PHYSIOLOGY AND TRANSLOCATION OF HERBICIDES

A. S. CRAFTS

Formerly University of California, Davis, U.S.A.

WEED CONTROL in many ways may be considered as applied plant physiology and applied plant biochemistry. Plant physiology has much to offer to weed control research and weed control in turn has contributed much to principles of plant physiology. This paper will consider some of the principles of plant physiology that are generally accepted, and are proving useful in interpreting weed control research.

One of the foremost achievements of modern plant physiology is the solution of the old problem of the mechanism of food movement in plants. Work at Davis with labelled tracers has shown that the mass-flow mechanism of rapid food movement in the phloem is the only one that will account for the distribution patterns obtained. And electron micrography of phloem by Esau has shown that the strands of cytoplasm that traverse the sieve plates are, in their natural state, tubular in nature, and hence will accommodate a stream flow through the sieve-tube lumina.

A second achievement of great significance in weed control is the demonstration that herbicides applied to leaves or stems move in this food stream from regions of synthesis to regions of utilization — that is, from source to sink of foods.

Absorption of herbicides must take place through foliage, that is, leaves and stems, or through roots. Foliar absorption apparently takes place along two routes, a lipoid route, and an aqueous route. Herbicides that enter via the lipoid route are pH limited. Anionic toxicants such as the dinitro compounds and the phenoxy acids move through the cuticle from solutions buffered to the acid side faster and in greater quantity than from neutral or alkaline solutions. This is because the acid reaction presents the parent undissociated molecules which are lipoid soluble for uptake through the cuticle.

Neutral molecules such as amitrole or maleic hydrazide do not respond to pH adjustment but enter most effectively into leaves having a high water content. Under these conditions the water continuum of the plant extends to the surface of the foliage and applied solutions make immediate aqueous contact. This favours rapid and complete uptake of water-soluble molecules.

In entering leaves and stems, herbicides must pass a number of barriers. First is the cuticle, a lipoid layer that presents permeability problems, and that on sclerophyllous plants presents a retention problem for lipoid soluble compounds. For example, an acre of live oak (*Quercus* spp.) or eucalypt (*Eucalyptus* spp.) trees has many pounds of cuticle and a pound or two of a phenoxy acid may well stay in solution in this lipoid layer and never reach the phloem for transport to the roots.

Beneath the cuticle are pectic and cellulosic layers into which the lipoid soluble molecules must pass and move. Dissociation of the acid molecules from buffered herbicide solutions help here. Finally, to enter the living protoplast the herbicide molecules must pass the plasmalemma membrane, the living, active outer layer of the protoplasm that is semi-permeable, and that has powers of

selectivity. Within this membrane a compound may be actively accumulated, it may be moved by protoplasmic streaming, it may be side-tracked into the vacuole, or it may be transported ultimately to the vascular strand for translocation via the assimilate stream.

Movement thus may involve diffusion which is rapid over short distances but which varies inversely as the square of the distance. It may involve protoplasmic streaming which accelerates the rate to a maximum of around 5 cm per hour. It involves transfer from chlorenchyma to border parenchyma to sieve tube which usually includes condensation from hexose sugars to sucrose and a corresponding cycling of phosphate. And, finally, it involves mass flow in mature sieve tubes along a gradient of hydrostatic pressure developed osmotically.

At this point two words that plant physiologists use in discussing translocation might be introduced. The first is symplast, a term which implies that all of the living protoplasm of a higher plant is a physiologic unit of cells, connected by protoplasmic connections in the pits. The other term is apoplast, the non-living cell wall phase which surrounds and contains the symplast. The plasmalemma is the outer limiting membrane surface of the symplast which is in intimate contact with the apoplast and via the apoplast with the environment. By the interaction of osmosis into the symplast and the resistance of the tensile apoplast to expansion, the plant develops turgor which enables it to grow against the force of gravity and to maintain a form favourable to photosynthesis and able to occupy not only the atmosphere but also the soil.

By means of these terms it is possible to distinguish two types of translocation, first symplastic, implying movement within the living system by diffusion and protoplasmic streaming within parenchyma and mass-flow within mature functioning sieve tubes, and second apoplastic movement through cell walls and dead xylem tracheary elements. It is known that foods, certain mineral nutrients, and several herbicides, including 2,4-D, amitrole and picloram, undergo symplastic movement from foliage to roots, shoot tips, cambium tissues and storage organs. It is also known that water, inorganic salts, and many herbicides, including substituted ureas, symmetrical triazines, benzoic acids and picloram, are carried from the roots to the tops by apoplastic movement via the xylem in the transpiration stream.

Next root absorption from the soil will be discussed. Solutes and water taken in by roots may move along cell walls from cortex to stele and ascend the stem in the transpiration stream. This is free space, or apoplastic movement and the principal barrier is the casparian strip of the endodermis. This strip is the barrier which enables the root to develop root pressure, often to a value of two or more atmospheres. It may be by dissolving in and diffusing through this structure that the substituted ureas and symmetrical triazines are so readily passed through roots and transported to tops in the transpiration stream.

Solutes and water, after diffusing through walls of the root hairs and cortical parenchyma, may be accumulated within the symplast. Within the symplast they are transported by diffusion and protoplasmic streaming across the cortex, the endodermis and pericycle and into the ground parenchyma of the stele. Here, because of the low O_2 , high CO_2 status, the solutes may be lost to the apoplast where they move in solution via the tracheary elements of the xylem to the tops. Mineral nutrients, dichloropropionic acid and picloram are examples of solutes that may move in this way.

Several barriers may interfere with uptake by roots and export to the tops. Since an acre-inch of soil may hold from 30,000 to 100,000 lb of water, a pound of chemical applied to an acre of soil as a herbicide is greatly diluted within the soil solution. This means that the gradient from soil to root is low, and diffusion will be slow.

Organic matter and clay colloids of the soil are known to have great capacities for absorption of many types of molecules. By comparing solution cultures of herbicide-treated plants with soil treatments, it is possible to show that toxicity is greatly reduced by adsorption.

Since transpiration is responsible for water movement within the xylem, transpiration rate is important as it determines the quantities of molecules presented to root surfaces for absorption. And so transpiration regulates the velocity of upward movement and thus the relative quantities translocated in comparison with the amounts absorbed *en route*.

A fourth barrier is the plasmalemma of the root cells. This membrane has the ability to discriminate between molecules—for example, potassium versus sodium, monuron versus 2,4-D. And finally the casparium strip, just as it resists leakage from stele to cortex of solution under root pressure, so may it interfere with free movement of molecules from cortex to stele via the apoplast. Molecules of 2,4-D apparently pass this barrier with difficulty if at all; triazines and substituted ureas seem to move through rapidly.

Transport via the transpiration stream is known to occur at velocities of up to 10 metres per hour. Water which makes up the bulk of the transpiration stream moves passively from soil through roots to foliage where most of it is lost to the atmosphere. Solutes, and particularly plant nutrients, are actively accumulated by root cells and moved symplastically into the stele where they leak into the apoplast and join the water in upward movement. Of the herbicides, those absorbed and moved symplastically seem to concentrate in root tips but not to move freely from living cells to apoplast and thence to tops via the xylem. Herbicides that move freely in the apoplast seem able to traverse this phase of roots and ascend readily to the foliage. Protham and 2,4-D are of the former type; triazines and substituted ureas are in the second category.

Finally, it should be emphasized that the phloem and xylem of plants are distribution systems. The function of the phloem is to deliver to all non-green cells those assimilates needed in their metabolism. And the function of the xylem is to distribute inorganic nutrients throughout the plant body and to transport water to growing issues, and CO₂-absorbing leaves so that growth and assimilation can go on in ways advantageous to the plant. The sieve tubes of the phloem are highly specialized cells, specialized for the function of rapid transport of the assimilate stream. They are living cells and so may be thought of as part of the symplast. The tracheary elements of the xylem lose their protoplasts upon maturation and hence are made up of non-living ligno-cellulose wall structures. They are a specialized phase of the apoplast. The functioning of both phloem and xylem are highly dependent upon the metabolic activities of phloem parenchyma, companion cells and xylem parenchyma cells.

Considering now the mode of action of herbicides, these compounds may be divided into two general categories, those that kill locally by contact action, and those that move from the tissues to which they are applied to express their toxic action in some other part of the plant.

Contact herbicides include acids such as sulphuric acid that kill by virtue of their high hydrogen ion concentration which rapidly destroys the plasmalemma membranes thus killing the cells. They include hydrocarbons such as diesel oil or Stoddard solvent that solubilize membranes and render cells permeable and leaky. They include heavy metals such as arsenic and copper that destroy enzyme systems. They include the pyridilium compounds that undergo photochemical change to give free radicals that are violent poisons to plant cells. And they include in-couplers of oxidative phosphorylation which destroy the energy converting systems of plant metabolism; such are the dinitro compounds.

Translocated herbicides include the growth regulators, for example, the phenoxy, benzoic and picolinic acids. These compounds alter the integrated growth processes to produce callous tissues, abnormal secondary roots, deformed leaves and distorted and inhibited terminal meristems. One way they kill plants is to bring about a premature obliteration of phloem and a plugging of the xylem. They include mitotic poisons such as propanil and chlorpropanil which interfere with cell division and destroy meristems. They include a number of compounds that block photo-oxidation reactions in leaves and cause rapid destruction of the living cells.

Of the translocated herbicides there are several categories. Those that are principally phloem mobile, include amitrole, maleic hydrazide, trichlorobenzoic acid and chloramben which are freely mobile, the phenoxy compounds that have limited mobility, and barban which moves only short distances. Those that move principally in the xylem are the substituted ureas, the symmetrical triazines and the nutrient calcium. Picloram and phosphate are able to move freely in both phloem and xylem. "Dacthal", pentachlorophenol and ioxynil move in neither of these systems. Thus, by determining the modes of action and translocation properties of herbicides, one may be in a position to prescribe formulations and application methods.

With the above information at hand, what can be visualized for the future? Certainly new compounds must continue to be synthesized, screened and tested. Autoradiography for studying translocation and comparative photosynthesis for determining selectivity are two valuable methods.

Minimum, maximum and optimum dosage should be determined for each chemical on each weed. Logarithmic applicators are essential for quick determination of these.

Formulation studies should be continued. It is known that large droplets are best for translocated herbicides, small for contact material. Nozzle design and particulating agents play rôles here.

Hydrogen-ion relations should be followed; these have proved important in the use of dinitro and phenoxy herbicides.

Surfactants present an ever-present challenge. Their use with diuron for cotton weed control constituted a breakthrough in weed control technology. Their exact rôles in the action of each new herbicide should be accurately determined. And basic physical research upon this ultimate mode of action should be continued. Finally, invert emulsions and particulating agents should be studied further. Both may play an important rôle in the action of translocated herbicides as well as controlling spray drift.

In soil application, careful comparisons of spray versus pellets should be carried on with all new materials. Soil incorporation should be studied further in order to find the most effective methods for application. Rainfall following application must be taken into consideration, as should volatility of the chemical. Incorporation has enabled growers in western United States to use soil-borne

herbicides that formerly were effective only in the eastern states where summer rainfall occurs.

And last, but not least, continued studies should be made on soil fumigants for these are able to kill deep rooted weeds, insects, and weed seeds, and to leave the soil rapidly so that cropping may be resumed. This is important on high-priced lands, and with valuable crops, soil sealing, plastic covers and other methods justify continued work.