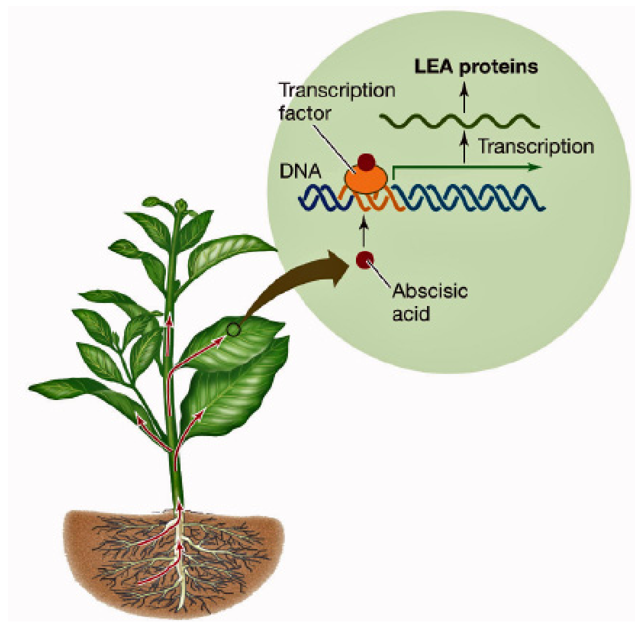
Plant Responses to Environmental Stress

Plants have a number of mechanisms to cope with stresses in their environment, which include such physical conditions as water (too much as well as drought), temperature (hot and cold), saline soils and oxygen deprivation, as well coping with biotic stresses such as predators and pathogens.

Physical Stresses in the Environment

Water

We have discussed previously how plants respond to potential dehydration, and in some cases, excess water, through a number of modifications, such as leaf drop, xeromorphic leaf structure, leaf or stem succulence, or sometimes for roots, deep taproots to find the water table. As mentioned in our discussion of chemical growth regulators, Abscisic acid monitors water condition in cells and leads to stomatal closure to minimize immediate water loss.

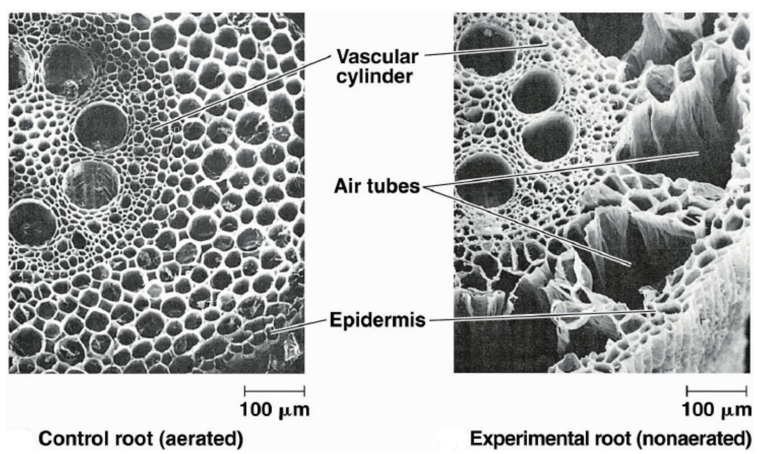


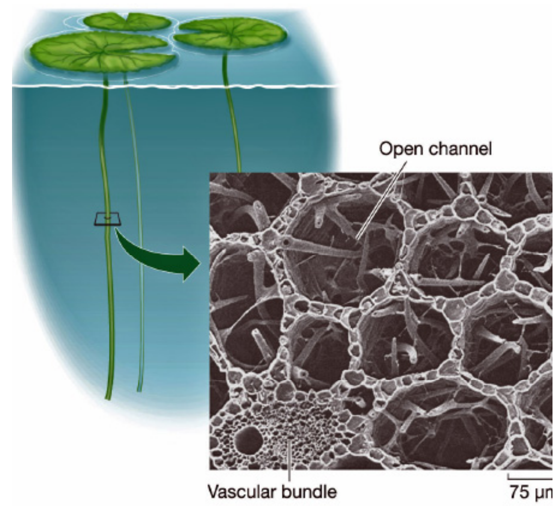
Abscisic Acid and LEA Proteins

Abscisic acid also initiates gene transcription for additional water conservation measures on the part of the plant. Of particular interest is the synthesis of LEA proteins (late embryogenesis proteins). LEA proteins occur naturally in maturing seeds as they desiccate for dormancy. The LEA proteins help to stabilize the membranes and other proteins of the dehydrated cells, but LEA genes can also help plants grow better during drought. Transgenic rice plants with the LEA gene are more drought tolerant than rice plants lacking LEA expression in shoot growth. The HARDY gene in Arabidopsis also promotes more root growth and thicker drought resistant leaves to improve water efficiency. The HARDY gene has also been incorporated into rice with success.

Oxygen

We mentioned in our root structures section the specialized roots, pneumatophores, that many swamp trees have to obtain oxygen in waterlogged soils. Some plants, such as cattails, have large air spaces in their stems and leaves so that oxygen can more readily diffuse towards roots. An in some experimental situations, plants respond to water-logged substrate with development of air spaces within the stem tissue. Unfortunately, many house plants die of suffocation when pots are set in saucers and water is allowed to sit in the saucer, causing the soil to become waterlogged. Such plants cannot develop adequate aeration.





Heat

Plants have poor heat-regulating mechanisms. Their metabolism, in particular, can be seriously impacted by hot temperatures. Although transpiration cools the plant through evaporation, when it’s hot the plant is most likely to have a water deficit, closing stomata, and that shuts down transpiration. Plants synthesize a class of proteins when temperatures are high, and these proteins may function to protect enzymes that would be denatured by the excess heat. These proteins are called **heat-shock proteins.**

Cold

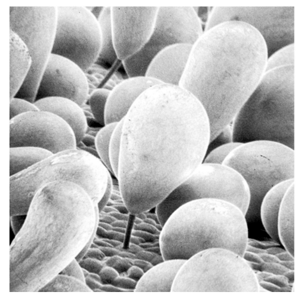
Plants produce more **unsaturated membrane fatty acids** in cold temperatures to maintain membrane fluidity needed for transport proteins. This process takes several days and works for gradual cooling. Most plants that withstand cold do so by dropping fragile parts prior to the cold onset, and going into dormancy, which includes lowering water content in cells. Sudden frosts have a serious impact on plant health. Ice crystals form in plant tissues when air temperatures fall below freezing and expansion can cause significant cell damage and death to fragile parts. Some plants are able to produce **antifreeze proteins** to retard growth of ice crystals within cells. Shallow roots of plants adapted to moderate cold can also be impacted by deep freezes. Many humans who live in Puget Sound suffer plant loss when their outdoor potted plants are subject to several days of below-freezing temperatures and roots freeze.

Salts

High concentrations of mineral salts in soil affect water potential and decrease water absorption. High concentrations of some mineral salts, such as sodium, are also directly toxic to plants. Some plants can produce organic solutes for distribution in root cells that maintain a more-negative water potential in the root cells to facilitate water movement from soil into the root. This is marginally effective for short term.

There are some plants, called halophytes that live in saline soils. Most have active salt glands in leaf epidermal cells that excrete salt. One plant, of very arid regions, called *Nolana*, has salt glands used to obtain water. Water from the atmosphere condenses on the salt secreted on the surface of the leaves. *Nolana* then actively transports the water into the leaf tissue.

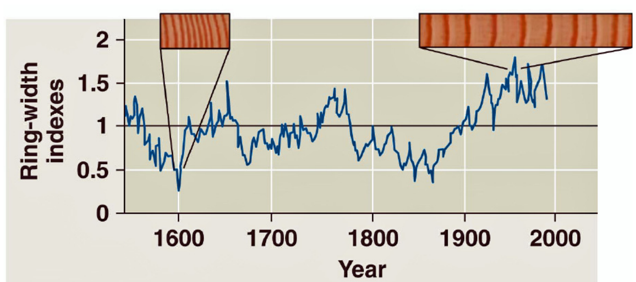
Mangrove Salt Excretion



Salt Glands

General Climate Response

The field of dendrochronology, or study of tree rings, examines long-lived tree species and their growth patterns, which correlates exceptionally well to general climate and climate change. Rings of both living and dead trees can be examined, using fine cores. For example, a forest of conifers in Mongolia has specimens available from the 1500's through today. Ring pattern indicates a general warming climate, with more growth (wider rings) during the past half century.



Moisture has similar effects on tree rings. In the state of Washington, specimens in the coastal rain forest have much wider growth rings than those of the Cascades. Looking more specifically, in Washington, growth rings lag one year behind the climate pattern. The precipitation in 2010 winter (largely snow pack) determines the early xylem growth for the spring of 2011. The reserves the tree was able to accumulate in the spring-summer of 2010, based on that winter's snow pack, provide the reserves for the spring early growth in xylem for 2011.

Plant Responses to their Biotic Environment

Plants are constantly under attack. The dermal tissues function to defend plants from mechanical damage, but are limited in their ability to do so. Predators with sharp mouthparts munch on plants, or penetrate through vulnerable spots. The mechanical protection afforded by spines, thorns and other offensive surface structures is also limited.

Plant Predators

Fungal spores readily enter through stomatal openings and take advantage of the spongy mesophyll to rapidly spread through the leaf tissue. Nematodes are infamous root parasites, biting through the epidermis. The ease with which aphids penetrate into phloem of soft tissues has been discussed previously. Following the strategy that the best defense is a good offense, plants respond to many predator attacks with a chemical offense, the secondary metabolites.

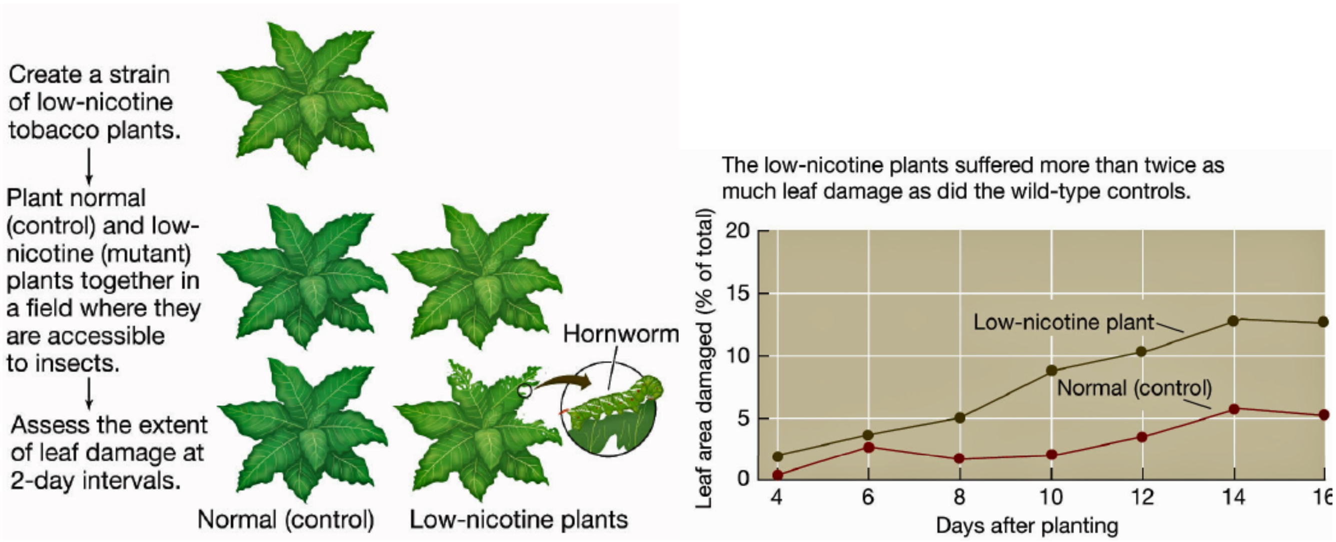
Chemical Toxins – Secondary Metabolites

The list of toxic plants is enormous. Plants, fixed in space, to survive, must ward off predation, and being distasteful and/or toxic to others is one of the best strategies. Over 3000 plant species produce cyanogenic glycosides that block the electron transport system of cell respiration. Hundreds of toxic alkaloids are produced in plants, some of which, such as nicotine, caffeine and morphine, have worked their way into human culture. Aromatic terpenes also repel potential predators.

To prevent the toxin from killing the plant, plants store their secondary metabolites in vacuoles isolated from the rest of the plant cell, but will be damaged by a predator chewing on the plant, thereby entering the predator's digestive tract. In some cases, the secondary metabolite in produced in a non-toxic form but gets converted in the predator's digestive tract, often by bacteria, into a toxic form.

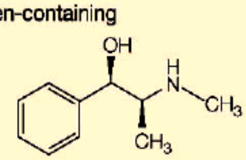
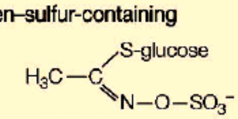
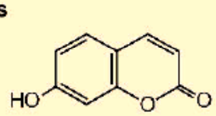
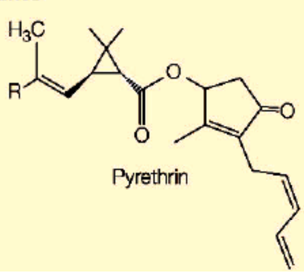
Plants also use secondary metabolites to prevent competition from other plants. A chemical secreted by roots of one plant may prevent root growth by other plants. Black walnut tree roots have such **allelopathy**. Toxins leached from leaves onto soil inhibit germination and growth by potential competitors. *Eucalyptus* secretions are so acidic that they can oxidize paint surfaces. Many desert plants, such as sagebrush, exhibit this form of allelopathy.

The success of secondary metabolites has been shown several times with predators and plants having varying amounts of the metabolite. Consistently the predator selects the plant with the least amount of the chemical to eat.



Tobacco Nicotine Levels and Tomato Hornworm Predation

Secondary Metabolites Used in Defense

CLASS	TYPE	ROLE	EXAMPLE
Nitrogen-containing  Ephedrine (an alkaloid)	Alkaloids Glycosides Nonprotein amino acids	Neurotoxin Inhibit electron transport Disrupt protein structure	Nicotine in tobacco Dhurrin in sorghum Canavanine in jack bean
Nitrogen–sulfur-containing  Methylglucosinolide	Glucosinolates	Inhibit respiration	Methylglucosinolate in cabbage
Phenolics  Umbelliferone	Coumarins Flavonoids Tannins	Block cell division Phytoalexins Inhibit enzymes	Umbelliferone in carrots Capsidol in peppers Gallotannin in oak trees
Terpenes  Pyrethrin	Monoterpenes Diterpenes Triterpenes Sterols Polyterpenes	Neurotoxins Disrupt reproduction and muscle function Inhibit ion transport Block animal hormones Deter feeding	Pyrethrin in chrysanthemums Gossypol in cotton Digitalis in foxglove Spinasterol in spinach Latex in *Euphorbia*

The Predator Retaliation

Some insect predators have evolved resistance to secondary metabolites and have incorporated them into their bodies to protect them from their predators. The monarch butterfly is perhaps the best example of the predator taking advantage of a toxic to protect itself from being consumed. *Heliconius*, a tropical butterfly has resistance to the cyanogenic glycoside of its “host” passion flower, and even converts the glycosides to unharmful molecules from which it obtains nitrogen. Some beetles destroy the toxin-containing lactifers in leaves and feast on the tasty parts.

Beetle damage to milkweed

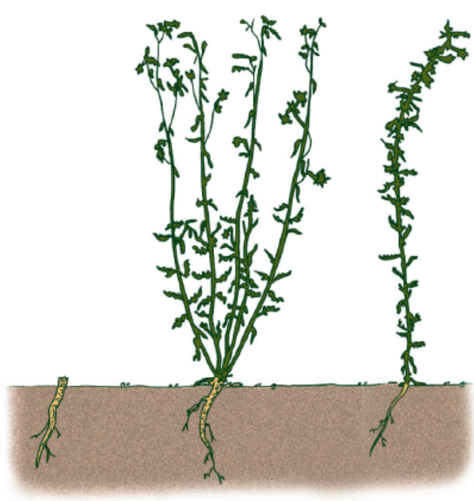
Monarch larva and adult

Mechanisms for Plant Wound Responses

Plants have a variety of mechanisms to inhibit predation. The secondary metabolites just mentioned are always present in the plant and act as effective deterrents once the predator recognizes that plant as something to avoid (or to take advantage of in the case of some, such as the Monarch and Heliconius butterflies).

Growing Better

A few plants respond to being eaten by herbivores by growing faster and better. For example, some plants, when browsed to the ground, respond by producing multiple shoots adventitiously. Dandelions respond to being decapitated in this manner. Where one shoot existed, after being "weeded", the remnant root may initiate three of four new shoots.

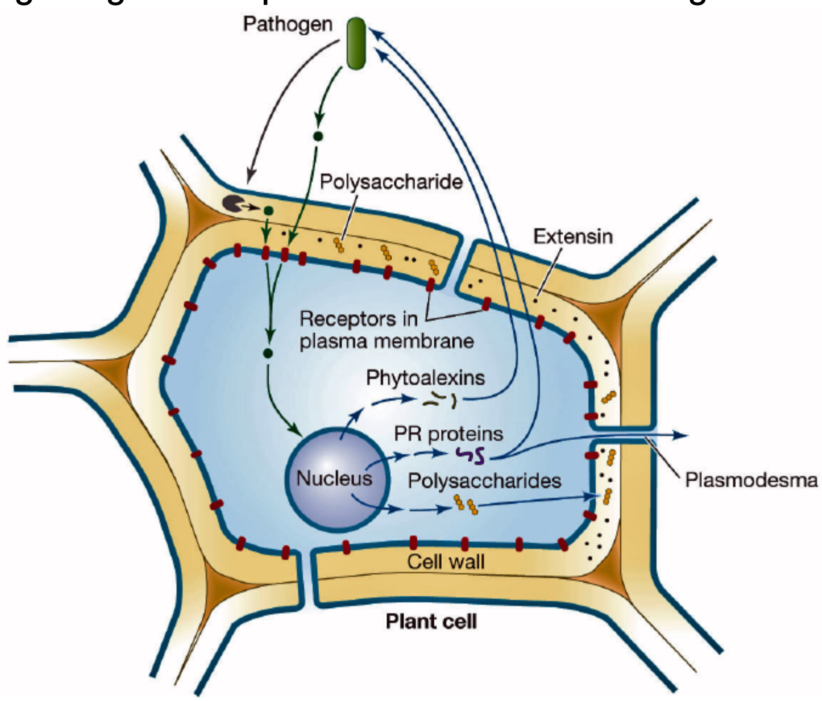


Response to being Overeaten – Normal Growth Pattern on Right

Induced Chemical Defenses

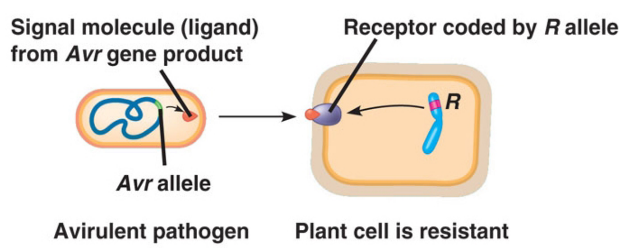
In addition to the always-present secondary metabolites, plants have rapid responses that are induced by the action of the predator or pathogen. These responses activate transduction pathways that lead to the production of chemical (and other) deterrents to predation and wounding. We shall examine a few of these.

General Plant Signaling in Response to Predator/Pathogen



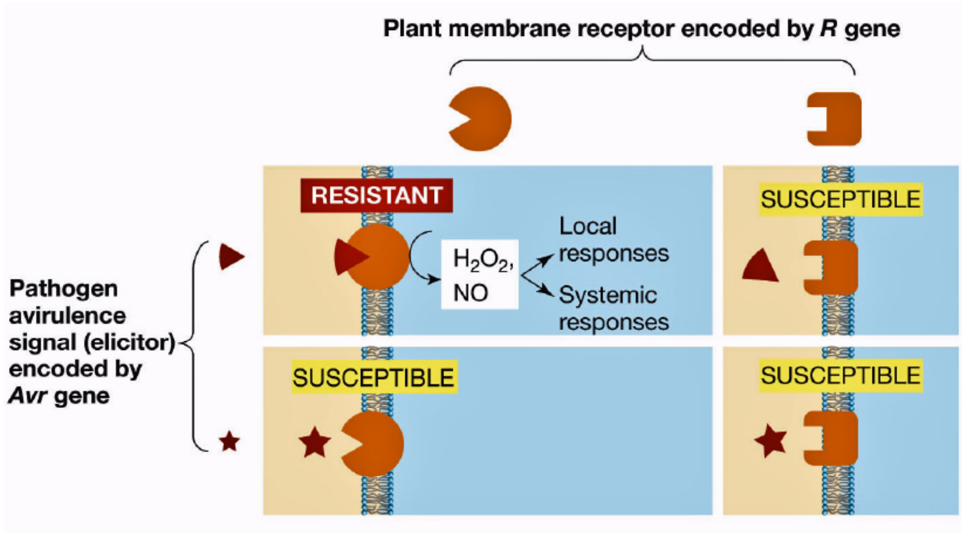
Genetically Determined Pathogen Response

Many plants have evolved some **pathogen resistance through specific gene recognition** that allows for some compromise in which a plant can permit some "munching" but prohibit virulent infestations. Both plant and non-virulent pathogens have genes that code for receptor proteins. The plant genes are called "**R**" genes and the pathogen's genes "***avr***" genes (for avirulence or non-virulence).



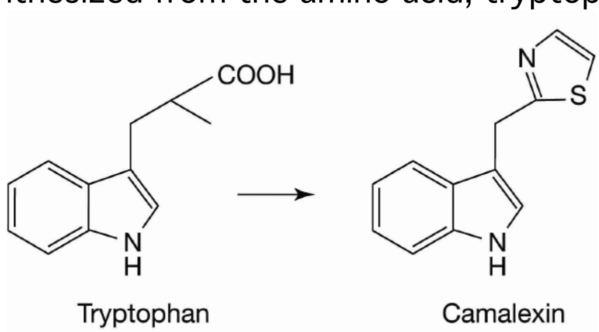
- The signal molecule that activates the transduction pathway may be produced by the pathogen, such as peptides found in a bacterium, or wall fragments of a fungus, or be cell wall components of the plant broken when the pathogen munched. **Oligosaccharins** in plant cell walls may function as the recognition and signaling molecules for these reactions. These signal molecules for the Avr and R receptors are often call **elicitors.**

- When the plant receptor protein and the pathogen receptor protein match, the plant mounts defenses against invasion by the pathogen.



The Hypersensitive Response

- The usual response mechanism with an **Avr-R** interaction is to produce antimicrobial agents, called **phytoalexins**, and **PR proteins** (pathogenesis-related proteins) in the infected tissues, a response known as the **hypersensitive response** (HR). One phytoalexin, **camalexin**, produced by *Arabidopsis*, is synthesized from the amino acid, tryptophan.



The PR proteins include enzymes that degrade the cell walls of bacterial and fungal pathogens. One PR protein is **chitinase**, which degrades the chitin walls of fungi. PR proteins also serve as **warning molecules** within the plant. PR protein response is less rapid than some other plant defenses.

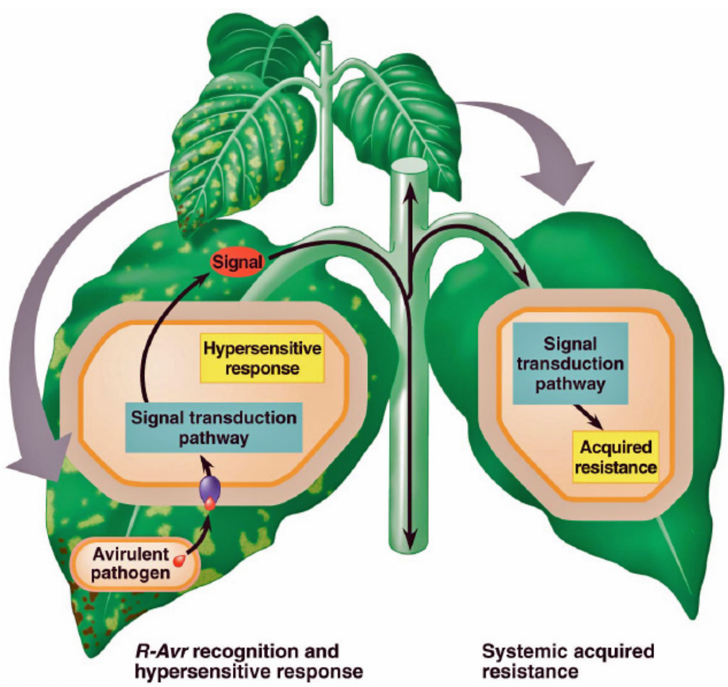
- Hydrogen peroxide and nitric acid are often synthesized immediately in the wound area that trigger events leading to cell death of the affected plant cells. These chemicals are often toxic to the pathogen as well.
- When a gene specific defense is successful, the plant typically seals off the infected area forming a **necrosis**, destroying both its own tissue and the pathogen.

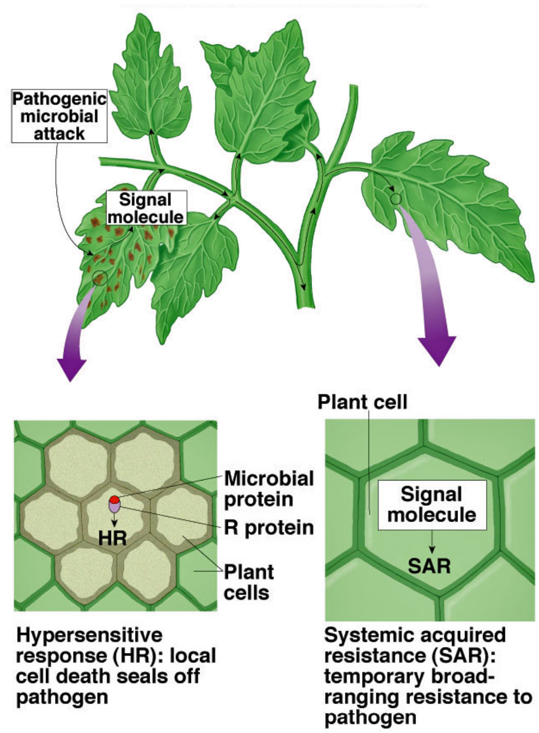
Fungus-induced necrosis

The Systemic Acquired Response
Not only can plants mount a defense in the infected area, but they also produce chemical signals in the infected area that are translocated to other parts of the plant to provide resistance to infection, as mentioned as one job of the PR proteins. This response is known as a **systemic acquired response** (SAR).

Salicylic acid, produced as part of the hypersensitive response to wounding, functions to activate a systemic acquired response. SAR resistance may be short-lived, or last as long as a growing season, and non-specific, but effective. Salicylic acid is particularly effective against some virus infections. Some plants produce the volatile **methyl salicylate**, which travels through air to both parts of the affected plant and to neighboring plants as a warning.

Salicylic acid may also be exported to other parts of the plant initiating defense Pathogen resistant protein (PR) synthesis.



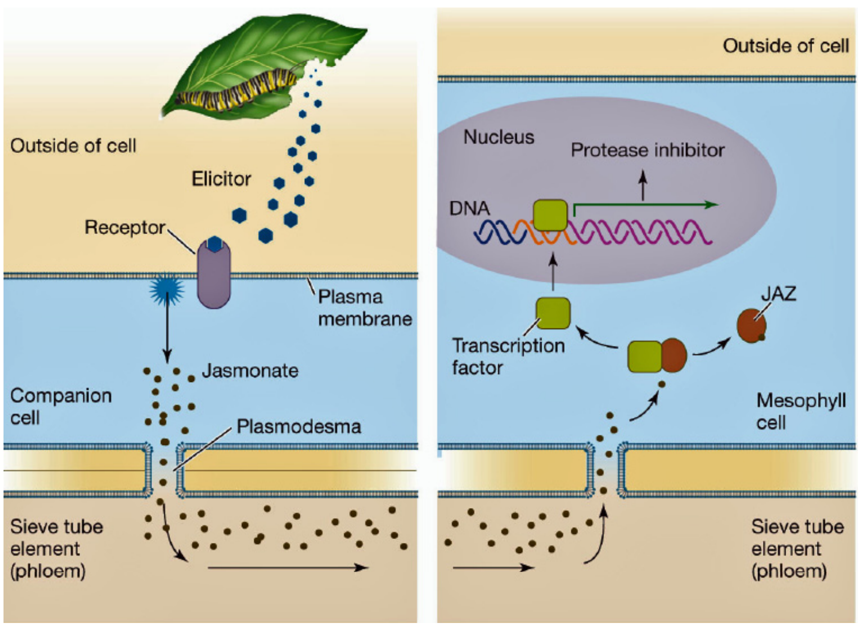


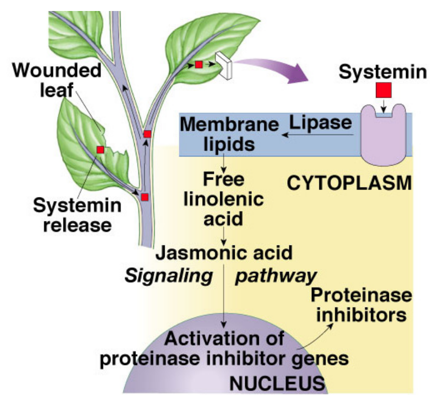
Specific Immunity to RNA Viruses

Viruses are among the most common plant pathogens, being able to infect both vertically (passed from generation to generation) and horizontally (through direct infection). Some plants have enzymes that can form double-stranded RNA from the viral RNA, and chop the double-stranded RNA into siRNA (small interference RNA), discussed briefly in Biology 211, to degrade the viral mRNA before it can be transcribed.

Jasmonic Acid and Wound Response

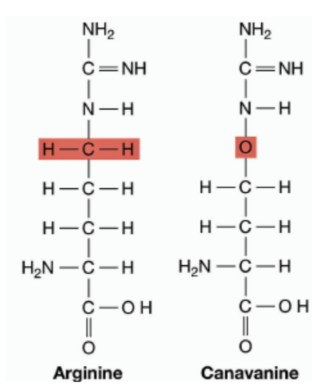
Another plant wound response to predator munching is achieved through signal transduction pathways activated by a small peptide, **systemin**, produced in the wound area in response to the predator's saliva. Systemin was first isolated from tomato plants. Systemin promotes fatty acids in the plasma membrane to be converted to **jasmonic acid.** Jasmonic acid moves through plasmodesmata to phloem sieve tubes throughout the plant and activates signal transduction pathways leading to proteinase inhibitors that bind to digestive enzymes of the predator.





Dietary Defense

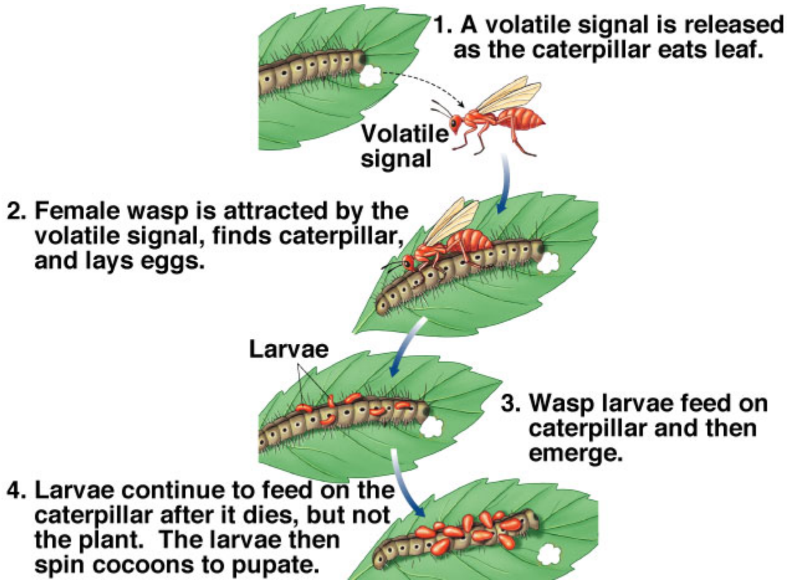
Some plants produce an amino acid (**canavanine**) that gets incorporated into larvae that die when they substitute it for an amino acid needed in protein synthesis.



Using Proxies

Plants, being clever, also take advantage of other organisms to destroy and/or deter the plant predator.

- Some plants can secrete volatile chemicals when injured by a larval predator that attract larvae parasites. In one example, the parasite, a wasp, lays its eggs on the larva. The developing wasp larvae feed on the plant pest for their own development, saving the plant from destruction.



- In an intricate symbiosis, the Acacia tree feeds and hosts ants, which protect the tree from potential predators and competitors. If a pest (or a clothes pin) touches the tree, the ants swarm to deter it or destroy it.

- Beans injured by predators secrete a volatile chemical that is detected by adjacent plants, which activate signal transduction pathways leading to the synthesis of defense molecules.

Lest you think that only insects, fungi and small organisms cause problems, browsing animals also cause much damage to plants. Deer, goats and most large browsing animals manage to alter the shape of their targets. Many is the tree denuded from the ground to the point where their predator's mouth parts can no longer reach. Humans often fence out potential browsers, and in the process, induce wound repair on the very trees they are using to help protect their other plants.

Deer damage

Wound healing in bark