Section 14: Host resistance

- Hosts may be less susceptible to attack (due to antibiosis and antixenosis) or may yield well despite attack (due to tolerance).
- Host resistance is important in reducing cost of pest control, may help protect environment by reducing pesticide use, and may help alleviate the onset of pesticide resistance.
- Host resistance used more for plant disease and nematode management because pesticides not so readily available or effective.

Constitutive versus induced resistance

- Both animals and plants have evolved mechanisms of resistance to attack by diseases and pests. That they don't always work is apparent, which can be seen by outbreaks of disease and pests. That they generally have an effect is less apparent, but also important.
- Constitutive resistance is best known, and is expressed by well-defined morphological and chemical deterrents to pest attack that occur consistently, and that can be selected for by plant breeders. It is species- or variety-specific. Induced resistance, which is stimulated by insect attack, is less well defined, but widespread.

Basis of resistance

- Antixenosis - a resistance mechanism that deters the colonization the host by the pest. Both biochemical and morphological factors may be involved. Also called non-preference.
- Antibiosis - a mechanism wherein the colonized host has deleterious effects on the pest's development, reproduction or survival.
- Tolerance - a mechanism wherein the insect infestation is supported without loss of host vigor.

- Hosts vary naturally in their susceptibility to attack. Sometimes resistance is based on more than one mechanism. Sources of variation may be natural or induced.
- The challenge is to enhance resistance quantitatively, but without loss of other important horticultural characteristics such as taste, fruit size, and color. Factors deterring insects may also affect humans (allelochemicals).
- Resistance is more evident in plant than animal hosts, the exception being trypanosomiasis-tolerant cattle in Africa.

Monogenic and polygenic resistance

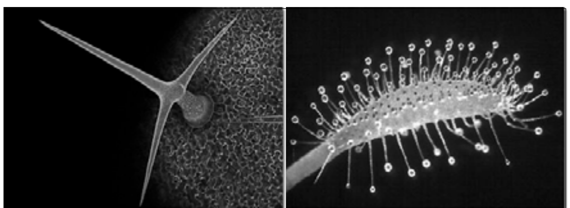
- Many plant characteristics are controlled by single genes. These are easily identified and transferred from source to recipient plants to improve them. Use both traditional (Mendelian) and molecular techniques. Called monogenic resistance.
- Other characteristics are more variable and controlled by many genes. Called polygenic resistance.
- Monogenic resistance more likely to break down. Often not selected for in breeding programs.

- Now possible to transfer some resistance factors, if protein-based, to plant using molecular techniques. This includes genes not of plant origin.
- Molecular techniques have the potential to speed up the process of breeding, which may take 15 years using conventional techniques.
- Genetically modified (GM) crops meet opposition in some areas.

Can you explain why the use of GM crops might seem undesirable to some?

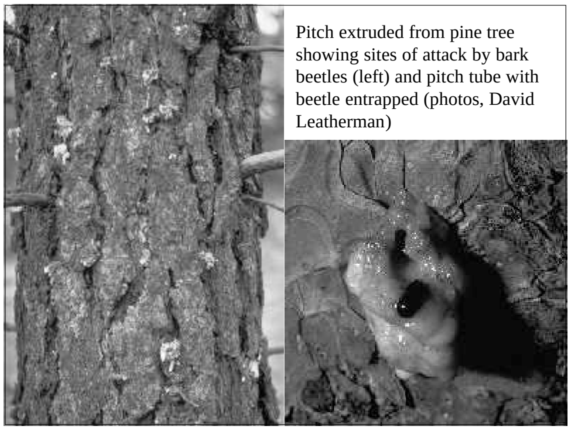
Specific mechanisms of resistance

- Color - affects acceptance (e.g., red cabbage avoided).
- Palatability at selection - often select botanically related plants due to secondary plant chemicals (e.g., mustard oils in crucifers).
- Hairiness - trichome density interferes with insect activities; sometimes spears them or, in the case of glandular trichomes, impedes movement (e.g., small insects such as aphids and whiteflies.



Trichomes, or leaf hairs, can be spiny (above left) or glandular (above right). Of course they vary in length and density. Often the trichomes affect the ability of phytophagous species to feed on the plant, but hairiness is not always beneficial because the parasitic and predatory insects found on plants also may be affected by trichome density (left photo, D.D. Kunkel; right photo, J. Runions)

- Waxiness - chemicals in wax on plant foliage may attract or deter insects (e.g., flea beetles, aphids).
- General shape - morphology of some plants is more suitable than others (e.g., cotton bract, pod proximity, nectaries).
- Gummosis - plant exudates such as gum, latex, and resins can afford protection by drowning, entangling, and extruding (e.g., pitch from conifers)
- Necrosis - tissue death in the immediate area of feeding; more important with sessile than mobile organisms

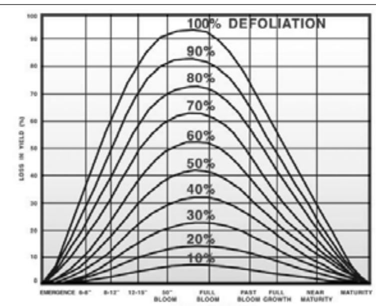


Pitch extruded from pine tree showing sites of attack by bark beetles (left) and pitch tube with beetle entrapped (photos, David Leatherman)

- Tissue hardness - epidermal cells vary greatly in their hardness, or how fast they become hard. Hard tissue can impede feeding (hence group feeding in some species) and silica levels in grasses is a resistance factor.
- Phenological resistance - this is a questionable form of resistance because it refers to hosts that are not susceptible at time of attack (e.g., early or late flowering).
- Toxins and feeding deterrents - chemicals that deter feeding or normal growth of the pest (e.g., the quinone DIMBOA in corn [maize]).

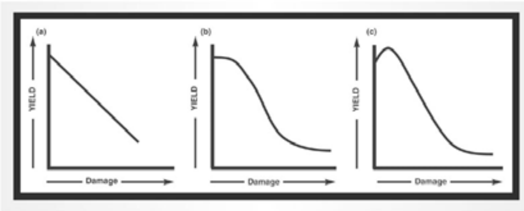
- Nutrition - insects are affected by the quality of the food they ingest, particularly the levels of soluble nitrogen (amino acids). Pests known to be susceptible to nitrogen, such as aphids and mites, are most likely affected.
- Extrinsic resistance - this is the interaction of hosts with other mortality factors such as biocontrol agents. The shape of structures may afford differing abilities of pests to hide, or for biocontrol agents to attack (e.g., appressed onion leaves allow onion thrips to shelter between the leaves).
- Symptom expression - some hosts fail to display symptoms of insect feeding due, often due to physiological insensitivity (e.g., hopperburn)

- Compensation - hosts differ greatly in their ability to recover from damage. Usually due to surviving host tissue or nearby plants being freed from competition, thereby growing larger.
  - Sensitivity varies among crop varieties, with crop health and cultural practices, but most importantly with type and timing of damage.
  - Typically, plants damaged early in their growth cycle have time to recover (compensate), and those late in their growth cycle have already produced fruits, tubers, etc. The most susceptible period is often the flowering/fruiting stages, when photosynthates are being shifted from foliage production to storage organs.



Graphic model of potato loss in relation to defoliation (10-100%) at various stages of the plant growth cycle. Loss is proportional to defoliation level. The period most susceptible to damage corresponds is the period of bloom (adapted from USDA Tech Bull 1581).

- Compensation may be partial, complete, or more than complete (over-compensation or growth stimulation).
- The nature of the response is a function of whether the pest causes direct or indirect damage.
  - Direct damage is damage to the harvested portion of the plant, such as the fruit of tomatoes or tubers of potatoes
  - Indirect damage is damage to the non-harvested portion of the plant, such as the roots of tomato or the foliage of potato. Typically, the crop can withstand more damage to the non-harvested portion without economic damage (loss).



Generalized forms of plant response to damage. Response “a” represents a very susceptible plant, wherein all tissue loss represents economic loss; this is typically due to direct pests. Response “b”displays insensitivity to some loss, a response typical of indirect pests. Response “c” shows over-compensation or yield stimulation at low levels of damage; this is more widespread than is commonly acknowledged.

Why doesn’t damage equal loss?

- Common misconception that all insect damage translates to loss.
  - Plants commonly produce more foliage and fruits than needed, shedding some early in the season. If some of these are damaged, no loss.
  - Some thinning may be desirable; chemical thinners applied to fruits to reduce number and increase size.
  - Pruning alleviates carbohydrate-based feedback that slows down or terminates growth, stimulating continued growth rather than senescence. It is equivalent to cutting your lawn regularly, which keeps the grass growing instead of producing seed.

Induced resistance

- Although some plants produce and store chemicals that deter herbivory by insects (a “static” defense), many times plants only produce defensive chemicals when they are attacked (an “active” defense).
- Active defense usually involves a systemic reaction; not only is the site of damage affected, but the entire plant.
- Induced defenses may not provide complete immunity, but may affect the ability of herbivores to grow or reproduce.
  - e.g., potatoes attacked by caterpillars produce proteinase inhibitors and polyphenol oxidase, which interfere with digestion and thereby limit the ability of insects to feed.

Signals for induction of resistance

- Signalling pathways used by plants to cause gene expression of resistance proteins are under investigation. Three types of genes seem to be involved:
  - Defense genes: code for proteinase inhibitors or secondary compounds
  - Signalling pathway genes: involved in production of volatile compounds used as signals
  - Metabolic genes: reroute metabolism to increase production of defensive compounds such as proteinases

  Key signals in induction are (in sequence):

  systemin, jasmonic acid, oligogalacturonic acid, and hydrogen peroxide

Jasmonic acid

- Application of jasmonic acid to plants stimulates levels of polyphenol oxidases and proteinase inhibitors after 3 days.
- Herbivore levels are decreased for 3 weeks.
- Nearly all insects affected, though aphids less so.
- For disease resistance induction, the product “Actigard” is being used commercially, and this may affect some insects.

Emission of volatile molecules

- Wounding response includes emission of volatiles.
- Local and systemic responses to wounding.
- Aldehydes, alcohols, esthers, and terpenoids are produced.
- Can have repellent or toxic effect, repel oviposition, attract predators and parasitoids.
- Insect feeding secretions, esp. chemical volicitin, also attract natural enemies.

Problems with plant resistance

- Might seem to be ideal way to manage pests, but often difficult to obtain, especially of multiple pests involved. Sometimes trade-off with other issues (e.g., disease resistance).
- Trade-off with desirable horticultural characteristics characteristics such as taste or color.
- Trade-off with yield; resistant crops usually yield less well. Can use insecticides when needed.
- Health hazard; some toxic properties not limited to pests.
- Interference with biological control.

More problems with resistance

- Trade-off in insecticide susceptibility; plants containing toxins may induce detoxification processes that make it harder to obtain kill with insecticides.
- Variability of resistance: populations of insects may vary in ability to overcome resistance; crop age, crop or nutrient management, and weather (temperature) may affect expression of resistance.
- Monogenic toxin-based, genetically modified (GM) crops may select for ability of pests to overcome resistance.

Insect biotypes

- Biotypes are groups of genetically identical organisms (insects).
- Asexually reproducing insects, especially aphids, tend to produce biotypes that can exploit different plant types, and overcome host resistance.
- Generally an issue with single-gene (monogenic) resistance, which is the most common form of resistance produced by plant breeders. Probably a greater problem as genetically engineered plants become more common, as these are monogenic.

Plant clones

- Clones are organisms descended from a common parent by mitotic division; meiosis not involved. Plants propagated by cuttings, budding, grafting, tubers, bulbs are clones.
- When genetically identical plants are infested by genetically identical insect biotypes, the stage is set for immediate resistance breakdown.
- Crops affected include perennial vegetables, potatoes and sweet potatoes, apples, peaches, rubber, bananas, sugarcane, pineapple, berry crops, some grass crops, and others.

Examples of insect biotypes (after Panda and Khush 1995).

Crop	Insect	No. of biotypes
Wheat	Maetiola destructor	9
	Schizaphis graminum	7
Raspberry	Amphorophora idaei	4
Alfalfa	Acyrthosiphon pisum	4
	Therioaphis maculata	6
Sorghum	Schizaphis graminum	5
Corn	Rhopalosiphum maidis	5
Rice	Nilaparvata lugens	4
	Nephotettix virescens	3
	Orseolia oryzae	4
Apple	Eriosoma lanigerum	3

Community-level resistance

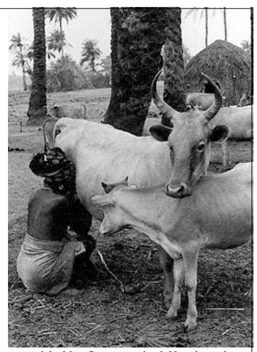
- Resistance of plant communities is derived from overall health and diversity. There are “windows of susceptibility.”
- Recovery ability related to plant health/growth rate.
- Age class diversity and species diversity, and low plant density desirable (thin stands to maximize growth rate).
- Eliminate high risk individuals (weak or harboring pests).
- Avoid predisposing factors (site, moisture, nutrition).

Resistance in vertebrate hosts

- Not very productive area, though interest level is high. Some selection for resistance in cattle has occurred naturally in Africa.
- Host immunity has potential to deter feeding or inhibit insect reproduction. Salivary glands and gut are major stimuli of antibodies. Also possible to generate tolerance through "immunization /vaccination." Most promising with ticks, but still imperfect.

Zebu cattle (below), though traditionally popular in Africa, are somewhat susceptible to trypanosmiasis, which is transmitted by tsetse flies. The more trypanotolerant breeds such as N'dama cattle (right) are increasingly popular in western Africa, but not the drier areas of central Africa.

provided by Georges Puilame



provided by Campagnie J. Van Lancker

Antitick plants

- Ticks climb grasses (and other plants) in order to attach themselves to passing animals (questing).
- Pasture grasses capable of repelling, trapping and killing ticks reported from Africa; trichomes deter climbing by ticks, and some grasses (e.g., Stylosanthes spp.) produce "viscous fluids" that poison ticks. In South America, molasses grass (Melinis minutiflora) also is repellent and deters climbing.
- Some shrubs are repellent and acaricidal (e.g., Gynandropsis gynandra) and farmers are encouraged to plant it around cattle pens. This shrub is eaten by people, goats and donkeys, so there appears to be no hazards associated with use.
- Emphasizes value in considering ethnobotany.

Status of host resistance

- Not as well developed as might be expected.
- Breeders focus on yield and other horticultural characteristics.
- Absence of complete resistance has discouraged some.
- Availability of inexpensive, effective insecticides has reduced need.
- Most useful for low value crops/subsistence agriculture.
- Current emphasis on genetic manipulation and control of breeding by commercial interests does not lead to polygenic resistance for low value crops and subsistence agriculture.

Repellents

- A natural product produced by some plants
  - Essential oils from wormwood, cedar, wintergreen, anise, eucalyptus, Cymbopogon grass, lemon grass, etc.
- Humans have sought repellents for biting flies since the earliest times, and they are mentioned in Roman and Greek writings.
- Oil of citronella (from Cymbopogon) first widely used repellent.
- DEET (diethyl toluamide) was developed in 1954, and remains the most effective product.
- Other synthetics are under development, and seem promising. Other natural repellents include soybean oil, geraniol, neem, castor seed oil, and lemon oil.

Advantages and disadvantages of repellents

- Intuitively, repellents should prevent disease transmission as well as annoyance.
- However, it is not necessarily substantiated by data.
- Repellents tend not to persist for very long, and are not systemic, so coverage is important.
- Efficacy varies among insects, and with product.
- Permethrin, though actually an insecticide, has some repellency, and is used on clothing.

Repellents for plant-feeding insects

- Repellents for plant feeders not as well developed as for animal/human feeders.
- Best known are products containing azadiractin, extracted from neem trees. Many products are available (also growth regulator and oviposition deterrent).
- Hot pepper wax contains extract of cayenne pepper, capsaicin.

Questions

- Can you distinguish among antixenosis, antibiosis, and tolerance in plants? Constitutive and induced resistance? Monogenic and polygenic resistance?
- Can you describe host resistance occur in animals?
- Can you list 10 specific mechanisms of resistance in plants?
- Describe injury compensation in plants
- Why is host plant resistance not used more frequently to manage pests?
- How can natural and synthetic repellents be used to confer resistance to attack?

Questions from supplementary readings

- Reading 21, Permethrin-treated uniforms
  - What 3 techniques are recommended by the French military health service for soldier protection.
  - Did repellent (DEET) use or permethrin impregnation of uniforms reduce the blood feeding by mosquitoes? Incidence of malaria? Probability of being bitten?
  - How often did these authors conclude it would be necessary to re-apply DEET?
  - Was there a benefit to having both DEET and permethrin impregnation?

Questions from supplementary readings

- Reading 22, Mosquito repellents
  - The natural products citronella, geraniol, and neem have been reported to have insect repellent properties. How did they fare in thes tests?
  - Did the synthetic repellents provide more protection that the natural products?
  - How many times per day would you need to apply the 3 most effective products to be assured of good repellency?