

INTRODUCTION TO NEOTROPICAL ENTOMOLOGY AND PHYTOPATHOLOGY

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Summary

Insects are among the most abundant and diverse organisms in terrestrial ecosystems, making up more than half of the earth's biodiversity. To date, 1.5 million species of organisms have been recorded, although around 85% of potential species (some 10 million) have not yet been identified. In the case of the Neotropics, although insects are clearly a vital element, there are many families of organisms and regions that are yet to be well researched. The high abundance and diversity of insects is the result of 400

million years of evolution, during which they have shown great adaptive capabilities, occupying different niches and ecosystems throughout the world. This evolution has been possible due to the presence of flowering plants, which insects use and interact with for alimentary, reproductive, biological control, pollination and habitat purposes. In phytopathology, plant diseases are analyzed; it is not surprising that insects are the vectors for many such diseases. We begin this study by giving an overview of the historic development of both disciplines: entomology and phytopathology, followed by a report of recent developments relating to insect evolution and biodiversity. The role these organisms play in vital ecosystem processes such as pollination and biological control is emphasized. Also stressed is the importance of recognizing global change and biodiversity loss as key elements for consideration of how to maintain ecosystem

integrity and prevent the mass extinction of insects by implementing public policies designed to preserve them.

1. Introduction

From the early days of agriculture, plant diseases—caused by mycoplasmas, viruses, bacteria, fungi, and parasitic angiosperms—have, along with insect pests, been considered an element that must be controlled in order for cultivated plants to provide their intended products. The idea of combating “the bad guys” that attack plants stems from an anthropocentric view of nature, as those organisms affecting plants valuable to man are part of a complex ecosystem that has been artificially modified and simplified for human use. Plants are considered healthy when they carry out all of their physiological functions. However, in nature all organisms are susceptible to being eaten or degraded by other organisms. In a natural system, plant populations maintain a certain biological integrity, and trophic level interactions formed by guilds or ecological assemblages of organisms interacting constantly within each ecosystem, maintaining a population dynamic between animals, plants, insects, fungi, bacteria, viruses, and mycoplasmas. The various organisms that feed on them as well—parasites, antagonists, commensalists, etc.—are part of the ecosystem. With human population growth and extensive and intensive agricultural practices, natural ecosystems have been modified and simplified into crop systems. Crops are affected by diseases and rampant insect pest population growth, because there are abundant food sources for reproduction and no natural enemies to exercise top-down control over them, as is the case in any natural system. It is in this scenario, human beings begin to struggle with diverse organisms that cause plant illnesses. Furthermore, attempts to mitigate or control the damage through physical means, either chemical or biological, often further disturb the original natural conditions.

Research on plant diseases arose from the human need to protect several crops that provide food or other products with economic value. Phytopathology, or plant pathology, is the science that studies the diverse agents that cause plant diseases. Disease in a plant can be understood as a physiological alteration or damage that affects its well being. The word is used in a broad sense when an organism affects a plant's health, be it mycoplasma, virus, bacteria, fungus, parasitic angiosperm, insect, mite, nematode, or other parasitic animal. When the problem arises due to adverse soil conditions caused by the scarcity of a particular nutrient, it is considered a disorder. The

term pathogen is commonly used in reference to live organisms that are causing damage to an entire plant or part of a host plant.

Thanks to scientific breakthroughs in understanding different pathogenic agents, research has become more diversified and specialized. Diseases caused by macro and micro parasites including insects, fungi, bacteria, viruses, and nematodes, among other agents, have been studied by entomologists, mycologists, parasitologists, bacteriologists, virologists, and nematologists. The introduction of phytopathology into any of these different fields requires an understanding of the basic concepts explained heretofore. Insects, being the most abundant and diverse animals on earth, are closely linked to the causal agents of several plant diseases. It is therefore vitally important to understand their biology, history, taxonomy, ecology, and evolution.

2. History

2.1. Phytopathology

In the nineteenth century, studies conducted by De Bary and Kuhn laid the foundations for modern plant pathology. Their descriptions were meticulous, and they proved the pathogenicity of a large number of microorganisms. Since the time of Linnaeus, it was known that pathogenic fungi were independent organisms. On the basis of this knowledge, in 1860 Pasteur provided a definitive refutation for the spontaneous generation concept; and in 1876 Koch proposed four postulates that would become crucial to pathogenic studies. In Europe, during this same period (1880), a Bordeaux mixture (lime-sulfur) was used to combat the downy mildew growing on grapevines (*Plasmopara viticola*) and in Ceylon (now Sri Lanka), to control coffee rust (*Hemileia vastatrix*). These advances aroused interest in studying disease control using chemical substances. The most commonly used were sulfur and copper sulfate; pathologists concentrated on finding the ideal dose and application period to effectively control parasites. However, continual crop reduction led to the search for other, more efficient chemical compounds. In 1934, Tisdale and Williams discovered dithiocarbamate fungicides—and in 1938, research began on cloranil-type quinines (tetrachloroparabenzoquinone). By 1943, diclone-type fungicides (2-3-dichloride-1-4 naphthoquinone) were being tested. This paved the way for the discovery of the antimetabolic mechanism of toxins; the concept of quelates was developed, and plant pathology research based on physiology and biochemistry began. At the same time, ecological studies shed light on the role of organisms in diseases involving parasite-host-environment interactions. Detailed knowledge of both fungus and insect pest life cycles showed that soil is an excellent medium for the transmission and survival of pathogenic fungi and many insect pests. During the second half of the 20th century, the parasite-host relationship was studied from a physiological and biochemical perspective, with analysis focusing on the mechanisms parasites use to penetrate a host and how it resists them. The “gene-for-gene” concept derived from Flor’s 1956 research on linen rust meant that “...for each gene conditioning the rust reaction on a host, there is a specific gene that conditions parasite pathogenicity.” Later, studies by Van der Plank broadened research on pests. Genetic and molecular biology research on many insect pests and parasitic fungi has brought benefits both to the field of entomology and plant pathology, with application to agricultural and environmental science.

2.1.1. Evolution of the Parasite-Host Relationship

A parasite is an organism that spends a substantial portion of its life in or on a host (or a small number of hosts), thus deriving nourishment and jeopardizing the survival and reproduction capacity of the host (Price 1977, Thompson 1994). The parasite-host relationship is interspecific and antagonistic; that is, the fitness of one of the interacting species increases as that of the other species decreases. Selection then acts on parasites, improving their chances to find appropriate hosts. Differences in how they feed influence the way that parasitic organisms specialize on hosts as well as how hosts defend themselves from parasites. Specialization can be defined as a limitation in the number of species with which a particular species interacts. Thus, an extreme specialist is one that depends on one species or a group of closely related species for survival and reproduction during much of its life cycle.

From an ecological perspective, all parasites share a common problem: they must satisfy their nutritional requirements and avoid all enemies on the host or they will die. They must adhere to the host, face physiological changes in it—sometimes induced by them—and compete with other predators or potential competitors; they must also deal with their own parasites without abandoning the host (Thompson 1994). On plants, parasites represent a specialized ecological niche that requires adaptations on the part of fungi. In molecular terms, these adaptations represent a dependency on the type of interaction that takes place between parasite and host, although the inactivation of plant defenses appears to be of primary importance (Heath 1987).

Mycologists and phytopathologists recognize two types of parasites: biotrophic and necrotrophic. The former is an organism that grows on another organism, in intimate association with its cytoplasm for all or part (during the development of one or several stages) of its life cycle, deriving energy from the live protoplasm. A necrotrophic parasite is also an organism that grows on another, but finally kills it; it completes its development by deriving energy from the dead cells of its host. Fungi can grow and reproduce in the absence of live protoplasm. They have an aggressive and destructive way of attacking and colonizing, frequently involving rapid growth rates and potent extracellular enzymes (Dick 1988, Hawksworth *et al.* 1996, Snell and Dick 1971, Ulloa and Hanlin 2006).

The success of biotrophic parasites depends on allowing the host to remain alive; this makes for a delicate balance between host and parasite (Savile 1979). The development of necrotrophic fungi is favored by a hypersensitivity response from the host, while in the biotrophic fungi; the response is hyposensitive to the host. Necrotrophic fungi can produce hormones but cannot alter translocation patterns, as tissue destruction sends a message to block infection sites. Necrotrophic fungi use tissues as substrates at the time of infection. In contrast, through alterations in translocation patterns, biotrophic fungi are able to use photosynthetic products and other byproducts of the infection. An obvious difference between biotrophic and necrotrophic pathogens is in the amount and type of hydrolytic enzymes secreted within host tissues. Necrotrophics produce plentiful amounts of enzymes of varying specificity, resulting in tissue degradation; biotrophics are known to cause a minimal amount of tissue damage (Heath 1987).

Although pathologists and mycologists have upheld the concept that specialization in the parasite-host interaction is determined by their genotype, they also support the idea that these interactions are mediated by environmental conditions (Savile 1976, Dick 1988, Hijwegen 1988, Isaac 1991, Lonsdale and Gibbs 1996). Thompson (1994, 1999, 2005) explains species co-evolution in his geographic mosaic theory, which is based on the fact that species distribution is not homogenous, so that a spatial mosaic of species richness is created. This theory takes into account other evolutionary theories: gene to gene, geographically structured races and mutualisms, succession cycles, recycling, alternance, diversification and escape, and lineage radiation theories. An ecological concern that has grown over time is the need to understand co-evolution as a progressive process, especially for the dynamics of biological communities that grow rapidly.

2.1.2. The Evolution of Phytopathogenic Fungi and Their Host Plants

Fungal parasite distribution is determined by the specificity and range of hosts as well as by environmental conditions that affect parasite distribution. Some parasite genera or species are always found on the same genera or species of host, while others are less selective and can develop ecological races that are associated with different host species or races (García-Franco 1996).

The coevolution of host and parasite involves not just one factor responsible for parasite diversification but a chain of adaptations. Other factors are a) topographic specialization relating to host tissue; b) biological specialization to a host environment, through parasite evolution in conjunction with the host involved; and c) sporadic successful leap over to a distantly related host. These jumps can be defined as transference from one host species to another, with or without genetic modifications (Pirozinski and Hawksworth 1988). Hijwegen (1988) considered the coevolution of plants and biotrophic parasites to be the evolution of a pathosystem that gives rise to a branched system. It constitutes a combination of evolutionary events and jumps to closely related taxa. Thus, fungal attacks on plants originate predominantly from factors relating to genetics, geographic overlap, and climate conditions. Specialized fungi are able to behave like phylogenetic taxonomists, choosing hosts on the basis of geographic overlap and favorable climate. Savile is a pioneer in the use of parasite-host data as a tool to shed light on the taxonomy and evolution of vascular plants (Savile 1970, 1976, 1979).

The affinity of rust fungi groups with plant groups is evident in Uredinales. In nature, we can encounter the entire gradient of relationships, be they on the host family, subfamily, genus, or species level. For example, within the Rosaceae family, the genus *Gymnosporangium* is a parasitic fungus characteristic of the Pomoideae subfamily (recorded on *Malus*, *Pyrus*, *Amelanchier*, *Aronia*, *Crataegus*, *Cydonia*, and *Sorbus*), but only on aecidiae in almost all Euroasian and North American species, the greatest diversity and host richness corresponding to North America. The subfamily Prunoideae (*Prunus*) is associated with the genus *Tranzschelia*, and the subfamily Rosoideae is associated with *Phragmidium* with the genera *Rosa* and *Potentilla*. The genus *Triphragmium* distinguishes species of *Filipendula*, causing Savile to suggest that it be placed in Rosoideae instead of the subfamily Spiraeoideae (Savile 1979). Leppik (1972) showed that rusts reflect an early biogeographic evolution of the Fabaceae

(Leguminosae). *Uromyces* (Pucciniaceae) prevails in the temperate northern regions on Faboideae; while several genera of Raveneliaceae are distributed in the tropics and southern region and are found mainly on Mimosoideae and Caesalpinioideae (Leguminosae). Examples of a parasite species on a host genus are *Hemileia vastatrix* on *Coffea* spp., *Cronartium conigenum* on *Pinus* spp., and *Melampsora lini* on *Linum* spp., among others.

Observation of this high degree of pathogenicity in the late 1970's has been applied to the implementation of biological control strategies against weeds that escape from natural enemies (parasites, grazers, and predators). This is the case of *Diabole cubensis* on *Mimosa pigra* (indigenous to America), considered monotypical (Cummins 1978). The weed was introduced into Australia, where it affected flora and fauna on huge areas, both agricultural and natural. Field exploration and observation in Latin America showed that *Diabole cubensis* appeared only on the previously mentioned host (Evans *et al.* 1995); for this reason, it was selected as a potential control agent.

2.1.3. Flor's Gene-For-Gene Theory

The gene-for-gene theory was proposed in 1956 by Flor, who studied genetics in linen cultivars that were attacked by the *Melampsora lini* rust. He demonstrated a close genetic relationship between host and pathogen. The theory is based on the concept that for each gene that determines the resistance of a linen plant, there is a specific, complementary gene in the rust that determines its virulence. For a host cultivar with only one resistance gene, there is a complementary single virulent gene in the pathogen; in certain cases, a host cultivar has two, three, or four such resistance genes, with a complementary two, three, or four virulence gene in the fungus.

Usually, although not always, resistance genes (R) in hosts are dominant, while susceptible ones (those lacking resistance) are recessive (r). In pathogens, non-virulent genes (A) are dominant, and virulent ones (a) are recessive. Therefore, there are four possible combinations for host-pathogen interactions. Three combinations--R-a, r-A, and r-a—cause compatible (susceptible) reactions, and infection is successful. One combination, R-A, results in an incompatible (resistant) reaction, and infection does not occur (Tarr 1972, Isaac 1991). Virulent genes appear in pathogens in response to new resistance genes in hosts. In other words, a new host resistance selects a new virulence in the pathogen. Hosts and pathogens are thus in a continuous state of coevolution (Tarr 1972).

Most plants are resistant to most pathogens: a potential pathogen finds most species outside its range of hosts. Non-host plants are therefore completely immune to infection, even when conditions are optimal for disease development, and even in the presence of abundant inoculum. Many plants do not get sick despite being theoretically susceptible, they can escape due the absent of the parasite or the ecological conditions are inadequate for infection. One example is *Phakopsora pachyrhizi*, a destructive fungus found in eastern Asia. Its presence has been recorded in southeastern Mexico, some Caribbean countries, South America, and Africa--but without its virulence (Cummins 1978). Soy in the U.S. is not parasited by *P. pachyrhizi* because the fungus is not found there (Hijwegen 1988). In other words, not all healthy plants are immune, but they can

show apparent resistance. Furthermore, if a plant is susceptible only when young or when blooming, and the pathogen is inactive or absent during that stage, the plant simply will not be infected. Temperature fluctuations and a lack in humidity so extreme as to lead to desiccation, will also affect the development and dispersal of a pathogen. Although some plants can escape, climatic change can cause an epidemic to begin (Isaac 1991).

Much research has been directed at creating resistant plant varieties, and the gene-for-gene theory has been corroborated. In 1963, Van de Plank introduced the term vertical resistance to describe a situation in which plants show high levels of resistance to a certain physiological pathogen race but are quite vulnerable to other races of the same organism. Some hosts frequently exhibit a hypersensitive response, usually during early infection; the pathogen is then unable to establish or multiply in the plant's tissue. This is known as resistance to specific races. In horizontal resistance, plants have a general resistance to pathogens; it involves a non-specific race of fungus that is controlled by a large number of genes (polygenic resistance). Horizontal resistance is useful on cropland in order to gradually reduce the spread of a disease.

The main objection to the gene-for-gene theory relating to microevolutionary reciprocal change is that it is based on examples from profoundly disturbed agrosystems that are not representative of natural ecosystems; furthermore, it cannot be applied to all agricultural systems (Pirozynski and Hawksworth 1988), and it places little emphasis on species ecology. Since the 80's, substantial data have been obtained on the nature and organization of plant cell walls and the alterations that they suffer when a parasite infects their cells. Through dying techniques, it can be observed how suberin, callose, lignin, and other phenolic compounds are deposited in the plant's cell wall in response to pathogens or abiotic stress (Chamberland 1994).

When a plant has recognized the presence of a particular pathogen through its gene-for-gene system, it can enlist a polygenic arsenal of other genes to defend it. A long-term study conducted by Burdon and Thrall (1999) on the dynamics of allele resistance frequencies and non-virulence within and among natural populations of Australian wild linen (*Linum marginale*) and the linen rust *Melampsora lini* suggest that a population with broad geographic structure can be essential to maintaining polymorphisms, which evolve simultaneously in plants and rusts. Gene-for-gene coevolution occurs in natural populations when the interaction between a host and parasite are controlled by genes that are vital to host resistance and when the parasite is non-virulent (Thompson 1999). However, gene-for-gene relationships are only one component of parasite-host coevolution.

2.1.4. Pathogenetic Mechanisms in Plant Parasitic Fungi and Hyperparasites

Alteration caused by a fungus in a host's cell walls is probable a key event in pathogenesis, as it allows pathogens to penetrate cell walls by secreting specific enzymes that degrade them. Several biochemical, histological, and cytochemical studies on the host-fungus interface have revealed that pathogenic fungi produce structures that allow penetration before the plant becomes infected and degrade its cell walls through mechanical pressure and enzymatic activity. Specialized cellular structures for cell wall

penetration are appressoria, haustoria, and microhyphae (Nicole *et al.* 1994).

Appressoria. For fungi such as rusts, *Colletotrichum* species, endophytes, and vesicle-arbuscular mycorrhizae, interaction with the host surface results in the formation of appressoria. These are described as formations from which a minute infection peg or germinal tube grows; it is capable of overcoming physical barriers posed by the host, such as cuticular layers, in order to penetrate it. It begins to form when the parasite's germinative tubes have stopped growing. The cell wall, cytoskeletal microtubules, and apical vesicles are probably involved in appressoria differentiation. They are frequently associated with stomatal penetration, although they have also been described penetrating a plant but leaving its surface intact (Isaac 1991). Several factors control the appearance and growth of appressoria, including temperature, plant exudates, and fungal genotype. Surface penetration by appressoria requires signals that can result in close adherence to the host substrate. The extracellular matrix of these structures contains specific proteins that are involved in the recognition and initiation of degradation in plant cell walls. Infection pegs or appressorial hooking begin at the appressorium and proceed to penetrate the host cell wall.

Haustoria. After the contact with the host has been established, the pathogen develops penetration pegs, vesicles and inter- or intracellular mycelium, marking the beginning of host tissue colonization. Haustoria are produced by fungi such as rusts, powdery mildews, downy mildews, and Exobasidiales. Ultrastructural research has distinguished several types of haustoria based on their morphology. In *Phytophthora*, they range from simple elongated shapes to structures that are similar to fingers. *Exobasidium* spp. haustoria are short and lobed, while those of *Cercosporidium* are finely branched. The haustorium wall is involved in recognizing resistant cultivars. Polysaccharides and glycoproteins are present in the haustorium wall and extrahaustorial matrix. A linked-glucose or manose have been found in the extracellular sheath. For example, in *Puccinia graminis* there are β -1,3 glucans, while in *Puccinia sorghi* there are linked β -1,6.

Microhyphae. Fungi may differentiate microhyphae, also called fine hyphae; they can extend for appreciable distances into host walls and cause their breakdown and/or to rupture.

Extracellular sheath. A wide range of fungi that include pathogens, saprophytes, endophytes, and mycorrhizal fungi produce a noticeable extracellular cover of material. It appears on a wide range of organisms, from *Peronospora* and *Sclerospora* to fungi from the major groups, including the obligate parasites (*Cronartium* and *Puccinia*) as well as wood-rotting fungi (*Phanerochaete*, *Rigidoporus*). Extracellular sheath formation occurs during a period of the fungal life cycle in response to certain physiological conditions, regardless of the type of illness that the fungus causes. In most cases, extracellular sheath appears as a fibrillar net, with fibrils arranged either densely or loosely around the hypha. The extracellular sheath adheres to the fungal structure and can establish a close junction between the host's mycelium and cell wall.

Chitin is the second most commonly found biodegradable polymer in nature. Present in almost all fungi, it is the principal component of the fungal wall. Chitinase has the

following general properties: active in slightly acidic pH, optimal high temperature of 30-50 °C, and high degree of stability due to glucosilation. Chitinases are inhibited by copper and mercury salts and competitively by chitobionolactone oxime and allosamidin. Chitinase activity is stimulated by partial proteolysis of microsomal fractions with commercial proteases such as trypsin or partially purified proteases. Chitinase has been implicated in several morphological and physiological processes that occur during the fungal life cycle. Furthermore, it appears to play a role in early stages of the parasite-host interaction in biotrophic and necrotrophic mycoparasitism. Chitinases have been reported in entomopathogenic fungi and arbuscular mycorrhizae. Chitine degradation involves two steps: 1) chitin microfibrilles are split by endo- or exochitinase, or by both simultaneously. Endochitinases divide chitin up randomly, resulting in light molecular weight soluble oligomeres of GlcNAc such as chitotetraose and chitotriose, the dimere chitobiose being dominant, and 2) the chitobiose is hydrolized into monomers of GlcNAc by β -1, 4 N-acetylglucosaminidase (Manocha and Balasubramanian 1994).

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Biographical Sketches

Arturo Bonet is an associate researcher in the Department of Entomology at the Instituto de Ecología A. C., Xalapa, Veracruz, Mexico. For a number of years he has devoted his time to the study of biological interactions (parasitoid-bruchid host–host plant) and the biological control of insect pests. His interest is in the Bruchidae attacking bean pulses and interacting parasitoids. He has promoted native parasitoids for biological control of bruchids in small farmer pulses storage.

Gloria Carrión was born in Mexico, where she received a PhD in Biological Science from the Universidad Nacional Autónoma de México (UNAM), specializing in mycoparasitic fungi of *Hemileia vastatrix* (coffee rust). She has taught at the Universidad Veracruzana's Faculty of Biology as Professor of Mycology and Ecology. In 1983, she became a Research Assistant at the Instituto de Investigaciones sobre Recursos Bióticos (INIREB), and in 1989 she joined the Instituto de Ecología A. C. as an Associate Researcher. Dr. Carrión has worked on many different projects focusing on parasitic fungi that affect native Mexican plants, principally Uredinales, with special attention paid to weed control. She has also worked on research involving mycoparasites that attack obligate parasitic fungi, insect parasites, and most recently on isolated fungi of the golden potato nematode (*Globodera rostochiensis*).