PLANT PHYSIOLOGY AND ANATOMY IN RELATION TO HERBICIDE ACTION

James E. Hill
Extension Weed Scientist

Physiology.

As we advance towards herbicides with greater selectivity and more plant toxicity, we will be required to know more about plant physiology and anatomy. All too often principles of plant physiology are dismissed as being too complicated to have any practical bearing on herbicide use. Yet many practices regularly used in the field to obtain proper herbicide selectivity, have their basis of selectivity in the physiology of the plant. Plant anatomy and plant physiology will be considered together in this discussion because plant structure and function are delicately interwoven in the living plant.

Plants react to herbicides within the normal framework of their anatomy and physiology. There are no plant processes and no structures specifically for herbicides. In fact, the lethal effects of different groups of herbicides are caused by an interference with one or more natural physiological processes in the plant.

A convenient way to look at herbicides as related to plant structure and function is to divide the physiological processes into three; 1) absorption, 2) translocation, and 3) site of action. The term absorption simply means uptake, or how a chemical gets into the plant. The term translocation means movement, how a chemical moves from the place where it is absorbed to the place where it will exhibit its legal activity. Lastly, the site of action refers to the process or location where the herbicide reacts to injure or kill the plant. Each of these physiological processes are examined below in relation to herbicide selectivity, the theme of the 1976 Weed School.

Absorption (uptake).

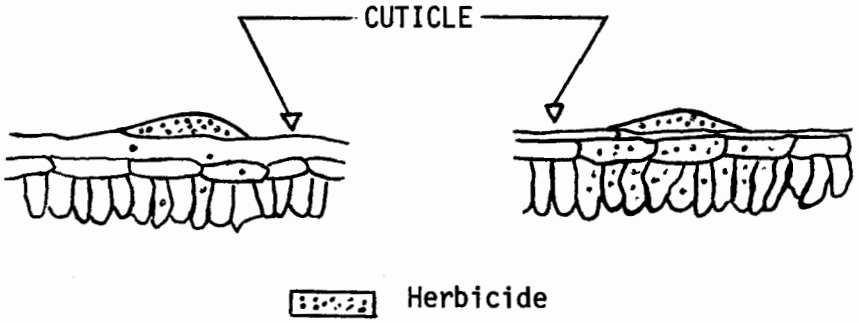
Herbicides are taken into the plant through the leaves and through the roots. Some herbicides can be absorbed only through the leaves and some can be absorbed only through the roots. Others can be absorbed both ways. Uptake into one or the other organs but not both illustrates how the physiological process, absorption, can be selective. Herbicides that are

absorbed by the roots are applied to the soil. In practice we refer to these types of chemicals as soil applied herbicides. Trifluralin is an example of a soil absorbed herbicide. Conversely, chemicals taken up by the leaves are applied to the foliar portion of the plant and referred to as foliar applied herbicides. Trifluralin, a root absorbed herbicide, applied to the leaves will normally not control weeds. In the same vein, herbicides taken in by the leaf are not usually applied to the soil, although there are circumstances where soil applied chemicals can be taken in through the emerging shoot.

How does root absorption occur? Chemicals are taken into plants by both passive and active uptake. Passive uptake occurs by diffusion from high to low concentrations and is not under close metabolic regulation by the plant. Active uptake requires an expenditure of energy by the plant and is metabolically regulated. Chemicals, including plant nutrients, are absorbed into the roots by both active and passive uptake. It is generally concluded that herbicides enter the roots in the same way as plant nutrients. If a mechanism is functioning for the uptake of nutrients then the plant will not be able to restrict an herbicide that is taken up in the nutrient stream.

The same principles that apply to root absorption also apply to leaf absorption. In contrast to root uptake however, absorption by the foliar portion of the plant is restricted by a physical barrier, the cuticle. The cuticle covers the above ground portion of the plant and prevents water and nutrient losses from the plant. As well as protecting the plant from internal losses, the cuticle also prevents some chemicals from entering the plant although others may move through with relative ease. The variability in chemical penetration is a result of the chemical makeup of the cuticle. The cuticle is a waxy non-cellular layer(s) that is lypophyllic or "fat-loving". Since the cuticle is lypophyllic, lipid or wax soluble chemicals are able to move through more easily while non-lypophyllic chemicals are not able to penetrate the cuticle. Some chemicals must be applied pre-emergence to the soil and enter through the roots because they cannot penetrate the cuticle. The chemical composition and structure of the cuticle may vary between plant species and thus can account for differences in herbicidal penetration and activity (Figure 1). The cuticle structure may also vary as a result of environmental conditions such as temperature, rainfall and light intensity. Thus herbicide activity on two plants of the same species grown in different environments may be changed.

Figure 1. Cuticle Variability and Absorption



Thick cuticle prevents absorption of herbicide.

Thin cuticle permits good absorption of herbicide.

Another factor regulating leaf absorption is the presence of stomata. The stomata are minute pores on the surface of leaves that allow gas exchange between the internal and external environment. Stomatal opening and closure is regulated by the plant and can be affected by light, heat, wind, chemicals and other factors. Stomatal penetration, is generally more rapid than cuticular penetration. These two modes of leaf uptake are not mutually exclusive and both may occur under appropriate conditions. The degree of stomatal entry by an herbicide is dependent on the number and size of the stomata, whether they are open or closed, and on the surface tension of the herbicide (Figure 2). Larger and more numerous stomata allow faster foliar uptake and closed stomata exclude licuids and gases. Chemicals or sprays with high surface tensions (like water) enter the stomata less rapidly than those with low surface tensions. This is why surfactants are frecuently added to spray solutions to break the surface tension.

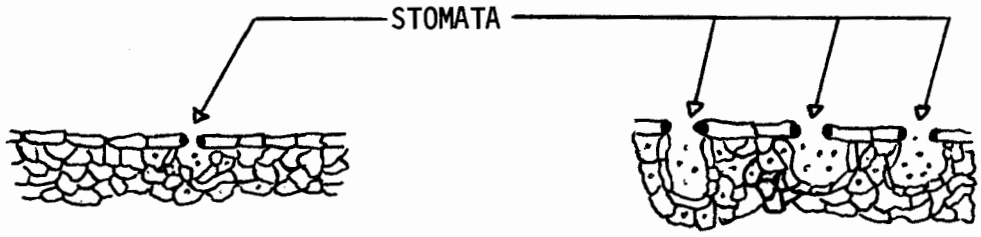
Translocation.

Movement of a chemical within the plant is called translocation. Herbicides may have no activity at the point of uptake but may be very potent inhibitors (or stimulators) in other parts of the plant. Therefore many chemicals must move once they enter the plant in order to exhibit their effect. Other herbicides do not move at all and still exhibit herbicide activity. Such non-mobile herbicides are called contact herbicides because they are potent at the site of uptake. Both foliar and root applied herbicides may be contact herbicides. Paracuat and dinitro are foliar contacts and trifluralin and EPTC represent root applied contacts.

How do herbicides move in the plants? A discussion of the structure and function of plant conducting tissues is necessary. Both living and non-living systems are found in the plant and each support a different process of translocation. The non-living part of the plant is called the apoplast. The cell walls, fibers, air spaces, water and the xylem, a conducting tissue, are part of the apoplast (Figure 3). The living part of the plant is called the symplast. The symplast includes the cells and their components including the phloem, also a conducting tissue.

The xylem and the phloem make up the vascular system in the plant. Both of these tissues can be likened to a series of pipes (cells) connected end to end and stacked together in a

Figure 2. Factors Regulating Stomatal Absorption



Few small stomata permit only poor absorption of herbicide.

Many large stomata allow good absorption of herbicide.

Herbicide

No wetting keeps stomatal absorption low.

Wetting agent favors good stomatal absorption.

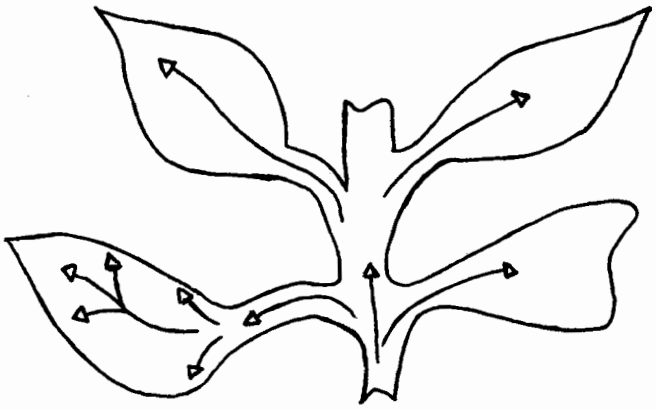
Figure 3. Components of the Apoplast and Symplast and the Direction of Herbicide Movement.

APOPLAST

(non-living)

cell walls
air spaces
fibers

- primary conducting tissue is xylem



Upwards and Outwards

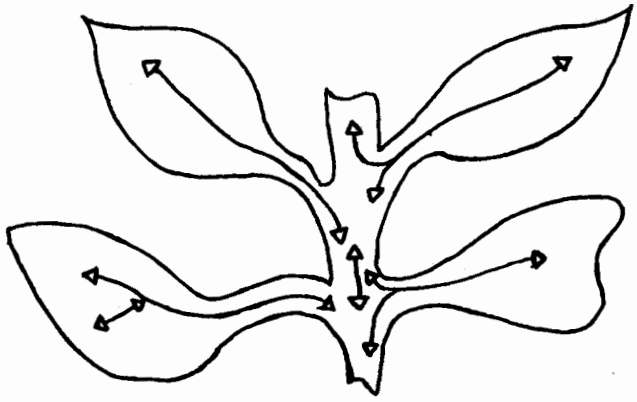
Never down

SYMPLAST

(living)

cytoplasm
nucleus
mitochondria
chloroplasts
other organelles
soluble enzymes
membranes

- primary conducting tissue is phloem



Both Directions (from where food is made to where food is needed)

bundle. These bundles, in fact called vascular bundles, reach throughout the plant from root to shoot. There are marked differences in the structure and function of the xylem and the phloem at maturity. These differences offer an anatomical and physiological basis for herbicidal selectivity. As xylem cells reach maturity they die, lose their cell cytoplasm, and the end walls dissolve away. In effect, they become hollow cylinders. In contract, phloem tissue remains alive at maturity. The end walls of phloem cells dissolve partially leaving small holes or sieve-like performations at each connection of the phloem pipeline. Through these sieve plates, as they are called, the cytoplasm of the cells can interconnect, making the phloem a continuous living tissue. The most important differences in xylem and phloem translocation as related to herbicide action is in what they transport and the direction of flow. The xylem conducts water from the roots to the shoots almost exclusively in an upward direction. The phloem conducts carbohydrates and other plant foodstuffs from the site of manufacture to the site of use in both directions. Phloem transport then, is from the source, where foods are manufactured or stored, to the sink, where foods are used. Examples of sources are the leaves, where the sun's energy is converted to food, or the seed which is a source of stored food for initial seedling growth. Examples of sinks would include growing points where new cells are being made, and roots where energy is needed for nutrient uptake and maintenance. Underground storage organs of perennials may be sources or sinks depending on whether they are accumulating food for winter storage (sink) or supplying food for new growth in the spring (sources). Would a herbicide that moves in the phloem be most effective against johnsongrass rhizomes in the spring; or later when the plant is mature?

How do the structure and function of plant conducting tissues affect herbicide movement? Some herbicides move easily into the non-living apoplast and are translocated in the xylem. Other herbicides enter the symplast and move in the phloem (Table 1). Some herbicides may move in both the apoplast and symplast to varying degrees, therefore it is not always possible to predict how herbicides will move in the plant. Herbicides that enter the xylem are conducted with the water and under all but very unusual conditions move only upward and outward. This means that a xylem-translocated herbicide applied to the leaves would rarely travel down and thus would not be a good choice for controlling perennial weeds with underground storage organs. In contract, herbicides applied to the leaf that readily enter

TABLE 1. TRANSLOCATION OF HERBICIDES IN THE APOPLAST AND SYMPLAST

Free mobility

In apoplast (non living)	In symplast (living)	In both
atrazine (AATREX®)	chloramben (AMIBEN®)	amitrole (AMIZOL®)
monuron (TELVAR®)	fenac (FENAC®)	dalapon (DOWPON®)
diuron (KARMEX®)	maleic hydrazide	dicamba (BANVEL®)
simazine (PRINCEP®)	MSMA (PHYTAR®158)	picloram (TORDON®)
bromacil (HYVAR-X®)	glyphosate (ROUNDUP®)	TBA
terbacil (SINBAR®)		
TCA		
pronamide (KERB®)		
pyrazon (PYRAMIN®)		
norflurazon (ZORIAL®)		
chlorpropham (FURLOE®)		
propham (CHEM HOE®)		
diphenamid (DYMID®)		
metribuzin (SENCOR®)		
phenmedipham (BETANAL®)		

Compounds that leak from roots: maleic hydrazide, TBA, dicamba, picloram and dalapon

Table modified from Ashton and Crafts 1973

TRANSLOCATION OF HERBICIDES

Limited mobility			
In apoplast (non living)	In symplast (living)	In both	Little or no mobility
dichlobenil (CASORON®)	2,4-D (Several)	naptalam (ALANAP®)	DCPA (DCPA)
diquat (DIQUAT®)	2,4-DP (Several)	diallate (AVADEX®)	2,4-DB (Several)
fluorodifen (PREFORAN®)	MCPA (Several)	EPTC (EPTAM®)	endothall (HYDROTHOL®)
paraquat (PARAQUAT)	2,4,5-T (Several)	bromoxynil (BUCTRIL®)	nitrofen (TOK®)
napropamide (DEVRINOL®)	2,4,5-TP (Several)	propanil (STAM®)	PCP
		pebulate (TILLAM®)	trifluralin (TREFLAN®)
		butylate (SUTAN®)	nitralin (PLANAVIN®)
		CDEC (VEGADEX®)	benefin (BALAN®)
		cycloate (RO-NEET®)	oryzalin (SURFLAN®)
		triallate (AVADEX BW®)	bensulide (BETASAN®)
			dinitramine (COBEX®)
			oxadiazon (RONSTAR®)

Compounds that leak from roots: maleic hydrazide, TBA, dicamba, picloram and dalapon

Table modified from Ashton and Crafts 1973

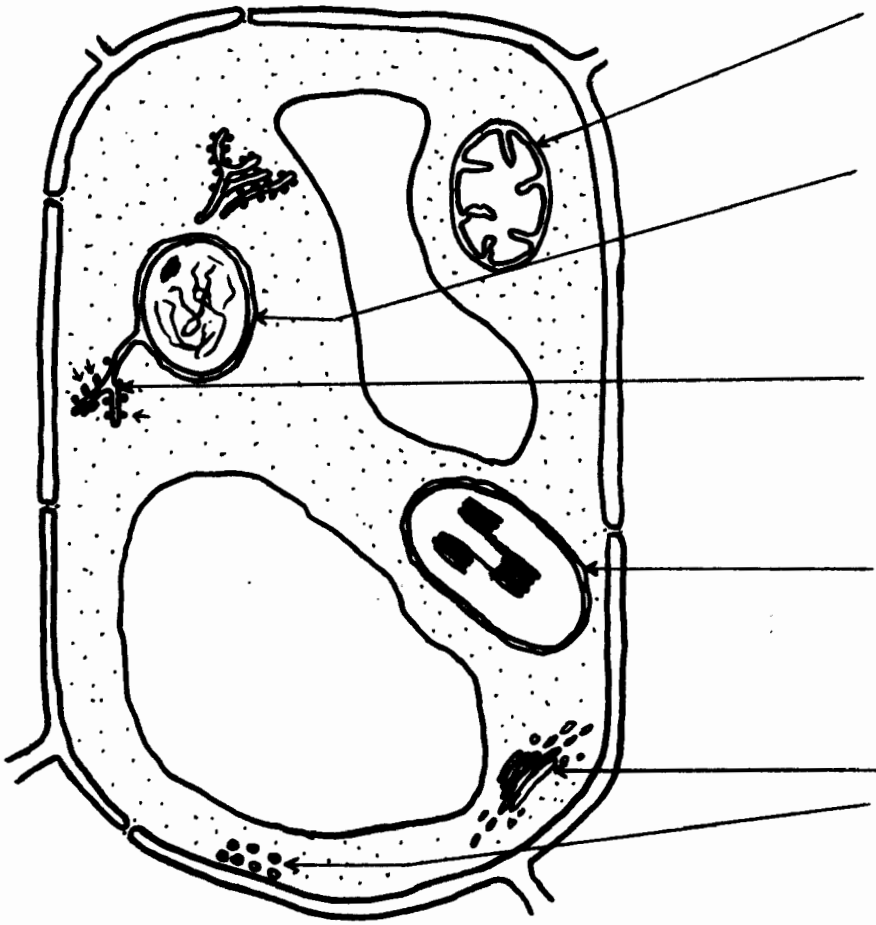
the symplast and translocate in the phloem may move up or down with the food from the source to the sink (Figure 3). Thus, phloem-translocated herbicides would be the most successful herbicides for perennial weed control where translocation to the roots or an underground storage organ is required for success. The importance of timeliness of application of phloem translocated materials becomes readily apparent. The control of perennial weeds by applications of herbicides that move in the phloem, for example, are most successful when the plant is actively manufacturing food and translocating it to the storage organs. Spraying too early in the spring when storage organs are sources and thus exporting foods would almost certainly result in poor weed control.

Site of Action.

Herbicide activity may occur at many levels in the plant. Some herbicide reactions are very general and some are quite specific. General types of reactions are those which interfere with whole systems, for example, the dissolution of plant cuticle waxes or the destruction of membranes. Weed oil is an example of a "whole plant" type of reaction. On the other hand, herbicides may have a very specific activity at the cellular or sub-cellular level in the plant. Although it is not necessary to know the details of how herbicides inhibit specific reactions in order to use them in the field, such knowledge is extremely useful in the development of new products. In addition, knowledge of specific reactions enables us to better understand why chemicals work under one set of conditions and not another. For example, would a photosynthetic inhibitor work in the dark, say on a germinating seed not yet emerged?

An initial discussion of how plants function at the cellular level is important in looking at modes and sites of action. All plants are made up of cells. The machinery of the cell consists of distinct units called organelles. Figure 4 illustrates a "typical" plant cell. Organelles usually serve different functions. Photosynthesis, the conversion of the sun's energy into food, is carried out by the chloroplast. Chloroplasts are organelles containing chlorophyll capable of trapping light energy for conversion to chemical energy. Herbicides that interfere with the chloroplast block the conversion of sunlight energy into food thus killing the plant. Mitochondria are another type of organelle distinct from the chloroplast and serving a different function. Mitochondria convert carbohydrate into energy and are found in animals as well as plants. Mitochondria function in the

Figure 4. Herbicide Interaction with Cell Structure and Function



Structure	Function	Herbicide Inhibition
Mitochondria	Respiration	dinitros organic arsonates nitriles
Nucleus	RNA synthesis DNA synthesis	substituted ureas triazines uracils phenoxys
Endoplasmic Reticulum and Ribisomes (⁝)	Protein synthesis	dinitrophenols substituted ureas dinitroanalins phenoxys
Chloroplast	Photosynthesis	substituted ureas triazines uracils dipryidyls
Golgi bodies	Cell wall synthesis	analines
Microtubules		DCPA

light and in the dark and thus provide energy to the plant at night when it is impossible to use the sun's light as a source of energy. Herbicides that interfere with mitochondrial activity may kill the plant in either the light or in the dark.

Herbicides that have been developed thus far interfere with a number of plant processes. Figure 4 diagrams the cell and the organelles that function in the cell, including the chloroplast and mitochondria. Figure 4 also shows where herbicides interfere with the function of organelles. The sites of action are not all-inclusive. Some herbicides may interfere with more than one process and our knowledge of how herbicides work is far from complete. However, the more that is known about the mode of action of various herbicides, the easier it will be to develop new, safe, and effective herbicides for weed control.

References.

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Weier, T. Elliot, C. Ralph Stocking and Michael G. Barbour. 1970. Botany. John Wiley & Sons, Inc.

Acknowledgements:

Figures 1 and 2 are taken from Circular 558, "Selective Chemical Weed Control" and CWC Weed School 1970 with permission from the authors.