4 pathogen effects on plant physiological functions

effect of pathogens on photosynthesis

Photosynthesis is a basic function of green plants that enables them to transform light energy into chemical energy which they can utilize in their cell activities. Photosynthesis is the ultimate source of all energy used in plant or animal cells, since, in a living cell, all activities except photosynthesis expend the energy provided by photosynthesis.

In photosynthesis, carbon dioxide from the atmosphere and water from the soil are brought together in the chloroplasts of the green parts of plants and, in the presence of light, react to form glucose with concurrent release of oxygen:

$$6\ CO_2 + 6\ H_2O \xrightarrow[\text{chlorophyll}]{\text{light}} C_6H_{12}O_6 + 6\ O_2$$

In view of the fundamental position of photosynthesis in the life of plants, it is apparent that any interference of pathogens with photosynthesis results in a diseased condition in the plant. That pathogens do interfere with photosynthesis is obvious from the chlorosis they cause on many infected plants, from the necrotic lesions or large necrotic areas they produce on green plant parts, and from the reduced amounts of growth, fruits, etc., produced by many infected plants.

In leaf spot, blight, and other kinds of diseases in which there is destruction of leaf tissue, photosynthesis is obviously reduced because of the reduction, through death, of the photosynthetic surface of the plant. Even in other diseases, however, plant pathogens reduce photosynthesis, especially in the late stages of diseases, by affecting the chloroplasts and causing their degeneration. The overall chlorophyll content of leaves in many fungal and bacterial diseases is reduced, but the photosynthetic activity of the remaining chlorophyll seems to remain unaffected. In plants infected by vascular pathogens, chlorophyll is reduced and photosynthesis stops even before the eventual wilting of the plant. Most virus, mycoplasma, and nematode diseases induce varying degrees of chlorosis. In the majority of such diseases photosynthesis of infected plants is reduced qreatly, in advanced stages of the disease the rate of photosynthesis being no more than one-fourth the normal rate.

effect of pathogens on translocation of water and nutrients in the host plant

All living plant cells require an abundance of water and an adequate amount of organic and inorganic nutrients in order to live and to carry out their respective physiological functions. Plants absorb water and inorganic (mineral) nutrients from the soil through their root system. These are generally translocated upward through the xylem vessels of the stem and into the vascular bundles of the petioles and leaf veins, from which they enter the leaf cells. The minerals and part of the water are utilized by the leaf and other cells for synthesis of the various plant substances, but most of the water evaporates out of the leaf cells into the intercellular spaces and from there diffuses into the atmosphere through the stomata. On the other hand, nearly all organic nutrients of plants are produced in the leaf cells, following photosynthesis, and are translocated downward and distributed to all the living plant cells by passing for the most part through the phloem tissues. It is apparent that interference by the pathogen with the upward movement of inorganic nutrients and water or with the downward movement of organic substances will result in diseased conditions in the parts of the plant denied these materials. These diseased parts, in turn, will be unable to carry out their own functions and will deny the rest of the plant their services or their products, thus resulting in disease of the entire plant. For example, if water movement to the leaves is inhibited, the leaves cannot function properly, photosynthesis is reduced or stopped, and few or no nutrients are available to move to the roots, which, in turn, become starved, diseased, and may die.

INTERFERENCE WITH UPWARD TRANSLOCATION OF WATER AND INORGANIC NUTRIENTS

Many plant pathogens interfere in one or more ways with the translocation of water and inorganic nutrients through the plants. Some pathogens affect the integrity or function of the roots and cause decreased absorption of water by them; other pathogens, by growing in the xylem vessels or by other means, interfere with the translocation of water through the stem; and, in some diseases, pathogens also interfere with the water economy of the plant by causing excessive transpiration through their effects on leaves and stomata.

EFFECT ON ABSORPTION OF WATER BY ROOTS

Many pathogens, such as the damping-off fungi, the root-rotting fungi and bacteria, most nematodes, and some viruses cause an extensive destruction of the roots before any symptoms appear on the aboveground parts of the plant. Root injury affects directly the amount of functioning roots and decreases proportionately the amount of water absorbed by the roots. Some vascular parasites, along with their other effects, seem to inhibit root hair production, which reduces water absorption. These and other pathogens also alter the permeability of root cells, an effect that further interferes with the normal absorption of water by roots.

EFFECT ON TRANSLOCATION OF WATER THROUGH THE XYLEM

Fungal and bacterial pathogens that cause damping-off, stem rots, and cankers may reach the xylem vessels in the area of the infection and, if the affected plants are young, may cause their destruction and collapse. Affected vessels may also be filled with the bodies of the pathogen and with substances secreted by the pathogen or by the host in response to the pathogen, and may become clogged. Whether destroyed or clogged the affected vessels cease to function properly and allow little or no water to pass through them. Certain pathogens, such as the crown gall bacterium (*Agrobacterium tumefaciens*), the clubroot fungus (*Plasmodiophora brassicae*), and the root-knot nematode (*Meloidogyne* sp.) induce gall formation in the stem and/or the roots. The enlarged and proliferating cells near or around the xylem exert pressure on the xylem vessels, which may be crushed and dislocated and, thereby, become less efficient in transporting water.

The most typical and complete dysfunction of xylem in translocating water, however, is observed in the vascular wilts caused by the fungi *Ceratocystis, Fusarium,* and *Verticillium,* and bacteria like *Pseudomonas* and *Erwinia.* These pathogens invade the xylem of roots and stems and produce diseases primarily by interfering with the upward movement of water through the xylem. In many plants infected by these pathogens the water flow through the stem xylem is reduced to a mere 2 to 4 percent of that flowing through the stems of healthy plants. In general, the rate of flow through infected stems seems to be inversely proportional to the number of vessels blocked by the pathogen and by the substances resulting from the infection. Evidently, more than one factor is usually responsible for vascular dysfunction in the wilt diseases. Although the pathogen is the single cause of the disease, some of the factors responsible for the disease syndrome originate directly from the pathogen, while others originate from the host in response to the pathogen. The pathogen can reduce the flow of water through its physical presence in the xylem as mycelium, spores, or bacterial cells and by production of large molecules (polysaccharides) in the vessels. The infected host may reduce the flow of water through reduction in the size or collapse of vessels due to infection, development of tyloses in the vessels, release of large-molecule compounds in the vessels as a result of cell wall breakdown by pathogenic enzymes, and reduced water tension in the vessels due to pathogen-induced alterations in foliar transpiration.

EFFECT ON TRANSPIRATION

In plant diseases in which the pathogen infects the leaves, transpiration is usually increased. This is the result of destruction of at least part of the protection afforded the leaf by the cuticle, increase in permeability of leaf cells, and dysfunction of stomata. Diseases like the rusts, mildews, and apple scab destroy a considerable portion of the cuticle and epidermis and this results in uncontrolled loss of water from the affected areas. If water absorption and translocation cannot keep up with the excessive loss of water, loss of turgor and wilting of leaves follows. The suction force of excessively transpiring leaves is abnormally increased and may lead to collapse and/or dysfunction of underlying vessels through production of tyloses and gums.

INTERFERENCE WITH THE TRANSLOCATION OF ORGANIC NUTRIENTS THROUGH THE PHLOEM

Organic nutrients produced in leaf cells through photosynthesis move through plasmodesmata into adjoining phloem elements. From there they move down the phloem sieve tubes and eventually, again through plasmodesmata, into the protoplasm of living nonphotosynthetic cells, where they are utilized, or into storage organs, where they are stored. Thus, in both cases, they are removed from "circulation." Plant pathogens may interfere with the movement of organic nutrients from the leaf cells to the phloem or with their translocation through the phloem elements and, possibly, with their movement from the phloem into the cells that will utilize them.

Obligate fungal parasites, such as the rust and mildew fungi, cause an accumulation of photosynthetic products, as well as inorganic nutrients, in the areas invaded by the pathogen. In these diseases, the infected areas are characterized by reduced photosynthesis and increased respiration. However, synthesis of starch and of other compounds as well as dry weight are temporarily increased in the infected areas, indicating translocation of organic nutrients from uninfected areas of the leaves or from healthy leaves toward the infected areas.

In some virus diseases, particularly the leaf-curling type and some yellows diseases, starch accumulation in the leaves is a common phenomenon. In most of these diseases, starch accumulation in the leaves is mainly the result of degeneration (necrosis) of the phloem of infected plants which is one of the first symptoms of these diseases. It is also possible, however, at least in some virus diseases, that the interference with translocation of starch stems from inhibition by the virus of the enzymes that break down starch into smaller translocatable molecules. This is suggested by the observation that in some mosaic diseases, in which there is no phloem necrosis, infected, discolored areas of leaves contain less starch than "healthy," greener areas at the end of the day, a period favorable for photosynthesis; but the same leaf areas contain more starch than the "healthy" areas after a period in the dark, which favors starch hydrolysis and translocation. This suggests that virus-infected areas not only synthesize less starch than healthy ones, but also that starch is not easily degraded and translocated from virus-infected areas, although no damage to the phloem is present.

effect of pathogens on host plant respiration

Respiration is the process by which cells, through enzymatically controlled oxidation (burning) of the energy-rich carbohydrates and fatty acids, liberate energy in a form that can be utilized for the performance of various cellular processes. Plant cells carry out respiration in, basically, two steps. The first step involves the degradation of glucose to pyruvate and is carried out, either in the presence or in the absence of oxygen, by enzymes found in the ground cytoplasm of the cells. The production of pyruvate from glucose follows either the glycolytic pathway, otherwise known as glycolysis, or, to a lesser extent, the pentose pathway. The second step involves the degradation of pyruvate, however produced, to CO_2 and water. This is accomplished by a series of reactions known as the Krebs cycle which is accompanied by the so-called terminal oxidation and is carried out in the mitochondria only in the presence of oxygen. Under normal (aerobic) conditions, that is, in the presence of oxygen, both steps are carried out and one molecule of glucose yields, as final products, six molecules of CO_2 and six molecules of water,

$$C_6H_{12}O_6 + 6\ O_2 \longrightarrow 6\ CO_2 + 6\ H_2O$$

with concomitant release of energy (678,000 calories). Some of this energy is lost, but almost half is converted to 20–30 reusable high-energy bonds of adenosine triphosphate (ATP). The first step of respiration contributes two ATP molecules per mole of glucose, and the second step contributes the rest. Under anaerobic conditions, however—that is, in the absence of oxygen—pyruvate cannot be oxidized but it instead undergoes fermentation and yields lactic acid or alcohol. Since the main process of energy generation is cut off, for the cell to secure the necessary energy a much greater rate of glucose utilization by glycolysis is required in the absence of oxygen than is in its presence.

The energy-storing bonds of ATP are formed by the attachment of a phosphate (PO_4) group to adenosine diphosphate (ADP), at the expense of energy released from the oxidation of sugars. The coupling of oxidation of glucose with the addition of phosphate to ADP to produce ATP is called oxidative phosphorylation. Any cell activity that requires energy utilizes the energy stored in ATP by simultaneously breaking down ATP to ADP and inorganic phosphate. The presence of ADP and phosphate in the cell, in turn, stimulate the rate of respiration. If, on the other hand, ATP is not utilized sufficiently by the cell for some reason, there is little or no regeneration of ADP and respiration is slowed down. The amount of ADP (and phosphate) in the cell is determined, therefore, by the rate of energy utilization; this, in turn, determines the rate of respiration in plant tissues.

The energy produced through respiration is utilized by the plant for all types of cellular work, such as accumulation and mobilization of compounds, synthesis of proteins, activation of enzymes, cell growth and division, defense reactions, and a host of other processes. The complexity of respiration, the number of enzymes involved in respiration, its occurrence in every single cell, and its far-reaching effects on the functions and existence of the cell, make it easy to understand why respiration of plant tissues is one of the first functions to be affected during infection by plant pathogens.

RESPIRATION OF DISEASED PLANTS

When plants are infected by pathogens, the rate of respiration generally increases. The increase in respiration appears shortly after inoculation, certainly by the time of appearance of visible symptoms, and continues to rise during the multiplication and sporulation of the pathogen. After that, respiration declines to normal levels or to levels even lower than those of healthy plants. Respiration increases more rapidly in infections of resistant varieties, but it also declines quickly after it reaches its maximum. In susceptible varieties, respiration increases slowly after inoculation, but it continues to rise and it remains at a high level for much longer periods.

Several changes in the metabolism of the diseased plant accompany the increase in respiration following infection. Thus, the activity or concentration of several enzymes of, or related to, the respiratory pathways seem to be increased. The accumulation and oxidation of phenolic compounds are also greater during increased respiration. Increased respiration in diseased plants is also accompanied by an increased activation of the pentose pathway and, sometimes, by considerably more fermentation than observed in healthy plants.

The increased respiration in diseased plants is apparently brought about, at least in part, by uncoupling of the oxidative phosphorylation. In that case no utilizable energy (ATP) is produced through normal respiration in spite of use of the existing ATP and accumulation of ADP which stimulates respiration. The required energy by the cell for its vital processes is then produced through other, less efficient ways including the pentose pathway and fermentation.

The increased respiration of diseased plants can also be explained as the result of increased metabolism in the plant. In many plant diseases, growth is first stimulated, protoplasmic streaming increases, and materials are synthesized, translocated, and accumulated in the diseased area. The energy required for these activities derives from ATP produced through respiration. The more ATP is utilized, the more ADP is produced and further stimulates respiration. It is also possible that the plant, because of the infection, utilizes ATP energy less efficiently than a healthy plant. Because of the waste of part of the energy, an increase in respiration is induced and the resulting greater amount of energy enables the plant cells to utilize sufficient energy to carry out their accelerated processes.

Although oxidation of glucose via the glycolytic pathway is by far the most common way through which plant cells obtain their energy, part of the energy is produced via the pentose pathway. The latter seems to be an alternate pathway of energy production to which plants resort under conditions of stress. Thus, the pentose pathway tends to replace the glycolytic pathway as the plants grow older and differentiate, and to increase upon treatment of the plants with hormones, toxins, wounding, starvation, etc. Infection of plants with pathogens also tends, in general, to activate the pentose pathway over the level at which it operates in the healthy plant. Since the pentose pathway is not directly linked to ATP production, the increased respiration through this pathway fails to produce as much utilizable energy as the glycolytic pathway and is, therefore, a less efficient source of energy for the functions of the diseased plant. On the other hand, the pentose pathway is the main source of phenolic compounds which play important roles in the defense mechanisms of the plant against infection.

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