

= Plant defense against herbivory =

Plant defense against herbivory or host @-@ plant resistance (HPR) describes a range of adaptations evolved by plants which improve their survival and reproduction by reducing the impact of herbivores . Plants can sense being touched , and they can use several strategies to defend against damage caused by herbivores . Many plants produce secondary metabolites , known as allelochemicals , that influence the behavior , growth , or survival of herbivores . These chemical defenses can act as repellents or toxins to herbivores , or reduce plant digestibility .

Other defensive strategies used by plants include escaping or avoiding herbivores in any time and / or any place , for example by growing in a location where plants are not easily found or accessed by herbivores , or by changing seasonal growth patterns . Another approach diverts herbivores toward eating non @-@ essential parts , or enhances the ability of a plant to recover from the damage caused by herbivory . Some plants encourage the presence of natural enemies of herbivores , which in turn protect the plant . Each type of defense can be either constitutive (always present in the plant) , or induced (produced in reaction to damage or stress caused by herbivores) .

Historically , insects have been the most significant herbivores , and the evolution of land plants is closely associated with the evolution of insects . While most plant defenses are directed against insects , other defenses have evolved that are aimed at vertebrate herbivores , such as birds and mammals . The study of plant defenses against herbivory is important , not only from an evolutionary view point , but also in the direct impact that these defenses have on agriculture , including human and livestock food sources ; as beneficial ' biological control agents ' in biological pest control programs ; as well as in the search for plants of medical importance .

= = Evolution of defensive traits = =

The earliest land plants evolved from aquatic plants around 450 million years ago (Ma) in the Ordovician period . Many plants have adapted to iodine @-@ deficient terrestrial environment by removing iodine from their metabolism , in fact iodine is essential only for animal cells . An important antiparasitic action is caused by the block of the transport of iodide of animal cells inhibiting sodium @-@ iodide symporter (NIS) . Many plant pesticides are glycosides (as the cardiac digitoxin) and cyanogenic glycosides which liberate cyanide , which , blocking cytochrome c oxidase and NIS , is poisonous only for a large part of parasites and herbivores and not for the plant cells in which it seems useful in seed dormancy phase . Iodide is not pesticide , but is oxidized , by vegetable peroxidase , to iodine , which is a strong oxidant , it is able to kill bacteria , fungi and protozoa .

The Cretaceous period saw the appearance of more plant defense mechanisms . The diversification of flowering plants (angiosperms) at that time is associated with the sudden burst of speciation in insects . This diversification of insects represented a major selective force in plant evolution , and led to selection of plants that had defensive adaptations . Early insect herbivores were mandibulate and bit or chewed vegetation ; but the evolution of vascular plants lead to the co @-@ evolution of other forms of herbivory , such as sap @-@ sucking , leaf mining , gall forming and nectar @-@ feeding .

The relative abundance of different species of plants in ecological communities including forests and grasslands may be determined in part by the level of defensive compounds in the different species . Since the cost of replacement of damaged leaves is higher in conditions where resources are scarce , it may also be that plants growing in areas where water and nutrients are scarce may invest more resources into anti @-@ herbivore defenses .

= = Records of herbivores = =

Our understanding of herbivory in geological time comes from three sources : fossilized plants , which may preserve evidence of defense (such as spines) , or herbivory @-@ related damage ; the observation of plant debris in fossilised animal faeces ; and the construction of herbivore mouthparts .

Long thought to be a Mesozoic phenomenon, evidence for herbivory is found almost as soon as fossils which could show it. Within under 20 million years of the first fossils of sporangia and stems towards the close of the Silurian, around 420 million years ago, there is evidence that they were being consumed. Animals fed on the spores of early Devonian plants, and the Rhynie chert also provides evidence that organisms fed on plants using a "pierce and suck" technique. Many plants of this time are preserved with spine-like enations, which may have performed a defensive role before being co-opted to develop into leaves.

During the ensuing 75 million years, plants evolved a range of more complex organs - from roots to seeds. There was a gap of 50 to 100 million years between each organ evolving, and it being fed upon. Hole feeding and skeletonization are recorded in the early Permian, with surface fluid feeding evolving by the end of that period.

== Co evolution ==

Herbivores are dependent on plants for food, and have evolved mechanisms to obtain this food despite the evolution of a diverse arsenal of plant defenses. Herbivore adaptations to plant defense have been likened to offensive traits and consist of adaptations that allow increased feeding and use of a host plant. Relationships between herbivores and their host plants often results in reciprocal evolutionary change, called co evolution. When an herbivore eats a plant it selects for plants that can mount a defensive response. In cases where this relationship demonstrates specificity (the evolution of each trait is due to the other), and reciprocity (both traits must evolve), the species are thought to have co evolved. The "escape and radiation" mechanism for co evolution presents the idea that adaptations in herbivores and their host plants have been the driving force behind speciation, and have played a role in the radiation of insect species during the age of angiosperms. Some herbivores have evolved ways to hijack plant defenses to their own benefit, by sequestering these chemicals and using them to protect themselves from predators. Plant defenses against herbivores are generally not complete so plants also tend to evolve some tolerance to herbivory.

== Types ==

Plant defenses can be classified generally as constitutive or induced. Constitutive defenses are always present in the plant, while induced defenses are produced or mobilized to the site where a plant is injured. There is wide variation in the composition and concentration of constitutive defenses and these range from mechanical defenses to digestibility reducers and toxins. Many external mechanical defenses and large quantitative defenses are constitutive, as they require large amounts of resources to produce and are difficult to mobilize. A variety of molecular and biochemical approaches are used to determine the mechanism of constitutive and induced plant defenses responses against herbivory.

Induced defenses include secondary metabolic products, as well as morphological and physiological changes. An advantage of inducible, as opposed to constitutive defenses, is that they are only produced when needed, and are therefore potentially less costly, especially when herbivory is variable.

== Chemical defenses ==

The evolution of chemical defences in plants is linked to the emergence of chemical substances that are not involved in the essential photosynthetic and metabolic activities. These substances, secondary metabolites, are organic compounds that are not directly involved in the normal growth, development or reproduction of organisms, and often produced as by-products during the synthesis of primary metabolic products. Although these secondary metabolites have been thought to play a major role in defenses against herbivores, a meta-analysis of recent relevant studies has suggested that they have either a more minimal (when compared to other non-secondary

metabolites, such as primary chemistry and physiology) or more complex involvement in defense.

Secondary metabolites are often characterized as either qualitative or quantitative. Qualitative metabolites are defined as toxins that interfere with an herbivore's metabolism, often by blocking specific biochemical reactions. Qualitative chemicals are present in plants in relatively low concentrations (often less than 2% dry weight), and are not dosage dependent. They are usually small, water-soluble molecules, and therefore can be rapidly synthesized, transported and stored with relatively little energy cost to the plant. Qualitative allelochemicals are usually effective against non-adapted specialists and generalist herbivores.

Quantitative chemicals are those that are present in high concentration in plants (5–40% dry weight) and are equally effective against all specialists and generalist herbivores. Most quantitative metabolites are digestibility reducers that make plant cell walls indigestible to animals. The effects of quantitative metabolites are dosage dependent and the higher the proportion of these chemicals in the herbivore's diet, the less nutrition the herbivore can gain from ingesting plant tissues. Because they are typically large molecules, these defenses are energetically expensive to produce and maintain, and often take longer to synthesize and transport.

The geranium, for example, produces a unique chemical compound in its petals to defend itself from Japanese beetles. Within 30 minutes of ingestion the chemical paralyzes the herbivore. While the chemical usually wears off within a few hours, during this time the beetle is often consumed by its own predators.

See Toxalbumin

===== Types of chemical defences =====

Plants have evolved many secondary metabolites involved in plant defense, which are collectively known as antiherbivory compounds and can be classified into three sub-groups: nitrogen compounds (including alkaloids, cyanogenic glycosides, glucosinolates and benzoxazinoids), terpenoids, and phenolics.

Alkaloids are derived from various amino acids. Over 3000 known alkaloids exist, examples include nicotine, caffeine, morphine, cocaine, colchicine, ergolines, strychnine, and quinine. Alkaloids have pharmacological effects on humans and other animals. Some alkaloids can inhibit or activate enzymes, or alter carbohydrate and fat storage by inhibiting the formation of phosphodiester bonds involved in their breakdown. Certain alkaloids bind to nucleic acids and can inhibit synthesis of proteins and affect DNA repair mechanisms. Alkaloids can also affect cell membrane and cytoskeletal structure causing the cells to weaken, collapse, or leak, and can affect nerve transmission. Although alkaloids act on a diversity of metabolic systems in humans and other animals, they almost uniformly invoke an aversively bitter taste.

Cyanogenic glycosides are stored in inactive forms in plant vacuoles. They become toxic when herbivores eat the plant and break cell membranes allowing the glycosides to come into contact with enzymes in the cytoplasm releasing hydrogen cyanide which blocks cellular respiration. Glucosinolates are activated in much the same way as cyanogenic glycosides, and the products can cause gastroenteritis, salivation, diarrhea, and irritation of the mouth. Benzoxazinoids, secondary defence metabolites, which are characteristic for grasses (Poaceae), are also stored as inactive glucosides in the plant vacuole. Upon tissue disruption they get into contact with α -glucosidases from the chloroplasts, which enzymatically release the toxic aglucones. Whereas some benzoxazinoids are constitutively present, others are only synthesised following herbivore infestation, and thus, considered inducible plant defenses against herbivory.

The terpenoids, sometimes referred to as isoprenoids, are organic chemicals similar to terpenes, derived from five carbon isoprene units. There are over 10,000 known types of terpenoids. Most are multicyclic structures which differ from one another in both functional groups, and in basic carbon skeletons. Monoterpenoids, containing 2 isoprene units, are volatile essential oils such as citronella, limonene, menthol, camphor, and pinene. Diterpenoids, 4 isoprene units, are widely distributed in latex and resins, and can be quite toxic. Diterpenes are responsible for making *Rhododendron* leaves poisonous. Plant steroids and sterols are also produced from

terpenoid precursors , including vitamin D , glycosides (such as digitalis) and saponins (which lyse red blood cells of herbivores) .

Phenolics , sometimes called phenols , consist of an aromatic 6 @-@ carbon ring bonded to a hydroxy group . Some phenols have antiseptic properties , while others disrupt endocrine activity . Phenolics range from simple tannins to the more complex flavonoids that give plants much of their red , blue , yellow , and white pigments . Complex phenolics called polyphenols are capable of producing many different types of effects on humans , including antioxidant properties . Some examples of phenolics used for defense in plants are : lignin , silymarin and cannabinoids . Condensed tannins , polymers composed of 2 to 50 (or more) flavonoid molecules , inhibit herbivore digestion by binding to consumed plant proteins and making them more difficult for animals to digest , and by interfering with protein absorption and digestive enzymes . Silica and lignins , which are completely indigestible to animals , grind down insect mandibles (appendages necessary for feeding) .

In addition to the three larger groups of substances mentioned above , fatty acid derivatives , amino acids and even peptides are also used as defense . The cholinergic toxin , cicutoxin of water hemlock , is a polyene derived from the fatty acid metabolism. ? @-@ N @-@ Oxalyl @-@ L @-@ ? , ? @-@ diaminopropionic acid as simple amino acid is used by the sweet pea which leads also to intoxication in humans . The synthesis of fluoroacetate in several plants is an example of the use of small molecules to disrupt the metabolism of herbivores , in this case the citric acid cycle .

In tropical Sargassum and Turbinaria species that are often preferentially consumed by herbivorous fishes and echinoids , there is a relatively low level of phenolics and tannins .

= = = Mechanical defenses = = =

Plants have many external structural defenses that discourage herbivory . Depending on the herbivore ? s physical characteristics (i.e. size and defensive armor) , plant structural defenses on stems and leaves can deter , injure , or kill the grazer . Some defensive compounds are produced internally but are released onto the plant ? s surface ; for example , resins , lignins , silica , and wax cover the epidermis of terrestrial plants and alter the texture of the plant tissue . The leaves of holly plants , for instance , are very smooth and slippery making feeding difficult . Some plants produce gummosis or sap that traps insects .

A plant 's leaves and stem may be covered with sharp prickles , spines , thorns , or trichomes- hairs on the leaf often with barbs , sometimes containing irritants or poisons . Plant structural features like spines and thorns reduce feeding by large ungulate herbivores (e.g. kudu , impala , and goats) by restricting the herbivores ' feeding rate , or by wearing down the molars . Raphides are sharp needles of calcium oxalate or calcium carbonate in plant tissues , making ingestion painful , damaging a herbivore 's mouth and gullet and causing more efficient delivery of the plant 's toxins . The structure of a plant , its branching and leaf arrangement may also be evolved to reduce herbivore impact . The shrubs of New Zealand have evolved special wide branching adaptations believed to be a response to browsing birds such as the moas . Similarly , African Acacias have long spines low in the canopy , but very short spines high in the canopy , which is comparatively safe from herbivores such as giraffes .

Trees such as coconut and other palms , may protect their fruit by multiple layers of armor , needing efficient tools to break through to the seed contents , and special skills to climb the tall and relatively smooth trunk .

= = = Thigmonasty = = =

Thigmonastic movements , those that occur in response to touch , are used as a defense in some plants . The leaves of the sensitive plant , *Mimosa pudica* , close up rapidly in response to direct touch , vibration , or even electrical and thermal stimuli . The proximate cause of this mechanical response is an abrupt change in the turgor pressure in the pulvini at the base of leaves resulting from osmotic phenomena . This is then spread via both electrical and chemical means through the

plant ; only a single leaflet need be disturbed .

This response lowers the surface area available to herbivores , which are presented with the underside of each leaflet , and results in a wilted appearance . It may also physically dislodge small herbivores , such as insects .

= = = Mimicry and camouflages = = =

Some plants mimic the presence of insect eggs on their leaves , dissuading insect species from laying their eggs there . Because female butterflies are less likely to lay their eggs on plants that already have butterfly eggs , some species of neotropical vines of the genus *Passiflora* (Passion flowers) contain physical structures resembling the yellow eggs of *Heliconius* butterflies on their leaves , which discourage oviposition by butterflies .

= = = Indirect defenses = = =

Another category of plant defenses are those features that indirectly protect the plant by enhancing the probability of attracting the natural enemies of herbivores . Such an arrangement is known as mutualism , in this case of the " enemy of my enemy " variety . One such feature are semiochemicals , given off by plants . Semiochemicals are a group of volatile organic compounds involved in interactions between organisms . One group of semiochemicals are allelochemicals ; consisting of allomones , which play a defensive role in interspecies communication , and kairomones , which are used by members of higher trophic levels to locate food sources . When a plant is attacked it releases allelochemicals containing an abnormal ratio of volatiles . Predators sense these volatiles as food cues , attracting them to the damaged plant , and to feeding herbivores . The subsequent reduction in the number of herbivores confers a fitness benefit to the plant and demonstrates the indirect defensive capabilities of semiochemicals . Induced volatiles also have drawbacks , however ; some studies have suggested that these volatiles also attract herbivores .

Plants also provide housing and food items for natural enemies of herbivores , known as " biotic " defense mechanisms , as a means to maintain their presence . For example , trees from the genus *Macaranga* have adapted their thin stem walls to create ideal housing for an ant species (genus *Crematogaster*) , which , in turn , protects the plant from herbivores . In addition to providing housing , the plant also provides the ant with its exclusive food source ; from the food bodies produced by the plant . Similarly , some *Acacia* tree species have developed thorns that are swollen at the base , forming a hollowing structure that acts as housing . These *Acacia* trees also produce nectar in extrafloral nectaries on their leaves as food for the ants .

Plant use of endophytic fungi in defense is a very common phenomenon . Most plants have endophytes , microbial organisms that live within them . While some cause disease , others protect plants from herbivores and pathogenic microbes . Endophytes can help the plant by producing toxins harmful to other organisms that would attack the plant , such as alkaloid producing fungi which are common in grasses such as tall fescue (*Festuca arundinacea*) .

= = = Leaf shedding and color = = =

There have been suggestions that leaf shedding may be a response that provides protection against diseases and certain kinds of pests such as leaf miners and gall forming insects . Other responses such as the change of leaf colors prior to fall have also been suggested as adaptations that may help undermine the camouflage of herbivores . Autumn leaf color has also been suggested to act as an honest warning signal of defensive commitment towards insect pests that migrate to the trees in autumn .

= = Costs and benefits = =

Defensive structures and chemicals are costly as they require resources that could otherwise be

used by plants to maximize growth and reproduction . Many models have been proposed to explore how and why some plants make this investment in defenses against herbivores .

= = = Optimal defense hypothesis = = =

The optimal defense hypothesis attempts to explain how the kinds of defenses a particular plant might use reflect the threats each individual plant faces . This model considers three main factors , namely : risk of attack , value of the plant part , and the cost of defense .

The first factor determining optimal defense is risk : how likely is it that a plant or certain plant parts will be attacked ? This is also related to the plant apparency hypothesis , which states that a plant will invest heavily in broadly effective defenses when the plant is easily found by herbivores . Examples of apparent plants that produce generalized protections include long @-@ living trees , shrubs , and perennial grasses . Unapparent plants , such as short @-@ lived plants of early successional stages , on the other hand , preferentially invest in small amounts of qualitative toxins that are effective against all but the most specialized herbivores .

The second factor is the value of protection : would the plant be less able to survive and reproduce after removal of part of its structure by a herbivore ? Not all plant parts are of equal evolutionary value , thus valuable parts contain more defenses . A plant ? s stage of development at the time of feeding also affects the resulting change in fitness . Experimentally , the fitness value of a plant structure is determined by removing that part of the plant and observing the effect . In general , reproductive parts are not as easily replaced as vegetative parts , terminal leaves have greater value than basal leaves , and the loss of plant parts mid @-@ season has a greater negative effect on fitness than removal at the beginning or end of the season . Seeds in particular tend to be very well protected . For example , the seeds of many edible fruits and nuts contain cyanogenic glycosides such as amygdalin . This results from the need to balance the effort needed to make the fruit attractive to animal dispersers while ensuring that the seeds are not destroyed by the animal .

The final consideration is cost : how much will a particular defensive strategy cost a plant in energy and materials ? This is particularly important , as energy spent on defense cannot be used for other functions , such as reproduction and growth . The optimal defense hypothesis predicts that plants will allocate more energy towards defense when the benefits of protection outweigh the costs , specifically in situations where there is high herbivore pressure .

= = = Carbon : nutrient balance hypothesis = = =

The carbon : nutrient balance hypothesis , also known as the environmental constraint hypothesis or Carbon Nutrient Balance Model (CNBM) , states that the various types of plant defenses are responses to variations in the levels of nutrients in the environment . This hypothesis predicts the Carbon / Nitrogen ratio in plants determines which secondary metabolites will be synthesized . For example , plants growing in nitrogen @-@ poor soils will use carbon @-@ based defenses (mostly digestibility reducers) , while those growing in low @-@ carbon environments (such as shady conditions) are more likely to produce nitrogen @-@ based toxins . The hypothesis further predicts that plants can change their defenses in response to changes in nutrients . For example , if plants are grown in low @-@ nitrogen conditions , then these plants will implement a defensive strategy composed of constitutive carbon @-@ based defenses . If nutrient levels subsequently increase , by for example the addition of fertilizers , these carbon @-@ based defenses will decrease .

= = = Growth rate hypothesis = = =

The growth rate hypothesis , also known as the resource availability hypothesis , states that defense strategies are determined by the inherent growth rate of the plant , which is in turn determined by the resources available to the plant . A major assumption is that available resources are the limiting factor in determining the maximum growth rate of a plant species . This model predicts that the level of defense investment will increase as the potential of growth decreases .

Additionally , plants in resource @-@ poor areas , with inherently slow @-@ growth rates , tend to have long @-@ lived leaves and twigs , and the loss of plant appendages may result in a loss of scarce and valuable nutrients .

A recent test of this model involved a reciprocal transplants of seedlings of 20 species of trees between clay soils (nutrient rich) and white sand (nutrient poor) to determine whether trade @-@ offs between growth rate and defenses restrict species to one habitat . When planted in white sand and protected from herbivores , seedlings originating from clay outgrew those originating from the nutrient @-@ poor sand , but in the presence of herbivores the seedlings originating from white sand performed better , likely due to their higher levels of constitutive carbon @-@ based defenses . These finding suggest that defensive strategies limit the habitats of some plants .

= = = Growth @-@ differentiation balance hypothesis = = =

The growth @-@ differentiation balance hypothesis states that plant defenses are a result of a tradeoff between " growth @-@ related processes " and " differentiation @-@ related processes " in different environments . Differentiation @-@ related processes are defined as " processes that enhance the structure or function of existing cells (i.e. maturation and specialization) . " A plant will produce chemical defenses only when energy is available from photosynthesis , and plants with the highest concentrations of secondary metabolites are the ones with an intermediate level of available resources . The GDBH also accounts for tradeoffs between growth and defense over a resource availability gradient . In situations where resources (e.g. water and nutrients) limit photosynthesis , carbon supply is predicted to limit both growth and defense . As resource availability increases , the requirements needed to support photosynthesis are met , allowing for accumulation of carbohydrate in tissues . As resources are not sufficient to meet the large demands of growth , these carbon compounds can instead be partitioned into the synthesis of carbon based secondary metabolites (phenolics , tannins , etc .) . In environments where the resource demands for growth are met , carbon is allocated to rapidly dividing meristems (high sink strength) at the expense of secondary metabolism . Thus rapidly growing plants are predicted to contain lower levels of secondary metabolites and vice versa . In addition , the tradeoff predicted by the GDBH may change over time , as evidenced by a recent study on *Salix* spp . Much support for this hypothesis is present in the literature , and some scientists consider the GDBH the most mature of the plant defense hypotheses .

= = Importance to humans = =

= = = Agriculture = = =

The variation of plant susceptibility to pests was probably known even in the early stages of agriculture in humans . In historic times , the observation of such variations in susceptibility have provided solutions for major socio @-@ economic problems . The grape phylloxera was introduced from North America to France in 1860 and in 25 years it destroyed nearly a third (100 @,@ 000 km²) of the French grape yards . Charles Valentine Riley noted that the American species *Vitis labrusca* was resistant to Phylloxera . Riley , with J. E. Planchon , helped save the French wine industry by suggesting the grafting of the susceptible but high quality grapes onto *Vitis labrusca* root stocks . The formal study of plant resistance to herbivory was first covered extensively in 1951 by Reginald (R.H.) Painter , who is widely regarded as the founder of this area of research , in his book *Plant Resistance to Insects* . While this work pioneered further research in the US , the work of Chesnokov was the basis of further research in the USSR .

Fresh growth of grass is sometimes high in prussic acid content and can cause poisoning of grazing livestock . The production of cyanogenic chemicals in grasses is primarily a defense against herbivores .

The human innovation of cooking may have been particularly helpful in overcoming many of the

defensive chemicals of plants . Many enzyme inhibitors in cereal grains and pulses , such as trypsin inhibitors prevalent in pulse crops , are denatured by cooking , making them digestible .

It has been known since the late 17th century that plants contain noxious chemicals which are avoided by insects . These chemicals have been used by man as early insecticides ; in 1690 nicotine was extracted from tobacco and used as a contact insecticide . In 1773 , insect infested plants were treated with nicotine fumigation by heating tobacco and blowing the smoke over the plants . The flowers of *Chrysanthemum* species contain pyrethrin which is a potent insecticide . In later years , the applications of plant resistance became an important area of research in agriculture and plant breeding , particularly because they can serve as a safe and low cost alternative to the use of pesticides . The important role of secondary plant substances in plant defense was described in the late 1950s by Vincent Dethier and G.S. Fraenkel . The use of botanical pesticides is widespread and notable examples include Azadirachtin from the neem (*Azadirachta indica*) , d-Limonene from Citrus species , Rotenone from Derris , Capsaicin from chili pepper and Pyrethrum .

Natural materials found in the environment also induce plant resistance as well . Chitosan derived from chitin induce a plant 's natural defense response against pathogens , diseases and insects including cyst nematodes , both are approved as biopesticides by the EPA to reduce the dependence on toxic pesticides .

The selective breeding of crop plants often involves selection against the plant 's intrinsic resistance strategies . This makes crop plant varieties particularly susceptible to pests unlike their wild relatives . In breeding for host plant resistance , it is often the wild relatives that provide the source of resistance genes . These genes are incorporated using conventional approaches to plant breeding , but have also been augmented by recombinant techniques , which allow introduction of genes from completely unrelated organisms . The most famous transgenic approach is the introduction of genes from the bacterial species , *Bacillus thuringiensis* , into plants . The bacterium produces proteins that , when ingested , kill lepidopteran caterpillars . The gene encoding for these highly toxic proteins , when introduced into the host plant genome , confers resistance against caterpillars , when the same toxic proteins are produced within the plant . This approach is controversial , however , due to the possibility of ecological and toxicological side effects .

== Pharmaceutical ==

Many currently available pharmaceuticals are derived from the secondary metabolites plants use to protect themselves from herbivores , including opium , aspirin , cocaine , and atropine . These chemicals have evolved to affect the biochemistry of insects in very specific ways . However , many of these biochemical pathways are conserved in vertebrates , including humans , and the chemicals act on human biochemistry in ways similar to that of insects . It has therefore been suggested that the study of plant insect interactions may help in bioprospecting .

There is evidence that humans began using plant alkaloids in medical preparations as early as 3000 B.C. Although the active components of most medicinal plants have been isolated only recently (beginning in the early 19th century) these substances have been used as drugs throughout the human history in potions , medicines , teas and as poisons . For example , to combat herbivory by the larvae of some *Lepidoptera* species , *Cinchona* trees produce a variety of alkaloids , the most familiar of which is quinine . Quinine is extremely bitter , making the bark of the tree quite unpalatable , it is also an anti fever agent , known as Jesuit 's bark , and is especially useful in treating malaria .

Throughout history mandrakes (*Mandragora officinarum*) have been highly sought after for their reputed aphrodisiac properties . However , the roots of the mandrake plant also contain large quantities of the alkaloid scopolamine , which , at high doses , acts as a central nervous system depressant , and makes the plant highly toxic to herbivores . Scopolamine was later found to be medicinally used for pain management prior to and during labor ; in smaller doses it is used to prevent motion sickness . One of the most well known medicinally valuable terpenes is an anticancer drug , taxol , isolated from the bark of the Pacific yew , *Taxus brevifolia* , in the early

1960s .

= = = Biological pest control = = =

Repellent companion planting , defensive live fencing hedges , and " obstructive @-@ repellent " interplanting , with host @-@ plant resistance species as beneficial ' biological control agents ' is a technique in biological pest control programs for : organic gardening , wildlife gardening , sustainable gardening , and sustainable landscaping ; in organic farming and sustainable agriculture ; and in restoration ecology methods for habitat restoration projects .

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