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The Rust Fungi

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The rust fungi are a monophyletic group of approximately 7000 species in the basidiomycota and are highly specialized obligate parasites of plants. The life cycle of rusts can be complex. Some rusts have up to five spore stages that alternate between haploid and dikaryotic nuclear conditions and that can occur on two taxonomically unrelated host plants. The rusts have evolved specialized structures that allow them to penetrate and obtain nutrients from living host cells. Biologic forms of a single rust species may differ in ability to attack different genera of host plants. Furthermore, within a single rust species they can be highly variable in ability to attack different genotypes of one host species. At the species level, genes that condition avirulence/virulence in rusts interact in a specific relationship with rust-resistance genes in plants. Many of the most important plant diseases in the world are caused by rust fungi.

Introduction

The rust fungi are obligate parasites of plants from which they obtain nutrients, and on which they reproduce and complete their life cycles. There are an estimated 7000 species of rust fungi that are parasites of plants from ferns to advanced monocots and dicots. Rust fungi cause diseases in economically important plant species such as cereals, legumes, composites and many trees. The rust fungi derive their name from the rust coloured masses of urediniospores that are clonally produced on plant hosts. The rusts are biologically fascinating since their life cycles can vary between two and five distinct spore stages that include haploid, diploid and dikaryotic nuclear conditions. Some rust species require two taxonomically unrelated hosts to complete their life cycle, whereas some species require only one host. Species of rusts have evolved so that they are highly specific to which plant species they can infect, colonize and reproduce on. **See also:** [Fungal Pathogens of Plants](#)

Because of their distinct appearance rusts of cereals were long noted in the historical records of antiquity (Arthur, 1929). Aristotle (384–322 BC) writes of rust being produced on grains by warm vapours, and of years with heavy damage to grain crops due to rust. Theophrastus (371–287 BC) also wrote of the effects of rust on cereals. The Roman festival of Robigalia was celebrated on 25 April when the

wheat was filling grain, to placate the rust god Robigo to reduce the damage caused by rust. Rusts were determined to be biological entities only in 1767 when Fontana and also Tozzetti considered rust to be parasitic plants of grain crops. **See also:** [Fungi and the History of Mycology](#)

Rust Life Cycles

Most rust fungi have complex life cycles. A common pattern of a rust life cycle, which is also the most complex, involves five distinct spore stages on two unrelated hosts. This life cycle is called macrocyclic for its complete suite of five distinct spores, and heteroecious, in that it requires two hosts for completion of the cycle. Details of these spore stages are shown in **Figure 1**. At the beginning of the growing season germination of teliospores (**Figure 1a**) commences. Teliospores were produced the previous growing season on the host plant and overwintered or oversummered, usually on dead host tissue, in dark brown or black pustules called telia. Teliospores are generally not very mobile, although, with some rust fungi, they can be carried long distances by wind or other agents. The diploid teliospores germinate in place and undergo meiosis to produce four or more haploid basidiospores (**Figure 1b**), which are forcibly ejected into the air. Basidiospores of heteroecious rusts cannot infect the telial host species and must travel to another host where they infect young, vigorous host cells directly through the cell walls. Basidiospores are fragile and cannot tolerate drying, hence they do not travel long distances, and are often released during the night and during seasons when moisture is plentiful. Basidiospores invade host tissues to produce haploid colonies that are called pycnia. The pycnia can be of two or more mating types. Within each pycnium are produced minute, simple pycniospores embedded in insect-attracting nectar on the host's

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Online posting date: 15th September 2009

ELS subject area: Plant Science

How to cite:

Kolmer, James A; Ordonez, Maria E; and, Groth, James V (September 2009) The Rust Fungi. In: Encyclopedia of Life Sciences (ELS). John Wiley & Sons, Ltd: Chichester.

DOI: 10.1002/9780470015902.a0021264

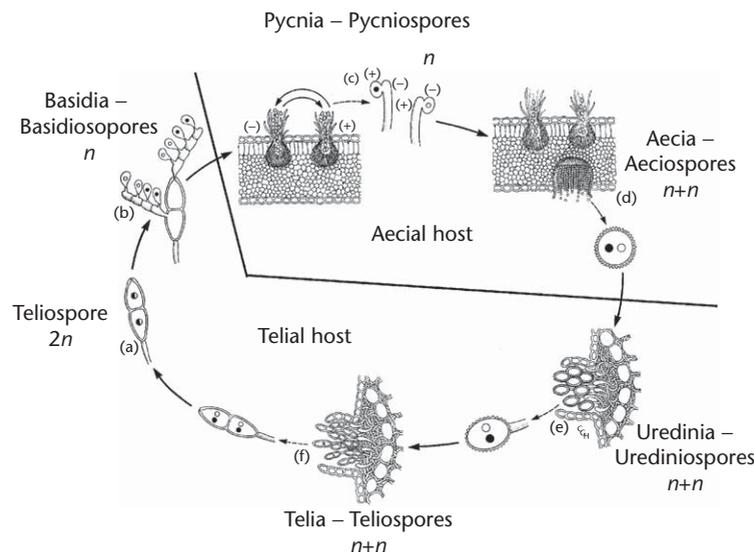


Figure 1 Life cycle of a macrocyclic-heteroecious rust. (a) mature, diploid teliospore, (b) basidia with basidiospores, (c) pycnial (spermatogonial) stage, (d) aecial stage, (e) uredinial stage and (f) telial stage. From Alexopoulos *et al.* (1996), drawn by Carol Gubbins Hahn.

surface – leaves, petioles, woody stems or flower parts and can be bright orange to (less often) colourless. Insects or surface moisture (rain or dew) distribute pycniospores on the host surface or between neighbouring plants, resulting in fertilization (Figure 1c), also called plasmogamy (the uniting of two cells to form a single cell with two genetically distinct, haploid nuclei). Once this occurs, the fungus forms the next spore stage (Figure 1d), the aecium and aeciospore, respectively. For rust species that infect leaves, this usually occurs on the lower leaf surface as dikaryotic hyphae (where each cell contains two separate, haploid nuclei) grow through the leaf and proliferate to form an aecial colony near the undersurface. Aecia do not usually occur singly, but in clusters, reflecting the pycnial clusters on the upper leaf surface. The colour of the aecial mass is often light orange. For many other rust species, aecial production may occur at the periphery of pycnial clusters or in the same areas where the pycnia occurred earlier. Dikaryotic aeciospores are usually produced in chains, within pustules that resemble groups of blisters or cups. Aeciospores have finely ornamented surfaces, composed of densely packed rounded projections or complex plates. Aeciospores are produced in quantity, and can travel long distances. This is necessary considering that they need to find another host. Once deposited on suitable host tissues, usually leaves, aeciospores germinate rapidly and usually invade cells through stomata. The resultant infection and colony formation results in another pustule called an uredinium, containing urediniospores (Figure 1e). This is the stage of the rust life cycle that is most familiar to plant pathologists because it is the only stage that is capable of repeating on the same host, and hence can increase rapidly through only a few generations, causing an epidemic. Urediniospores are produced singly, on stalks. Stalks do not remain attached to the spore when it is released, however. Similar to

aeciospores, urediniospores are dikaryotic. Late in the growing season when plant derived nutrients are declining, uredinia convert to telia (Figure 1f), and produce increasing numbers of teliospores as they begin to darken. These teliospores are thick-walled and resistant to cold or drying, and they serve as the resting stage for the fungus through the dormant state of the host. **See also:** Basidiomycota; Fungal Spores

The macrocyclic heteroecious life cycle is common, but many rust fungi have evolved shortened life cycles in various ways, usually in response to a shortened growing season for the hosts, due to high latitude, high altitude or desert conditions (Savile, 1953). Most, but not all, rust biologists assume that the most complex life cycles are primitive, and shortened cycles are more evolutionary advanced forms derived from the complex types. A complex terminology has been developed to describe the many ways in which abbreviated life cycles occur. In general, very short life cycles composed of three or fewer spore stages are referred to as being microcyclic, and life cycles that remain on a single host are called autoecious. Rusts with a single stage of urediniospores are asexual, most likely due to the loss of the alternate host. Sometimes the host ranges of the telial and aecial stages may not correlate to plant families. Naturally occurring macrocyclic, heteroecious rust fungi can have broad ranges of many genera of hosts, sometimes in several families for the aecial host, but a narrow range for the telial host, such as in *Puccinia andropogonis*, or the opposite, such as with *Puccinia coronata*. It seems obvious that host range depends on ecological factors, such as host diversity and proximity over the size of the geographical range over which the rust fungus occurs. Aecial hosts of heteroecious rust fungi must be relatively proximal to the telial host (Savile, 1976) since basidiospores travel shorter distances than aeciospores. This often leads to geographic-

and host-specific forms of each species, most of which have not been elucidated adequately.

Commonly a heteroecious, macrocyclic rust species has a correlated autoecious, microcyclic form that occurs only on the aecial host. In virtually all cases when this occurs, telia of the microcyclic form are found instead of aecia on the aecial host. This pattern has been formalized as Tranzschel's Law (Cummins and Hiratsuka, 2003). It has been proven to be useful in confirming alternate hosts of those heteroecious rusts that have a correlated microcyclic form, because the teliospores are identical in the two forms.

Phylogeny and Taxonomy of Rust Fungi

Rust fungi are in the phylum Basidiomycota, the same class of fungi as mushrooms, since they produce haploid basidiospores on basidia. Based on basidial morphology, some classifications place rust fungi in the subclass heterobasidiomycetes since the mature basidia have two sections, the basal hypobasidium and the epibasidium that bears the basidiospores on the sterigmata. Webster (1980) places rust fungi along with smut fungi in *Teliomycetes* based on their similar basidial characteristics. Using DNA sequence data from the large ribosomal subunit (Swann *et al.*, 2001) established three classes: *Urediniomycetes* that included the rusts, *Ustilaginomycetes* that included the smut fungi and *Hymenomycetes*, that included mushrooms and shelf or bracket fungi. Within *Urediniomycetes*, the rusts account for 95% of the species. The rust fungi in the order *Uredinales* are a distinct monophyletic group within *Urediniomycetes*.

Classification of rust families was traditionally based on morphology of the telium and teliospores (Alexopoulos, 1962). Three families were described based on telium morphology: species in *Melampsoraceae* have sessile (non-stalked) teliospores that are formed in columns in the telium; species in the *Pucciniaceae* have stalked teliospores that are produced in a single layer in the telium and species in the *Coleosporiaceae* do not form a promycelium but karyogamy and meiosis occurs directly within the teliospores that become septate during the germination process. Using telial morphology, in addition to spermogonial type, and characteristics of the urediniospores and aecia, Cummins and Hiratsuka (2003) proposed 13 families of rust genera.

Aime (2006) examined representative species from the 13 families proposed by Cummins and Hiratsuka (2003) for sequence variation in the 18S and 28S nuclear rDNA regions. Three major suborders were delineated: *Urediniineae* had species that had the aecial stage on angiosperms with pedicellate teliospores; *Melampsorineae* had species of heteroecious types with aecial stage on gymnosperms with sessile teliospores and *Mikronegeriineae* had species with aecial stage usually on nonpine gymnosperms and in microcyclic types the teliospores functioned as urediniospores, with short pedicellate or sessile teliospores. The 13

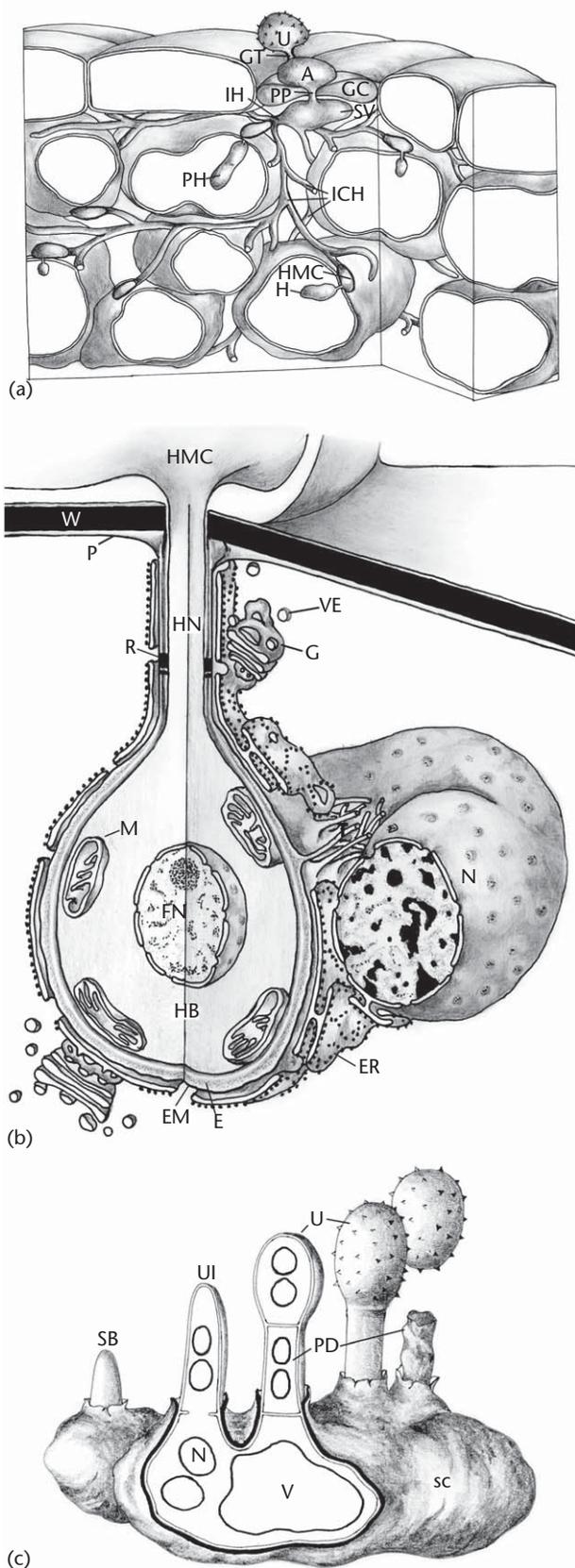
families proposed by Cummins and Hiratsuka (2003) were placed into the three suborders. Aime (2006) concluded that at the family level host associations were indicative of rust phylogeny and that morphological characteristics were not necessarily good predictors of the familial relationships.

Identification of individual species of rust fungi can be extremely difficult. In many cases only one or two spore stages may be present on a single host. In the case of heteroecious rusts, the identity of the alternate host may not be known. Arthur (1934) considered it essential to identify the host plant first before using his taxonomic keys that were largely based on spore morphology. Some researchers have preferred to use a broad species concept emphasizing spore and structural morphology, regardless of the host on which the rust occurred. As an example, Eriksson (1899) described leaf rust on wheat as *Puccinia triticina*, a single species, with telial host range largely restricted to wheat. Cummins and Caldwell (1956) based on overlapping teliospore morphology included leaf rust of wheat in the species complex of *Puccinia recondita* that had telial hosts on several species of grasses, wheat and rye, and had alternate hosts in the families *Ranunculaceae* and *Boraginaceae*. Anikster *et al.* (1997) determined that leaf rust of wheat that produced pycnial infections only on *Thalictrum speciosissimum*, was largely restricted to common hexaploid wheat and tetraploid durum wheat for telial hosts, and was sexually incompatible with members of *P. recondita* that had alternate hosts in the *Boraginaceae* such as *Anchusa* spp. Based on the sexual incompatibility and the distinct telial and pycnial host ranges, leaf rust on wheat is once again considered a separate species (*P. triticina* Eriks.) from leaf rusts on rye and other wheat relatives.

The Biotrophic Infection Process

As obligate parasites, the rusts are completely dependent on the presence of living plant hosts to reproduce and complete their life cycles. As biotrophs, the rusts are specially adapted to obtain nutrients from living plant cells. Axenic culture of wheat stem rust (*Puccinia graminis*) has been accomplished (Williams, 1984) as mycelia, urediniospores and teliospores were produced in culture. However, the results were inconsistent since not all isolates could be successfully cultured and the mycelia from the axenic cultures was not necessarily genetically identical to the progenitor urediniospores.

Uredinia are the economically important disease stage for many rusts. Urediniospores that are carried in wind currents are deposited on the host surface, usually by a rainfall event. The infection process for some *Puccinia* spp. (Staples and Macko, 1984) and *Uromyces* spp. (Mendgen and Hahn, 2002) has been studied in detail. The urediniospores imbibe water, swell and produce a germ tube after coming into contact with a film of free water on the plant surface (Figure 2a). After 4–6 h a germ tube is produced. For many rusts growth and orientation of the germ tube is



controlled by a thigmotropic response to the topography of the host surface (Wynn and Staples, 1981). The germ tubes continue to elongate until they come into contact with a stoma. Rusts are very specific to the host topography and stoma, rusts inoculated onto nonhost plants do not locate the stoma, or may not even properly germinate. Once the stomata is found, the germ tube stops elongating and at the tip of the germ tube an appressorium is formed over the stoma. This is followed by formation of a penetration peg from the appressorium that pushes through the stoma to enter the intercellular space within the host leaf or stem in which a substomatal vesicle is formed. Some rusts including stem rust of wheat, barley and oat (*P. graminis*) requires some light to be present to form a substomatal vesicle since the rust responds to increased concentrations of CO₂. Infection hyphae grow from the substomatal vesicle towards the mesophyll cells. The tip of the infection hyphae is delimited by a septum and forms a haustorial mother cell after coming into contact with the mesophyll cell wall. A penetration peg is formed from the haustorial mother cell, which allows the formation of the haustoria that is invaginated between the host cell wall and the extra-haustorial membrane that is derived from the host cell plasma membrane (Figure 2b). Nutrient uptake occurs across the extra-haustorial membrane. The host cells are likely manipulated by signals from the haustoria to maintain viability in order to allow the transport of sugars and amino acids across the extra-haustorial membrane into the haustoria. Additional haustoria are formed when other infectious hyphae come into contact with mesophyll cell walls. At 7–10 days after the initial infection, mycelia in the host tissue forms sporogenous cells in the intercellular space under the epidermis. Spore buds from the sporogenous cells break the surface of the epidermis (Figure 2c). The urediniospore initial, the pedicel and ultimately urediniospores are successively formed on the emergent spore buds (Harder, 1984). See also: [Coevolution: plant–Microorganism](#)

Host Specificity in Rusts

One of the most important characteristics of plant rusts is their exceptionally high degree of host specificity. This

Figure 2 Diagrammatic representation of infection structures of a cereal rust fungus. (a) Uredinal infection structures at 60 h. U, urediniospore; GT, germ tube; A, appressoria; GC, stomatal guard cell; PP, penetration peg; SV, substomatal vesicle; IH, infection hyphae; PH, primary haustoria; ICH, intercellular hyphae; H, additional haustoria. Drawn by James Chong. Reproduced from Harder (1984). (b) Cross section of invaded host cell at the site of penetration to show three-dimensional representation of a mature haustoria and association with host cell organelles. E, EH, extra-haustorial matrix; EM, extra-haustorial membrane; ER, endoplasmic reticulum; FN, fungal nucleus; G, golgi body; HB, haustorial body; HMC, haustorial mother cell; HN, haustorial neck; M, mitochondria; N, host nucleus; P, plasmalemma; R, ring neck; T, tubule complex; V, vesicle; W, host cell wall. Drawn by James Chong. Reproduced from Harder and Chong (1984). (c) Urediniospore formation on a cereal leaf. U, urediniospores; SC, sporogenous cell; SB, spore bud; UI, urediniospore initial; PD, pedicel; N, nucleus; V, vacuole. Drawn by James Chong. Reproduced from Harder (1984). Used with permission from Elsevier.

complexity occurs at many levels. Plants are resistant to almost all rusts that they would naturally encounter, and would be a suitable host to perhaps only a few rust species. Owing to their economic importance, the cereal rusts have been studied extensively for host specialization. Collections of *P. graminis* (stem rust) obtained from infected wheat plants are only slightly pathogenic to oat and rye plants. Conversely collections of *P. graminis* from oat and rye are only weakly pathogenic to wheat. The biological level of *forma specialis* (f. sp.) is used to describe separation of rusts based on host association within a single species (Anikster, 1984). Thus *P. graminis* f. sp. *tritici* is the form that attacks *Triticum aestivum* (wheat), *P. graminis* f. sp. *avenae* attacks *Avena sativa* (oat) and *P. graminis* f. sp. *secalis* attacks *Secale cereale* (rye). Furthermore, within *forma specialis* on a single host species, there also exists genetic variants for virulence to different resistance genes in host plants of a single, compatible species. Physiologic races of rust differ in virulence to host-resistance genes. Stakman and Piemeisel (1917) showed that different single uredinia derived isolates of *P. graminis* f. sp. *tritici* differed for virulence when tested with a diverse set of wheat cultivars. Flor (1971) in his landmark studies working with flax rust caused by *Melampsora lini* determined that genes in the host that expressed resistance and genes in the rust that expressed avirulence were highly specific in their interaction and corresponded to each other in a one to one relationship. This specific interaction between genes in the host and rust parasite known as the gene for gene relationship has become a central principle in the general field of plant pathology as other plant pathogens other than rust fungi such as bacteria, oomycetes and ascomycete fungi, interact with their hosts in the same manner. Genes in plants that condition resistance to specific rust races encode for proteins that often contain a nucleotide-binding site (NBS) and series of leucine-rich repeats at the C-terminus (Huang *et al.*, 2003). In flax rust, the AvrL567 protein is transported across the host cell membrane and interacts with gene products from the corresponding host-resistance gene to condition an incompatible response (Dodds *et al.*, 2004; Ellis *et al.*, 2007) which is often expressed as hypersensitive death of host cells, or as small uredinia surrounded by necrosis or chlorosis. Compatible interactions between the host and rust occur when the plant cannot recognize the rust as either rust isolates lack the specific avirulence genes, or host plants lack the specific resistance genes. **See also:** [Hypersensitive Response in Plants](#); [Resistance Genes \(R Genes\) in Plants](#)

Examples of Rust Fungi

Coffee rust: *Hemileia vastatrix* Berk. & B.

The most important disease of the coffee tree worldwide is caused by the rust fungus *Hemileia vastatrix*. Coffee rust causes premature drop of the infected leaves that results in significant yield loss, specially in the season following



Figure 3 Uredinial infection of *Hemileia vastatrix* (coffee rust). Photo courtesy of Howard Schwartz.

infection. The disease was first observed in 1861 in East Africa and later appeared in Sri Lanka in 1867. Coffee plantations in southeast Asia were devastated by *H. vastatrix* and replaced with tea plantations. It is believed that coffee rust was responsible for the switch to tea as the main social beverage of the British (Schieber and Zentmeyer, 1984). Coffee rust is present in all major coffee-producing countries.

Infection by *H. vastatrix* occurs mainly on the leaves of the coffee tree (**Figure 3**), although occasionally young stems and berries can also be infected. Urediniospores penetrate through the stomata on the abaxial surface of the leaves and yellow-orange coloured lesions develop later. New maturing urediniospores emerge through the stomata, rather than breaking through the epidermis of the leaves to form pustules, which is characteristic of most other rust fungi. The lesions can coalesce and form large necrotic spots as they age, and the leaves drop off prematurely (Agrios, 2004). The fungus can sometimes produce teliospores that germinate and give rise to basidia and basidiospores, however, the alternate host of *H. vastatrix* is not known (Coutinho *et al.*, 1995). The pathogen survives through continuous urediniospore cycles on the coffee plant.

White pine blister rust: *Cronartium ribicola* J. C. Fisch. ex Rabenh

The rust fungus *Cronartium ribicola*, native to Asia, has become one of the most important diseases of forests in North America affecting five-needle pines after it was introduced from Europe in 1906 (Tainter and Baker, 1996). It is a heteroecious macrocyclic rust that produces spermogonia and aecia on white pine and uredinia and telia on wild and cultivated currant and gooseberries of the genus *Ribes*.

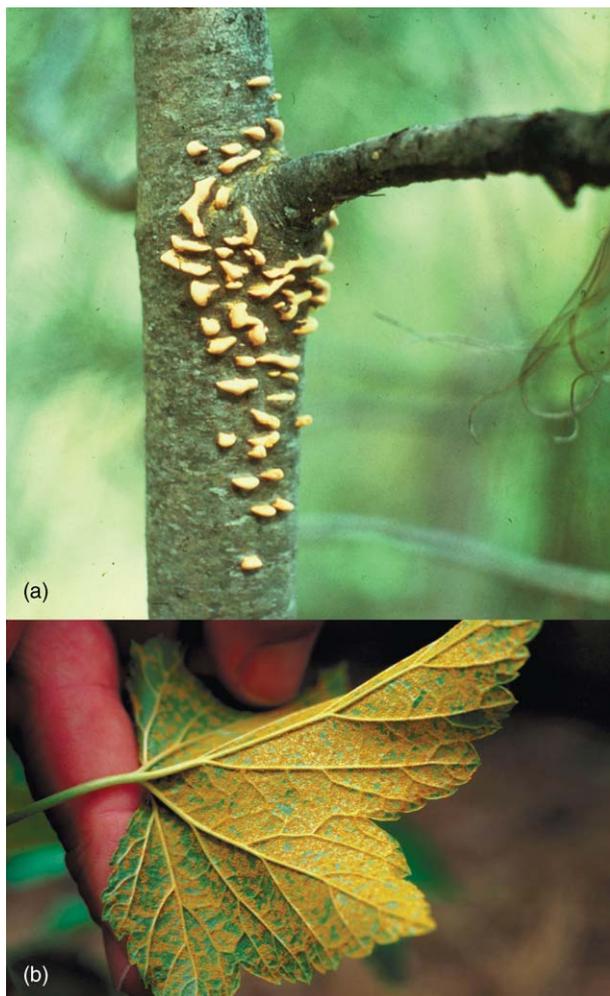


Figure 4 (a) Aecial infection of *Cronartium ribicola* (white pine blister rust) on pine tree. USDA Forest Service, Ogden UT. (b) Uredinia of *Cronartium ribicola* on *Ribes* sp. Robert Anderson, USDA Forest Service.

The disease cycle of *C. ribicola* can take years to complete. Basidiospores infect through the stomata of the pine needles, and the fungus grows intercellularly into the branch to form a swollen canker. In the spring of the following year spermogonia are produced, although a longer latent period can occur. Aeciospores erupt through the bark of the pine from blister-like lesions at the edge of the canker where spermogonia were formed the previous year (Figure 4). Aecial infections are perennial on pines as the fungus continues to spread into healthy bark until the death of the branch or stem. Aeciospores are carried long distances by wind and infect *Ribes*, on which uredinia and telia are produced. Teliospores germinate *in situ* to produce basidiospores that infect pine, completing the life cycle (Hansen and Lewis, 1997).

The white pine blister rust control programme started in 1909, which included *Ribes* eradication and quarantine measures has been considered the most extensive forest disease control effort in the history of US forestry.

However, in 1967 after millions of dollars were spent and only limited success was achieved, the programme was finally terminated (Maloy, 1997).

Hollyhock rust: *Puccinia malvacearum* Bert.

The hollyhock rust is a microcyclic fungus that only produces teliospores and basidiospores and completes its life cycle on one host. It is the most common disease that affects hollyhock *Alcea rosea*, but it can also infect other species of the Malvacearum family (Walker, 1969). *P. malvacearum* was first found in Chile in 1852 but it is now distributed worldwide. All green parts of the hollyhock plant are susceptible. The rust fungus can survive as mycelium in overwintering plants or as teliospores on dead or living tissue. The teliospores give rise to basidiospores that can be wind blown to infect neighbouring plants or can reinfect the same host. Basidiospores penetrate the cuticle directly and the mycelium grows between and inside the plant cells. The rust appears as reddish-brown pustules on the underside of the leaves, whereas on the corresponding upper leaf surface yellow to orange discoloration is present (Pirone, 1978). Sanitation is essential for disease control, as all infected plant tissue must be removed to avoid overwintering of the inoculum.

Wheat rusts: *Puccinia graminis* f. sp. *tritici* Pers., *P. triticina* Eriks. *P. striiformis* Westend

There are three rust diseases on wheat. Stem rust is caused by *P. graminis* f. sp. *tritici*, leaf rust by *P. triticina* and stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (Figure 5). *P. graminis* f. sp. *tritici* and *P. triticina* are macrocyclic heteroecious rusts with uredinia and telia occurring on wheat, and pycnia and aecia occurring on the alternate hosts *Berberis vulgaris* (common barberry), and *T. speciosissimum* (meadow rue), respectively. Uredinia and telia of *P. striiformis* occur on wheat; however, the alternate host has never been found. All three wheat rusts can cause disease on a continental level as urediniospores can be carried for thousands of kilometres in the prevailing wind currents. The wheat rusts are also highly variable, as many different physiologic races have been described for all three. Stem rust of wheat caused major epidemics in the United States from 1900 to the mid-1950s with millions of dollars in losses. The barberry eradication programme that started in 1919 has largely eliminated the alternate host of the pathogen. Stem rust has not been a major disease on wheat in the United States since the mid-1950s due to resistant wheat cultivars and removal of the alternate host. Leaf rust is the most common and widespread disease of wheat in North America and worldwide. The alternate host *T. speciosissimum* is restricted mainly to areas of southern Europe and southwest Asia but is absent in almost all other wheat-producing regions of the world. The leaf rust fungus usually reproduces through continuous cycling of urediniospores on wheat. Stripe rust is most commonly found in regions where wheat matures under cool and moist

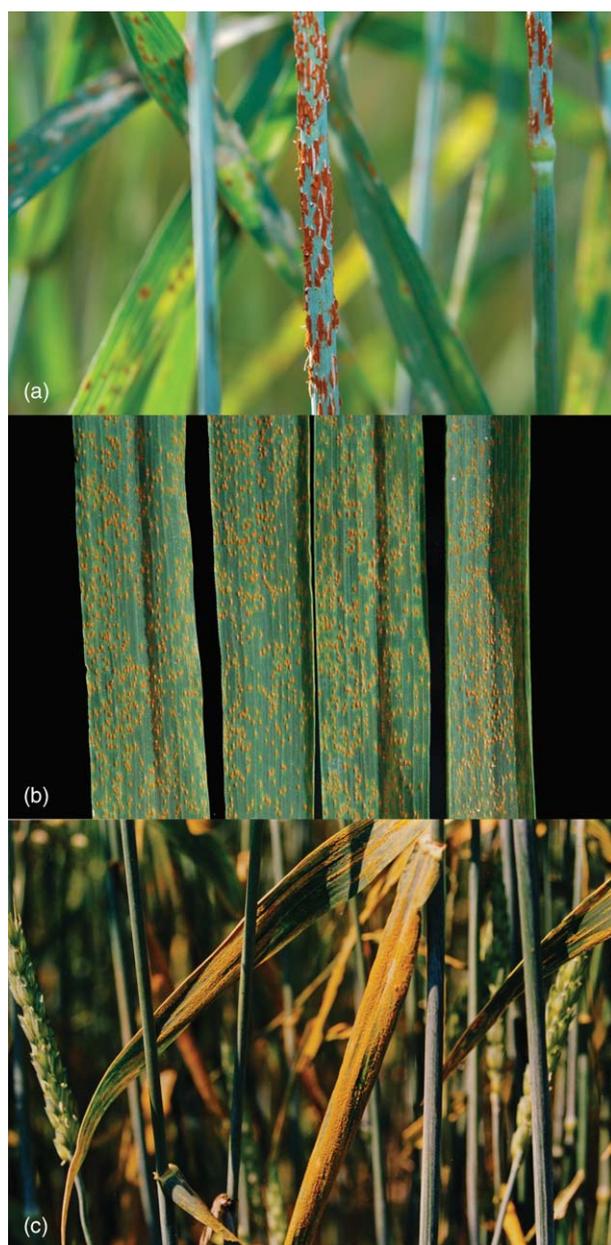


Figure 5 (a) Stem rust caused by *Puccinia graminis* f.sp. *tritici* on wheat – photo by Yue Jin –USDA-ARS. (b) Leaf rust caused by *P. triticina* on wheat – photo by James Kolmer. (c) Stripe rust caused by *P. striiformis* f. sp. *tritici* on wheat – photo by James Kolmer – USDA-ARS.

conditions, and uredinia are produced in yellow stripes between the leaf veins. Isolates of *P. striiformis* f. sp. *tritici* that are adapted to warmer temperatures have been recently described (Milus and Seyran, 2006). The three wheat rusts generally have slightly different optimum temperature and moisture conditions for infection and preference of tissue to colonize, giving each pathogen different niches on the same host. Stem rust infects mainly the stems and heads of wheat, leaf rust infects the leaves and stripe infects the leaf and heads. Extensive efforts have been made to

control the wheat rusts through breeding wheat cultivars with rust resistance (Roelfs *et al.*, 1992). **See also:** *Triticum aestivum* (Wheat)

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