur, however, in the more mature lower leaves, although these also contain translocated infectious virus particles. Some of these particles remain infectious in these mature leaves for at least 2 weeks without multiplication of the virus unless the leaves are wounded to initiate infection (*52*). These results suggest that the virus particles are unable to leave the dead elements in the older leaves although they are able to do so in the younger ones.

By introducing virus particles deeply within the stem, infections initiated many feet above are caused by the particles introduced rather than by new particles formed at the site of introduction (*57*).

Still another technique for virus introduction has been used to study virus translocation. Southern bean mosaic virus may be introduced deeply in the stems of pinto bean plants by means of graft unions. This introduction results in an even more extensive invasion of the receptor bean plant (pinto variety) than is observed when the previously discussed methods of introduction are used. This technique results in rapid long-distance transport of virus particles, probably in the phloem as well as in the xylem of the pinto bean plant (*58*). In this way, the closest approach to a systemic invasion by southern bean mosaic virus in pinto bean has been obtained. Nevertheless, preliminary data indicate that the mobility of southern bean mosaic virus is not as complete as it is in a systemic host, even after virus particles enter both xylem and phloem.

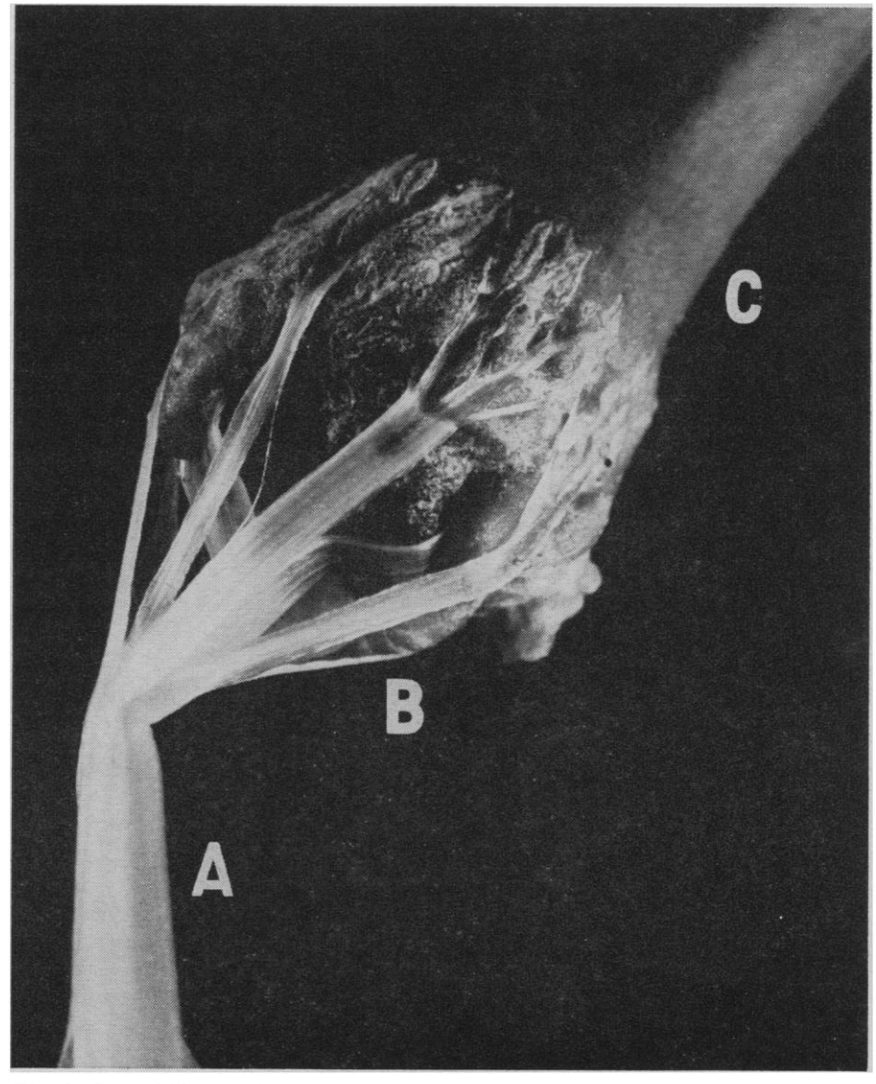


Fig. 3. Steam-killed portion of a bean stem (*A*) connected only by strands that include dead water-conducting cells (*B*) with the upper living portion of the plant (*C*). Southern bean mosaic virus particles passed upward from the lower living part of the plant through (*A*) to (*C*) and above, demonstrating translocation of this virus in the nonliving water-conducting cells.

Summary

To summarize our consideration of translocation, it is evident that plants have very effective translocation systems capable of rapidly moving very small particles, such as potassium ions, which are only about 2 angstroms in diameter, or of moving relatively large particles, some even as long as 20,000 times the diameter of a potassium ion. At the small end of the size scale the dimensions of particles may not influence their translocation, but when particles farther up the size scale (molecules) are involved, dimensions may become more important. At the large end of the size scale (macromolecules), dimensions may be critical. Although we have learned some facts about mechanisms involved in translocation, many questions still remain. The answers that afford an understanding of translocation from a broad viewpoint will necessarily explain how plants translocate particles that vary so widely in size as well as in other characteristics.

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British Achievements in X-ray Crystallography

Knowledge of the precise geometry of molecules opens new possibilities for understanding chemical reactions.

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X-ray crystallography is a technique by which the arrangement of atoms in various types of substances, and particularly in crystals, is deduced by studying the manner in which these substances scatter a beam of x-rays. This study became possible when the German scientist von Laue discovered x-ray diffraction by a crystal in 1912. The rays from a roentgen-ray tube were concentrated in a narrow beam by passing them through a fine hole, and when this beam fell on a crystal, and the scattered rays were recorded by a photographic plate, the photographs showed a symmetrical pattern of spots. Von Laue correctly interpreted this effect as due to the "diffraction" of x-ray waves by the regular pattern of atoms in the crystal.

This discovery was a crucial event in the history of science. In addition to proving conclusively that x-rays are electromagnetic waves like light, and leading to the study of the characteristic x-ray wavelengths emitted by the elements, which played a key part in subsequent research into atomic structures, it made it possible to analyze the structure of matter in a new and very powerful way.

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