Economically important plant parasites: rusts and smuts

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Abstract

Rusts (Pucciniomycotina) and smuts (Ustilaginomycotina) are the two most diverse groups of plant-pathogenic basidiomycetes. With a worldwide distribution, many of these phytopathogens are economically important, destroying many commonly cultivated crops. In this chapter we review both the historical and modern views on the classification and systematics of rusts and smuts, describe their biology and life cycles, highlight their relationship with host-defense response mitigation, and provide examples of pathogens that pose a threat to our modern agriculture.

Introduction

Rusts and smuts are agriculturally important plant pathogens, collectively parasitizing maize, wheat, sorghum, oats, barley, sugarcane, cereals, ryegrass, coffee, apples, pears, and hawthorn, among other lesser-known crops. They have earned their names from the rusted-like or dirty-powdery appearance of infected pant tissues. For both these groups of fungal pathogens, the emergence of powdery sori is a vital waypoint in their reproductive life cycles. As biotrophic, phytopathogenic members of the phylum Basidiomycota, the life strategies of rusts and smuts are somewhat similar; however, the reproductive structures, number of reproductive stages, and even the number of hosts infected during a single life cycle vary between the two groups. While the terms "rust" and "smut" are more suitably used as descriptors for a particular set of life cycle phenotypes, and less so as terms to define particular groups or species, the majority of fungi that utilize these reproductive strategies are found in two particular classes. For this reason, it is not uncommon to see the terms "rust" and "smut" used in a phylogenetic manner.

Ustilaginomycetes, for example, are sometimes referred to as "true smuts" due to their collective ability to produce teliospores, some of which do so in smutty masses called **galls** where clusters of teliospores can collectively burst out in plumes and float on the wind to reach new hosts. However, recent research has identified new species within Ustilaginomycetes with entirely different reproductive strategies, e.g., *Violaceomyces palustris* (Albu et al., 2015). Similarly, the second class, Pucciniomycetes, which encompasses all rust fungi, contains four orders of non-rust fungi as well. Furthermore, there are plenty of species that follow a typical smut life cycle but do not fall into either of these classes, e.g., the *Microbotryum violaceum* "anther smut" species complex that was first identified as *Ustilago violacea* based on its smut life cycle (Day & Garber, 1988) but is classified in a separate class, Microbotryomycetes.

Classification and systematics

Basidiomycota, the second largest phylum of Fungi, consists of four subphyla, Agaricomycotina, Wallemiomycotina, Pucciniomycotina, and Ustilaginomycotina (He et al., 2022). The latter two contain rust fungi (Pucciniomycotina) and smut fungi (Ustilaginomycotina), the two most diverse groups of plant-pathogenic basidiomycetes. Unsurprisingly, the classification and systematics of both groups have experienced considerable changes throughout the history of mycology.

Subphylum Ustilaginomycotina

Smut fungi are members of the subphylum Ustilaginomycotina within the phylum Basidiomycota, with the vast majority of the 1800 species of these plant pathogens restricted to the geographic distribution of their hosts. It is estimated that smut fungi originated in the Ordovician period (˜450 mya) from teliospore-forming ancestors (Riess et al., 2016). As a group, they experienced rapid diversification after the emergence of angiosperms, their primary hosts. Historically, mycologists described all plant pathogenic basidiomycetes that replace the various organs of their host plants with dusty masses of dark-colored thick-walled teliospores, which germinate to form basidia, smut fungi. However, recent phylogenetic and ultrastructural studies have demonstrated that smut fungi are a polyphyletic group of organisms (Begerow et al., 2006). The term "smut" is now applied to define the morphology and life history of a fungus rather than to reflect its position on the tree of life. While the majority of smut fungi are members of Ustilaginomycotina, teliospores, a defining characteristic of a "smut" life cycle, can also be found in other groups of fungi, e.g., rust fungi (Pucciniales), anther-pathogenic Microbotryales (Pucciniomycotina), as well as in entirely different phyla of the Fungal Kingdom, e.g., the ascomycete *Schroeteria* parasitizing *Veronica* seeds and the Entorrhizomycete *Talbotiomyces* forming galls on the roots of *Limeum*.

Most smut fungi are parasites of angiosperms, with the highest proportion of taxa associated with monocotyledonous plants, in particular grasses and sedges, accounting for 45% and 13% of all known smut species, respectively (Vánky, 2002). Out of the 1,800 known species of smut fungi, few are found on non-angiosperm plant groups. *Melaniella* on spikemosses, *Exoteliospora* on ferns, and *Uleiella* on conifers are some examples. The remaining diversity of smut fungi is distributed on various other plant families, mostly herbaceous hosts. Interestingly, Orchidaceae, the largest family of flowering plants, is not known to have any associated smut pathogens (Vánky, 2002).

Like many other groups of biotrophic plant pathogenic fungi, smuts generally follow the restricted ranges of their hosts. Thus, identification of smut fungi without the aid of molecular genetic tools often relies on proper identification of its host plant. Consequently, the classification of smuts has been largely based on host range data. Many species, e.g., those in the genera *Entyloma*, *Ustilago*, and *Anthracoidea*, possess very limited morphological characteristics for species descriptions. Diverse host information has therefore been used as a proxy metric in the delimitation of smut species belonging to these genera, often supported by molecular studies (Savchenko et al., 2014; Savchenko et al., 2013; Kruse et al., 2018).

The first higher-level classification of smut fungi has roots in the system proposed by Tulasne and Tulasne in the early 19th century, by which smut fungi have traditionally been divided into two families, Tilletiaceae and Ustilaginaceae, based on their patterns of teliospore germination (*Tulasne, L.-R.; Tulasne, C. 1847: Mémoire sur les Ustilaginées comparées aux Urédinées. Annales des Sciences Naturelles, Botanique, 3e Série 7: 12-127. - Biota of NZ*, n.d.). Later studies on the smut ultrastructural characters, and most recently on evolutionary relatedness based on the multi-gene or genomic data, showed that the two-family system did not adequately reflect evolutionary relationships in this group (Bauer et al., 1997; Bauer et al., 2008). Since then, a completely different classification for these organisms, one aligned with revolutionary changes in the classification of Basidiomycota as a whole, has been purposed. The current classification system of smut fungi considers ultrastructural characteristics of host-parasite interactions, the septal pore apparatus, and the biochemical composition of cell walls to be the main synapomorphies on the level of phyla, classes, and orders (Begerow et al., 2006; Begerow et al., 2014; Hibbett et al., 2007; Wang et al., 2014). These classifications made using synapomorphies are then further corroborated with DNA sequence data. For instance, Ustilaginomycotina, the main subphylum where smuts are found, has a distinctive cell wall composition with a dominance of glucose and an absence of xylose, which separates them from two other subphyla of Basidiomycota, Agaricomycotina and Pucciniomycotina. At present, there are four classes of smut fungi within Ustilaginomycotina, two of them, Malasseziomycetes and Moniellomycetes, do not include any teliospore-forming phytopathogens, while the other two, Ustilaginomycetes and Exobasidiomycetes, each harbor a large diversity of life forms, including typical "smuts" along with various anamorphic yeasts and non-smut pathogens of plants (Wang et al., 2014; Kijpornyongpan et al., 2018). The latter two are presented in more detail below.

Ustilaginomycetes is the largest class of smut fungi that unites morphologically and ecologically diverse organisms. Most of the species belonging to this class share the characteristic of "typical" smut: a brownish or blackish mass of thick-walled teliospores on various parts of infected plant tissues. There are four orders within this class, Ustilaginales, Urocystidales, Uleiellales, and Violaceomycetales, with the former two being the largest. Ustilaginales includes predominantly grass-pathogenic smut fungi responsible for the destruction of leaves and inflorescences of infected plants that were historically subdivided between the genera *Ustilago* and *Sporisorium*. They have recently been split into several monophyletic groups based on their molecular data and sorus morphology characteristics (McTaggart et al., 2012). Ustilaginales includes some of the most agriculturally relevant pathogens of crops, e.g., *Ustilago maydis* on corn, *U. nuda* on oats, and *U. scitaminea* on sugarcane (Martınez-Espinoza Alfredo D et al., 2002). Interestingly, this order includes the only edible species of smut fungi, *U. maydis* (Huitlacoche) and *U. esculenta* (Jiaobai) (Valverde et al., 1995; Chung & Tzeng, 2004). Unlike the Ustilaginales, the second order of Ustilaginomycetes, Urocystidales, is comprised of morphologically diverse species of fungal pathogens with colored teliospores formed in the flowers, leaves, or stems of infected plants. It includes genera producing singular spores (e.g., anther smut pathogens of monocots from the genus *Antherospora*, as well as a genus with spores organized into spore balls and surrounded by sterile cells, *Urocystis*. Similar to the Ustilaginales, the above-genus classification of Urocystidales is poorly understood and awaits phylogenomic studies (Begerow et al., 2006; Bauer et al., 2008; Wang et al., 2014).

Exobasidiomycetes is the most morphologically and ecologically diverse class of smut fungi, consisting of species with dark-colored teliospores, e.g., *Tilletia*, characteristic of the typical smut phenotype, taxa with hyaline smut spores embedded into the plant host tissue, e.g., *Entyloma*, as well as non-smut pathogens of plants, e.g., *Exobasidium* and anamorphic yeasts, e.g., *Tilletiopsis* (Begerow et al., 2006). Within this class, several groups deserve special attention. Members of Tilletiales have dark pigmented and often ornamented teliospores, some of which are capable of producing the fishy-smelling compound trimethylamine. The odor created by these spores is so powerful that infected plants can be detected several feet apart. Genera *Tilletia* and *Erratomyces* include important pathogens of grasses and legumes, respectively (Castlebury et al., 2005). Species belonging to Exobasidiales are non-smut pathogens of angiosperms lacking the teliospore stage of their life cycle, although it is believed they have evolved from the teliospore-forming ancestors. Most of them are pathogens of woody plants with the highest diversity found on members of the Ericaceae family of flowering plants. One species of these pathogens, *Exobasidium vaccinii*, is an economically relevant pathogen that infects the leaves, fruits, and stems of blueberries (Begerow et al., 2002). Last but not least, *Entyloma*, the sole member of the order Entylomatales, consists of species nearly indistinguishable morphologically. *Entyloma* parasites infect dicot hosts using hyaline teliospores to embed themselves into host plant tissues. The light-colored spores found on vegetative organs of plants infected by Entylomatales are often obscure and can be confused with plant pathogenic ascomycetes (Begerow et al., 2002). The highest diversity of

Entyloma species is found on Ranunculaceae, the butter cup family, and Asteraceae, the daisy family, of plants with *E. cosmi* and *E. helianthin* recently discovered as newly emerging pathogens of garden cosmos and sunflowers.

Subphylum Pucciniomycotina

Rust fungi belong to Pucciniomycotina, the third subphylum of Basidiomycota, which in addition to the rusts includes parasites of plants, insects, and other fungi, as well as saprotrophic yeasts, among others (Aime et al., 2014). Pucciniomycotina can be distinguished from Ustilaginomycotina by their simple septal pores and different cell wall compositions. Pucciniales, the order that includes all the rust fungi, is the most species-rich in the entire subphylum and comprise about 7,800 species (one-third of all described basidiomycetes), 170 genera, and 18 families worldwide (Aime & McTaggart, 2021). Rust species are obligate pathogens of a variety of plants, including lycopods, ferns, gymnosperms, and angiosperms, and are known to favor narrow host ranges. As a group, rust fungi are very old inhabitants of our planet, having originated 167–316 million years ago (Aime et al., 2018). Before the application of molecular phylogenetic studies, it was originally believed that early divergent rust genera emerged as a result of parasitizing early divergent host families through coevolution between rusts and their hosts, with fern rusts being the most ancient. However, recent molecular phylogenetic analyses have demonstrated otherwise, showing that the most recent extant common ancestor of modern rust fungi diversified on early-diverging gymnosperm hosts instead (Catherine Aime, 2006).

Rust fungi as a group share a set of characteristics that are unique within the Kingdom Fungi. They have complex life cycles that include alternation of generations, which separate in time and space, gametothalli (spermogonial and aecial) stages, and sporothalli (uredinial and telial) stages. Many species that follow a typical rust lifestyle require two unrelated hosts (heteroecism) and are capable of producing up to five different reproductive morphs within a single life cycle (Aime et al., 2014). Unsurprisingly, these characteristics have contributed to the development of numerous classification systems for rust fungi, making the systematic classification of rust fungi at the species level somewhat controversial. Since the early 20th century, some mycologists have followed a biological species concept based on time- and labor-consuming cross-inoculation experiments that allow for the grouping of species with similar morphological characteristics into narrowly defined species according to their host-specificity (Fischer, 1939; Fischer, 1943). Special emphasis has often been put on the measurements of spore sizes to characterize biological species in this way. The consequence of this approach has led to the classification of numerous species nearly indistinguishable from one another morphologically with rather narrow host ranges. That being said, some rust species possess a very high degree of phenotypic variability. So much so that spore morphology is dependent on which alternate host was utilized during cross-inoculation experiments. This situation becomes even more complicated by often overlapping host ranges and/or secondary losses of certain life cycle stages in many of these organisms. As a result, considerable disagreement on species delimitation still exists.

The higher-level classification of Pucciniales has undergone many changes since the early 20th century. Originally called "Uredinales", Pucciniales were divided into three or four families based on the behavior of their basidium and the presence of pedicels on teliospores. Later on, Cummins and Hiratsuka (*Illustrated genera of imperfect fungi-fourth edition. Barnett y Hunter. pdf.pdf*, n.d.) placed a greater emphasis on the morphology of spermogonium for classification, combining basidium and pedicel information with teliospore and telial morphology, resulting in the most widely used familial classification system of rust fungi at the time, which included 13 families. Only recently has the phylogenetic significance of various criteria applied by earlier classification systems been evaluated with molecular data. The resulting modern classification system of Pucciniales currently includes seven suborders and 18 families of rust fungi (Aime & McTaggart, 2021).

Suborder Rogerpetersoniineae was created to accommodate the earliest divergent extant rust species found so far – *Rogerpetersonia torreyae* that causes systemic infection of *Torreya* pines in California. The pathogen is known only from its gametothallus form and is believed to have lost the ability to produce a sporothallus. Suborders Micronegeriineae, Araucariomycetineae, and Skierkineae are three other early diverging lineages of rusts. Many species within these suborders form the gametothallus on gymnosperms (Aime & McTaggart, 2021).

The three remaining suborders of rust fungi, Melampsoriineae, Raveneliineae, and Urediniineae, account for a much greater diversity of rust species and are predominantly parasites of angiosperm hosts. *Melampsoriineae* consists of mostly macrocyclic and heteroecious species with gametothalli associated with conifers, and teliospores that germinate after a period of dormancy. Suborder Raveneliineae includes many tropical species that form elaborate, multi-celled teliospores. It is the second richest lineage of rust fungi in terms of taxonomic diversity and is one of the poorest studied. *Ravenelia* and *Phakopsora* are the largest genera within the group found predominantly in the tropics as parasites of various legumes and their relatives. Both genera are primarily autoecious (Aime & McTaggart, 2021). The most recently diverged suborder of Pucciniales, and the most species-rich suborder, is Urediniineae. There are ˜70 genera and more than 5,000 species recognized within the group. Urediniineae represents a rapidly radiating lineage that has undergone multiple losses of morphs, e.g., aecial, spermogonial, or sometimes their uredinial stages. It includes the two largest genera of rust fungi, *Puccinia* and *Uromyces* (Aime & McTaggart, 2021). Both genera include many economically important pathogens, e.g., *P. graminis* and similar grass-parasitizing species with 2-celled teliospores and macrocyclic or autoecious life cycles and *Uromyces appendiculatus* amongst other similar pathogens of legumes with one-celled teliospores and predominantly autoecious life cycles.

The modern classification of rust and smut fungi reflects many of the challenges facing mycologists in their attempts to determine phylogenetic relationships among these organisms, and is therefore far from a complete model. One of the main contributing factors is the lack of readily available molecular data, which is, more often than not, hard to obtain. The shear diversity of smut and rust species includes a large portion of individuals that have been found only once, particularly those of tropical lineages. Thus, additional collections and continued advances in molecular genetics technology are required to reveal the true evolutionary relationships within the lesser-studied groups of Pucciniales and Ustilaginomycotina.

Host-defense mitigation

Unlike animals, which possess the ability to alter their behaviors to aid in disease prevention, plants have evolved to instead rely on their capacity for creating vast profiles of chemical compounds to combat the infection and the spread of disease. This is facilitated in part by their larger ploidy number compared to animals. Extra copies of DNA have long been understood to allow for a greater degree of mutations while simultaneously preserving functional copies of genes responsible for essential cellular processes. Over time, plants have utilized this advantage to evolve a complex array of molecular strategies to ward off invading bacterial, fungal, and oomycete pathogens. Therefore, in order for fungal pathogens to successfully infect and complete their life cycle within an ever-adapting population of plant hosts, they too must continually evolve strategies to overcome emerging molecular defenses. Evolution therefore selects for pathogens better suited to inhibit the defense response of their hosts, but likewise favors hosts better suited to ward off invading pathogens. The result is an intense relationship between hosts and their fungal pathogens, locked in a never-ending molecular arms race, an evolutionary tug-of-war that over time has led to the intense host-specialization frequently observed in these groups of fungi.

A great example of the coevolution resulting from reciprocally selective pressures was first described by Harold Henry Flor in the 1940s. In his work, Flor described the inheritance of resistance to the rust *Melampsora lini*, a fungal pathogen of flax (Flor, 1947). Using a classical genetics approach, Flor was able to demonstrate that the success of pathogenicity within the host was heavily correlated with pairings between genes from the host, referred to as **resistance genes**, and genes from the pathogen, referred to as **avirulence genes**. Flax that inherited resistance genes were much better at fending off infection by *M. lini*, while *M. lini* that inherited avirulence genes were much more successful at infecting flax hosts. As many resistance and avirulence genes function by coding for products that directly impact one another, either through the detection of effectors secreted by foreign pathogens at the cell surface in the case of resistance genes, or through the direct inhibition of these reporters proteins in the case of avirulence genes, this relationship is now referred to as the **Gene-for-Gene Hypothesis**. Changes to the protein structure in either resistance or avirulence products therefore act as potential selective pressures for changes in their counterpart, fine-tuning pathogens to particular hosts over time.

While a strict gene-for-gene relationship is not found in every fungal pathogen/plant host pairing, all species of plant-infecting fungal pathogens, also known as **phytopathogens**, secrete bioactive compounds to both manipulate and otherwise overcome the plant defense responses of their hosts. While some phytopathogenic fungi, e.g., the ascomycete *Monilinia laxa* also known as "brown rot", are **necrotrophic** having evolved to infect their hosts in a comparatively destructive manner by overwhelming their hosts in a matter of days through extensive necrotic damage to host tissues, rusts and smuts take a slightly more sophisticated approach towards pathogenicity. While necrotrophs feed on the decaying tissues of the host through external digestion, a hallmark of the fungal kingdom's **heterochemohetotrophic** nature, rusts and smuts are **biotrophic**, having evolved to siphon nutrients from living hosts tissues. Like the necrotrophic fungi, biotrophic fungi also metabolize compounds from their hosts to survive; however, biotrophic fungi siphon carbon directly from the living hosts by reprogramming plant cells to produce or convert compounds into nutrients required by the fungus, allowing the host to subsist as well. To do so, many biotrophic fungi, including several species of rusts and smuts, produce **haustoria**, slender projections that emerge from the hyphae of the fungal pathogen to help it both anchor itself to the host and act as a small straw-like aperture to absorb nutrients from living tissues. By utilizing a more measured life strategy, biotrophic fungi create a long-term relationship with infected hosts, maintaining a constant source of nutrients while causing little damage to the host. However, while this biotrophic approach leads to a more sustainable source of nutrients for the pathogen, the process of surviving in or on a living host requires mechanisms to constantly manage plant defense responses. This introduces evolutionary pressures that often lead to the emergence of host-specific effectors needed to shut down the defense response machinery. Over time, the specialization of fungal effectors often leads to a narrowed compatible host range. In fact, some of the fungal pathogens most successful at managing host-defense responses, e.g., some members of the smut pathogen species complex *Microbotryum violaceum* which are able to grow inside their hosts without triggering chlorosis in the plant tissues at all, are relegated to a single host having coevolved an intense host specificity (Hood et al., 2019).

Regardless of their approach, all plant pathogens must evolve to overcome a gauntlet of plant defenses, the first of which begins with their entry into the waxy cuticle of the plant cell wall. Plant cells have several protective layers that play a role in defense, the first of which is their sturdy cellulose cell wall, and behind it, the apoplast. The **apoplast** is an extracellular space outside of the plasma membrane, fortified by the cell wall and containing a sophisticated network of polysaccharide polymers and glycoproteins. The apoplastic space contains fluid that circulates throughout the cell wall, facilitating quick communication between cells. This flow expediates the mobilization of defense response proteins upon detection of an intruder should they penetrate the outer defenses. The apoplastic space also contains signals used to recognize foreign cells, e.g., **Microbial-Associated Molecular Patterns** (**MAMPs**), or damage to the cell, e.g., **Damage-Associate Molecular Patterns** (**DAMPs**), both of which can upregulate the plant's defense response. They do so in association with the **Pattern Recognition Receptors** (**PPRs**), a diverse group of transmembrane proteins that have evolved to recognize a wide array of pathogen-related molecules, many of which are essential to the pathogen lifecycle and subsequently exhibit comparatively low levels of change. Examples of core molecules that can trigger activation of the PPRs include β-glucans, peptidoglycans, and eicosapolyenoic acids which identify fungal, bacterial, and oomycete pathogens, respectively. Upon detection of a pathogen, plants activate genes that code for the secretion of their own bioactive compounds through either traditional ER-Golgi-mediated secretion of proteins, a pathway that relies on secretion signals at the beginning of the polypeptides, or through the use of small extracellular vesicles to secrete leaderless compounds into the extracellular space. These molecules include both antimicrobial compounds like chitinases that degrade the fungal cell walls of invading pathogens and callose which fortifies the site of infection and strengthen the damaged plant cell wall.

The apoplast is therefore the front line of the struggle between the pathogen and the host. It is here that invading fungal tissues secrete molecules known as **effectors** which attempt to bind to and manipulate the physiology of the plant host, nullifying the recognition signals used by the plant amongst other effects. To successfully infect the host, the invading fungal pathogen must use these effectors to shut down the defense machinery before the plant is able to mount a strong enough response. Plants have therefore evolved to counteract these molecules by producing secondary receptor proteins known as **resistance proteins** that can detect the deployment of effecter molecules. While the initial immune response stimulated by the recognition of foreign compounds in the cells by PPRs is sometimes strong enough to fight off early-stage infections alone, the recognition of effector molecules by resistance proteins signals a much stronger defense response in the cells, usually triggering localized compartmentalization and cell death in attempt to quarantine the infection. During this process, the plasmodesmata are closed and mitogen activated protein kinases release reactive oxygen species within minutes.

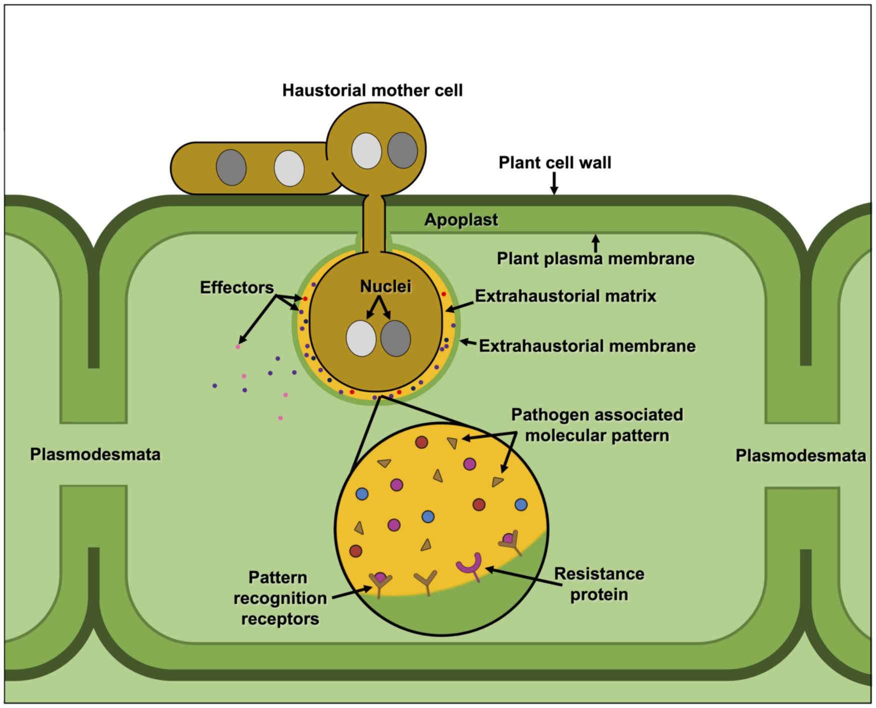

Figure 1: Penetration of surface plant tissue by the fungal appressorium. The haustorial mother cell protrudes into the apoplastic space of the plant cell and secretes myriad fungal effectors. These effectors are used to suppress plant defense responses by interfering with pattern recognition receptors; however, they may also trigger pathogen-associated molecular recognition via resistance proteins. Figure made with BioRender.

To overcome these defenses, fungal pathogens secrete hundreds of compounds to enter the plant cell, disable primary and secondary defense mechanisms, or otherwise mask themselves by modifying their own recognition factors. These arsenals of secreted molecules are still being described in many fungal pathogen species, as many have evolved as the result of unique coevolutionary relationships. The genomes of host-specific pathogens therefore often contain sets of proteins with yet undescribed roles, lacking recognition sequences used for bioinformatic analyses, e.g., Pfam domains or GO terms. Nevertheless, these effectors often share a few unifying trends. These proteins are usually small, less than 250 amino acids, and are frequently subject to rapid changes at the protein level due to evolutionary pressures imposed by their hosts. Despite their largely inconspicuous nature, there are also many examples of conserved effectors that can be identified across related species of fungal phytopathogens. By comparing closely related species of host-specific fungal pathogens, groups of core secreted effectors that tend to play a more central role during infection can be observed, examples of which include secretory lipases and pectinesterases, that act to modify the cell wall and allow for entrance into the plant host. The conserved nature of core effectors makes them more likely to play a universal role during infection, e.g., the mechanical entrance into the host, while unique or more species-specific effectors are more likely to be involved in the modification of species-specific plant defense responses.

Once colonized, established fungal pathogens can begin to manipulate their hosts to better suit their reproductive life cycles. This process often involves the secretion of molecules that interact with phytohormones, including the "**Big Five**" plant hormones, auxin, cytokinin, gibberellin, ethylene, and abscisic acid, and other important molecules like salicylic or jasmonic acids. By manipulating the host's hormones, fungal pathogens can affect the development and growth of plant tissues, as well as further inhibit the plant immune response.

Biology and life cycles

The Smuts (Ustilaginomycotina)

The general smut reproductive life cycle begins with a single teliospore. **Teliospores** make up the short-lived diploid phase of the smut life cycle and are the only structures capable of surviving outside a living host for more than a couple months. The hardiness of the teliospore's thick protective coating aids in its primary function, transmission to a new host. Teliospores are able to overwinter in a dormant state, biding their time until conditions are just right for emergence on a new host; however, in some species, e.g., *Ustilago nuda*, teliospores have also been discovered within the developing seeds of their previous hosts, indicating that some smut diseases can transfer vertically in tandem with host reproduction. Placement of teliospores within the seeds of infected hosts not only preemptively establishes a future host for disease transmission, but also provides the spores an extra layer of protection from the seed coat. While *U. nuda* may have evolved to match its spores with the offspring of their current hosts, many other species of smut have instead evolved to rely on abiotic factors for dispersal, e.g., rain and/or wind. Several species of smuts, e.g., those from the genus *Antherospora*, also utilize other biotic factors, e.g., insects, as carriers from plant to plant. These spores can either be transported to other hosts directly from the sori by utilizing winged insects for transportation, effectively hijacking the plants natural reproductive process, or through wingless insects that pick up spores from the soil and climb new plants. Some species of herbivorous insects have even been observed facilitating the entry of fungal spores into new hosts through the damage caused by predation, although this phenomenon has not yet been described specifically in rust or smut pathogens (Pfliegler et al., 2020).

Once the fungal spore is situated on a new host, and conditions are right for reproduction, the teliospore germinates. Upon germination, teliospores undergo meiosis, producing the four interconnected haploid cells characteristic of the Basidiomycetes fungi, a **basidium**. Each of these interconnected haploid cells is capable of undergoing mitosis to produce a free single-celled haploid **basidiospore**, marking the smuts transition into the yeast-like, single cell stage of its life cycle. These basidiospores are in turn able to reproduce asexually through budding while conditions are still favorable for asexual growth, usually driven by the abundance of readily accessible small-chain carbohydrate molecules. Successfully established colonies of basidiospores, sometimes referred to as the **primary mycelium**, will continue to reproduce asexually until conditions change, at which point basidiospores will transition into the mating phase. This transition can be caused by a variety of factors, including nutrient availability, temperature, or hormonal changes in the host during flower production.

During the mating stage, cells of opposite mating types release mating type-specific pheromones. These pheromones elicit the formation of **conjugation tubes**, projections of the cell that are capable of fusing with compatible mating partners. When matching conjugation tubes of mating partners meet, the two cells are jointed together through the fusion of their plasma membranes, a process known as **plasmogamy**. The resulting conjoined cells effectively form a tunnel through which the DNA of one mating type can be transferred to the other. Shortly after plasmogamy, a third structure containing both parental nuclei, still separated at this stage, is formed. The resulting "dikaryotic" cell will form the infectious hyphal structure capable of penetrating plant tissues and infiltrating the host. This infectious hyphal structure gives rise to the **secondary mycelium**, which spreads throughout various plant tissues. Using the secondary mycelium, smuts are able to colonize an entire plant host through a single site of infection; however, severe infection is often localized to a specific part of the plant in which different species have evolved to specialize.

Once infection has been established, the fungus enters the endophytic stage of its lifecycle and begins to absorb nutrients from the host. After the fungus has absorbed enough energy, and conditions are favorable for sexual reproduction, reproductive structures are formed. The reproductive structures of smut fungi can develop in various plant tissues depending on the species, with most appear in the flowers or fruits of the host. It is within these newly formed reproductive structures that fusions of the two nuclei through **karyogamy**, which have up until this point have remained separated in the dikaryotic cells, finally occurs and a new generation of teliospores are formed. In some species, e.g., *Ustilago maydis*, fusion of the nuclei occurs during the production of spores while in others, e.g., *Tilletia tritici*, the spores remain dikaryotic until just before germination. The resulting spores are called **teliospores** and are produced in specialized structures called sori that ultimately give the plant its smutted appearance for which the smuts are named. In most genera of smuts, the fertile teliospores separate into new individual spores; however, some genera, e.g., *Urocystis*, *Doassansia*, and *Thecaphora*, do not separate but rather form multicellular, intertwined clumps of interconnected spores in a spherical structure called a **spore ball**. Each spore ball contains multiple teliospores in various arrangement, shapes, and sizes, depending on the species. *Burrillia*, for example, have colorless spore balls, while *Thecaphora* (*Sorosporium*) are light brown and *Clintamra* spores are black. Other species, e.g., *Heterotolyposporium*, have hyaline spores held together by small hyaline cells (Vánky, 1998). Production of the next generation of teliospores completes the life cycle of these fungi by returning the smuts to their diploid phase in preparation for dispersal to new hosts.

While the formation of the sorus is an important step in the infectious life cycle for many species of smut fungi, not all smuts are known to make them. *Exobasidium vexans*, for example, has a shortened life cycle, skipping the formation of telia and teliospores and instead relying on rapidly growing hyphae that compact to form a hymenial layer capable of forming **clavate basidia** and basidiospores directly. The hymenial layer is also capable of forming conidia-producing **conidiophores**, providing an asexual avenue for wind-borne spores to spread to other hosts (Sen et al., 2020).

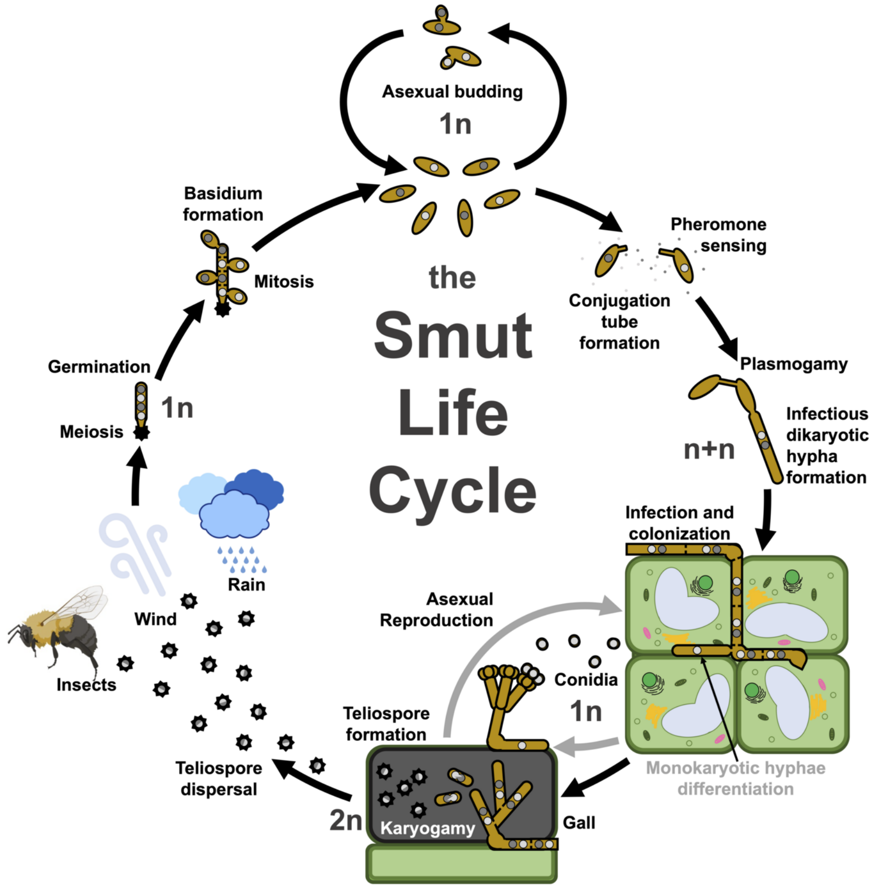

Figure 2: A general illustrated life cycle for smut fungi. The cycle begins as teliospores are transferred to a new host. These teliospores germinate to form basidia, which will act as progenitors for the single-celled stage of the life cycle. These cells undergo asexual reproduction when nutrients are readily available but switch into sexual reproduction when nutrients become scarce. Through pheromone sensing and conjugation tube formation, these cells fuse plasma membranes to form infectious dikaryotic filaments that colonize the host. These cells can either differentiate into monokaryotic hyphae, producing asexual conidia, or form gall structures where new teliospores are created to complete the cycle. Figure made with BioRender.

The Rusts (Pucciniale, previously Uredinales)

When comparing the smut life cycle to that of the rusts, the main difference we see between the two is the complexity and number of **sori** formed during infection, a result from adapting to infect multiple hosts. In fact, aside from Pyxidiophorales, a small ascomycetous order within Laboulbeniomycetes (Haelewaters et al., 2021; *Laboulbeniomycetes, enigmatic fungi with a turbulent taxonomic history*, n.d.), rust fungi are the only known species of fungi that require two unrelated hosts to complete its life cycle. These structures produce various types of infectious spores, each specializing in a particular portion of the rust life cycle. Altogether, rusts can produce up to five distinct types of spores.

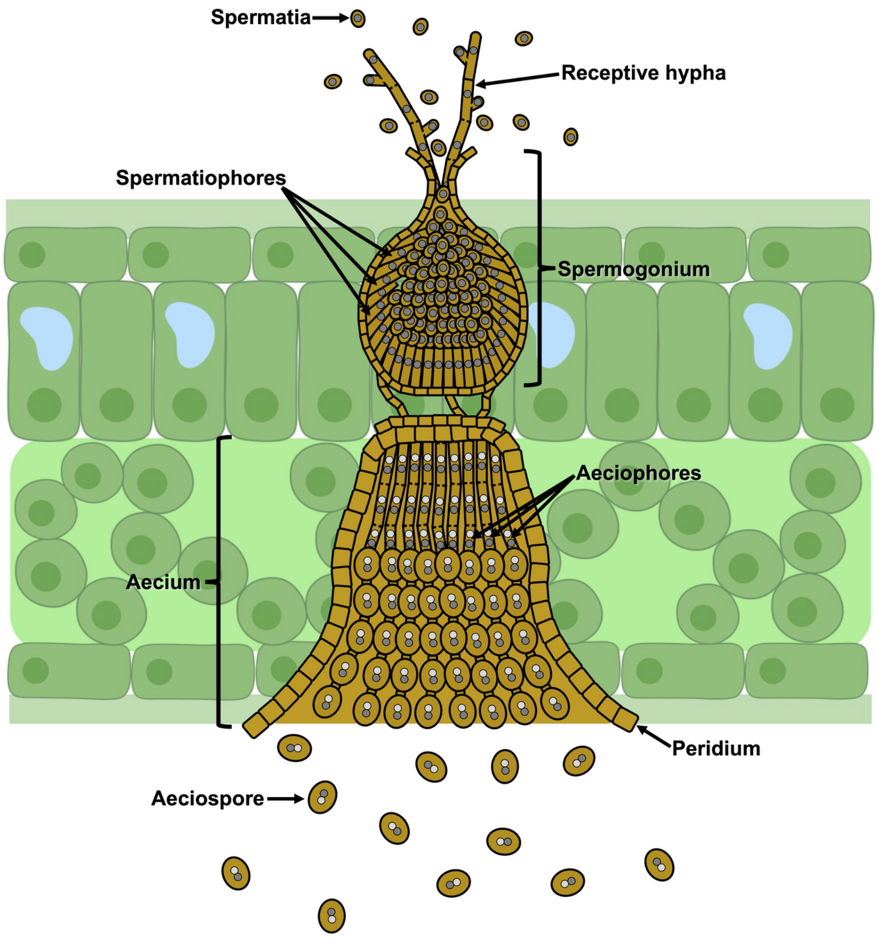

Figure 3: The basic structures of rust spermogonia and aecial sori. Spermogonia represent the first stage in the life cycle of rust fungi, and they appear on the primary host. They produce spermatia capable of binding with the hyphae from other spermogonia to form dikaryotic aecia. These cup-like structures are then able to produce infectious aeciospores that germinate on a secondary host to form a dikaryotic mycelium. Figure made with BioRender.

Rusts that require two hosts to complete their life cycle are called **heteroecious** rusts, while rusts that can complete their life cycle on a single host are referred to as **autoecious** rusts. Some autoecious rusts, while not requiring it, can infect multiple hosts as well. Like the smuts, the rust life cycle starts with a dikaryotic teliospore; which are often multi-celled, depending on the genus. In order to infect a new host, these cells must undergo karyogamy to fuse into diploids capable of meiosis, resulting in the emergence of infectious basidia equal to the number of cells in the teliospore. These basidiospores are then transferred to their first host, referred to as the **gametothallus host**, through wind, rain, or insect vectors. Once delivered to new host, the basidiospores germinate forming hyphae that penetrate the plant and begin to siphon off nutrients from the plant tissues before entering the **spermogonial stage**, a reproductive stage during which sexual sori called **spermogonia** are formed. Spermogonia rely on insects or plant surface moisture to transfer **spermatia** to receptive hyphae found in spermogonia located on another region of the plant, or in some cases on a different host plant.

Typically, the transfer of a pycniospore to a new spermogonium results in plasmogamy, initiating the dikaryotic stage of the rust life cycle and facilitating diversity through sexual recombination. The resulting dikaryotic hyphae starts the **aecial stage** in which hyphal cells spread through the plant tissue to the underside of infected leaves and form aecia. **Aecia** are sori that produce dikaryotic spores, **aeciospores**, used to infect a **secondary host**. Transfer of these aeciospores to an appropriate secondary host results in germination and establishment of a new dikaryotic biotrophic mycelium. This mycelium spreads locally through the plant tissues and gives rise to **uredinia**, a type of sori similar to aecia but it produces dikaryotic spores called **urediniospores**. Furthermore, unlike aeciospores which help to transition to a different species of host, urediniospores re-infect the secondary host repeatedly as long as the growth conditions are favorable. These aeciospores and urediniospores often appear as bright rusty looking spots on infected hosts, earning the "rust fungi" their name. It is important to note that during both of these stages the spores remain dikaryotic. It is not until the formation of the teliospores that fusion of the nuclei can occur to form the short true diploid phase and complete the rust life cycle. While these teliospores are very similar to urediniospores in nature, sometimes even produced in the same pustule, their emergence often requires specific environmental cues.

This broad overview of the rust life cycle captures the complexity of all possible reproductive stages; however, not all species of rusts undergo the full five spore cycle. In fact, there are three different reproductive strategies that have evolved amongst the rusts. Rusts that undergo all five phases of spore formation as therefore described as following a **macrocyclic** life cycle, while species that lack the uredinial stage are described as following a **demicyclic** life cycle, and species that follow the far more reduced life cycle containing only the telial and, sometimes, spermogonial stages are termed as **microcyclic**. Furthermore, even macrocyclic rusts may maintain other spore stages rather than proceed to the uredinospore stage climate conditions when climate conditions are favorable and an abundance of secondary hosts are available.

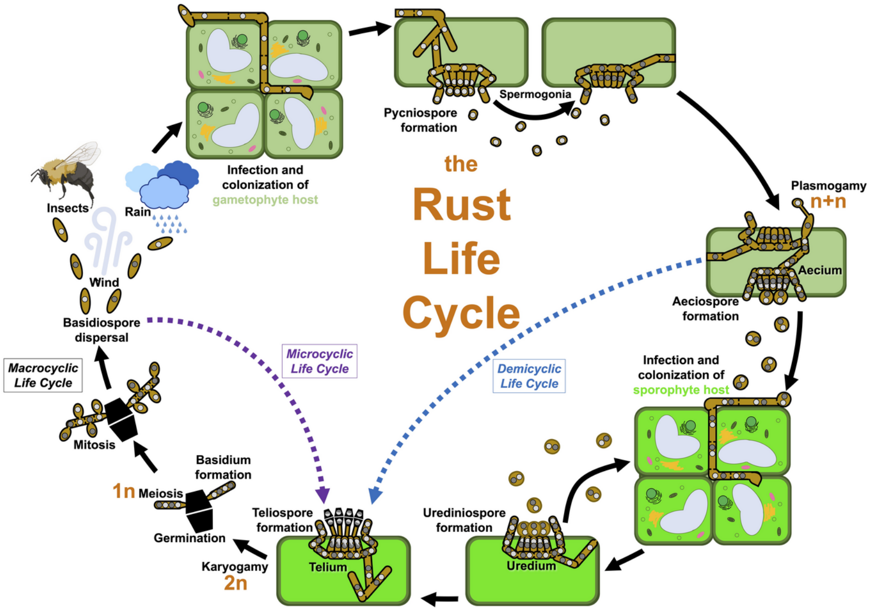

Figure 4: A general illustrated overview of the three major rust life cycles. Microcyclic rusts follow the simplest life cycle, infecting only a single host. In this life cycle, pycniospores colonize the plant tissue to form new telia for the production of the next generation of meio spores (teliospores). Demicyclic rusts utilize a much longer, multi-host life cycle, with teliospores forming basidia on a primary gametophytic host. This infection is facilitated by haploid hyphae, also referred to as the primary mycelium. These haploid chains give rise to spermogonia, capable of fusing their spores, sometimes referred to as pycniospores in Uredinales but more generally called spermatia, with the receptive hyphae of other spermogonia. The fusion of these cells forms dikaryotic aecia that produce infectious aeciospores. These dikaryotic spores infect a second host, also called the sporophytic host, and form dikaryotic hyphae, also known as the secondary mycelium. From here, the dikaryotic hyphae directly form telia that produce teliospores. Finally, the macrocyclic rusts follow a very similar life cycle to demicyclic rusts, with the addition of a uredinial stage following the establishment of the secondary mycelium. Just as in the microcyclic rusts, these structures are able to reinfect secondary hosts through the formation of urediniospores. Figure made with BioRender.

Economically important smut and rust fungi

Smuts and rusts are some of the world's most common plant pathogens, well known to humans for their ability to parasitize crops. Early records of smuts and rusts date back to at least the classical period of the Greco-Roman world, as Romans held the agricultural festival "Robigalia" on April 25 to place offerings to the god/dess of blight, rust, and mildew (Robigo/us) to curry favor and ward off crop disease, including rusts that at the time were referred to as "rubigo" (*On agriculture, with a recension of the text and an English translation by Harrison Boyd Ash : Columella, Lucius Junius Moderatus : Free Download, Borrow, and Streaming : Internet Archive*, 1934). However, it was not until the 1700s that rusts were formally recognized as disease agents in Europe. Among the economically important plants infect by rusts and smuts are cereals, fruit trees, vegetables, small grains, and many ornamentals. Massive expenditures are incurred every year by farmers who purchase systemic fungicides and resistant crop varieties in efforts to control the proliferation of smut and rust fungi.

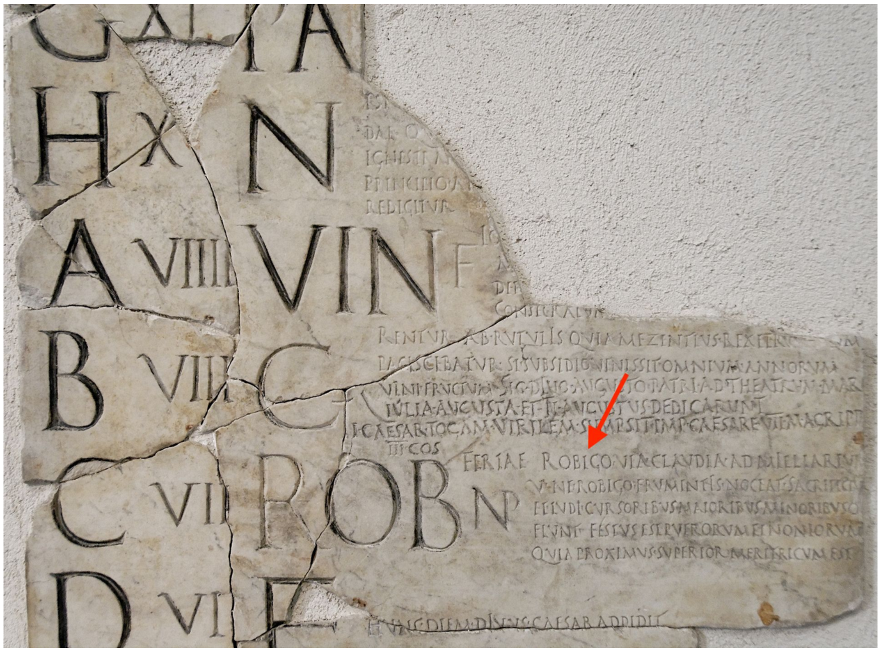

Figure 5: A section of the Fasti Praenestini, a calendar created by the Roman grammarian Marcus Verrius Flaccus in Palestrina (ancient Praeneste), Italy. The calendar lists the Roman "Robigalia" festival (as ROB) during which the main ritual involved the sacrifice of a dog to honor the god Robigus (sometimes depicted as feminine, Robigo) and protect their fields of grain from rust diseases, which they referred to as "rubigo". The Fasti Praenestini is part of the collection of Palazzo Massimo alle Terme, Museo Nazionale Romano. Photo: Marie-Lan Nguyen, Wikimedia Commons.

Smut fungi are distributed worldwide and, in many regions, having caused chronic agricultural losses, in some cases devastating as much as 25% of yield. Nowadays, significant economic damage is seen in the areas of the Middle East, Africa, and South Asia, where farmers sow chemically untreated seeds. In the rest of the world, direct yield losses caused by smuts are generally below 2%, largely due to the availability of resistant crop varieties, such as wheat cultivars Bill, Globus, and Sherman, and fungicide seed treatment by carboxin, or its derivatives. Some of the more agriculturally relevant smut fungi are those of cereal crops, e.g., *Ustilago hordei* and *U. nuda* on barley, *Tilletia caries*, *T. controversa*, *T. indica*, and *Urocystis tritici* on wheat, and *U. maydis* on corn (Bonde et al., 1997; Kumar et al., 2022; Vánky, 2002). The infected plants produce malformed inflorescences and, as a result, are unable to produce seeds. Smuts also cause severe disease outbreaks of other cultivated plants as well, with some of the more well-known examples being *U. scitaminea* on sugarcane, *Sporisorium reilianum* on sorghum, *Thecaphora solani* on potatoes, *T. frezii* on peanuts, *Urocystis cepulae* on onions, and *Entyloma helianthi* on sunflowers (Vánky, 2002). In addition to the yield losses, the economic importance of smuts is also associated with the quarantine restrictions imposed by various governments in order to mitigate contamination and stem the spread of the disease. For example, *Urocystis tritici*, the causal agent of flag smut of wheat, is a regulated pathogen in many countries around the world. It was first discovered in South Australia in 1868, and in less than forty years there were records of its presence in the wheat-producing regions of Italy, China, Japan, India, South Africa, and the United States. In the United States, flag smut was a significant problem in the Pacific Northwest until the 1960s when the fungicide seed treatment became the standard of modern-day agriculture (Savchenko et al., 2017). Since the majority of these smut fungi continue to persist in low numbers of hardy spores lying dormate in the soil, they can resurface to cause substantial losses, particularly to organic farms. This has introduced substantial challenges for countries, such as those in Europe, where all plant material used for organic agriculture must be produced with organic farming methods, i.e., all the seed used for planting in organic farms must have been produced by organic fields, restricting the use of conventional seed from plants that were previously treated with pesticides regardless of subsequent farming practices. While many plant-infecting fungi cause devastation to farmers by destroying their products, smut fungi are among the few plant pathogens with demonstrated application as food items themselves. The swollen corn kernels filled with the teliospores of *U. maydis*-infected maize, also known as huitlacoche, is a culturally important food in Mexico, and is becoming an increasingly popular delicacy in other parts of the world. This makes *U. maydis* one of the few fungal pathogens that may actually increase the value of infected crops (Valverde et al., 1995). *Ustilago esculenta,* a similar smut fungus that produces edible galls on the stems of the Manchurian wild rice *Zizania latifolia* has also been intentionally cultivated for more than 1,500 years in Eastern Asia (Chung & Tzeng, 2004).

Unlike the smuts, which are considered a “forgotten disease of the past” in many parts of the world, rust fungi remain notoriously damaging plant pathogens, capable of aggressively spreading through many species of cereals, legumes, and trees. Several species of rust fungi that infect strains of wheat are of immense economic importance (Yamaoka, 2014). *Puccinia graminis* for example*,* the causal agent of wheat rust, was once known as one of the most devastating crop pathogens worldwide due to its ability to produce large numbers of infectious urediniospores well suited for spreading through the air (LEONARD & SZABO, 2005). Since the 1960s, however, no major stem rust epidemic has occurred in the United States or Europe as a result of the development of genetically resistant wheat cultivars and the stabilization of rust races by the elimination of its asexual host during the barberry eradication campaign (Jin, 2005). However, it seems that the battle with the stem rust is not over yet, since a new virulent race, named Ug99, first detected in Uganda in 1999, has been spreading the world. Most of the modern cultivars lack resistance to Ug99, making its potential spread a very big concern for the global agriculture (Singh et al., 2011). Several other rust species causing serious crop losses are worth mentioning. *Puccinia striiformis* for example, also known as stripe rust or yellow rust, is a pathogen of wheat and barley that operates under a life cycle requiring alternation between grasses and barberry hosts. Historically, this pathogen was found in high-altitude areas of the Himalayas with cool, humid summers and was of limited importance in barley cultivation. However, in the last few decades, it has adapted to warmer temperatures and is creating devastating epidemics in warmer climates where wheat is grown (Chen, 2020). Currently, about 90% of the world’s wheat production is susceptible to *P. striiformis*, and the global economic losses are estimated to be more than $1 billion annually. *Puccinia triticina,* the agent of leaf rust, is perhaps the last of the “big three” rust pathogens of wheat. It is considered the most common among all rusts and thrives in all wheat-growing regions with mild summers (*Global status of wheat leaf rust caused by Puccinia triticina - Euphytica*, 2011). Unlike *P. graminis* and *P. striiformis,* this fungus alternates between wheat and *Thalictrum* spp., although the uredinial stage is the most common and teliospores are rarely formed.

Many species of agriculturally significant rust fungi are also infection non-cereal crops. Members of the genus *Gymnosporangium* are important pathogens of pears, alternating between *Juniperus* spp. and pear trees. *Hemileia vastatrix* is another tree specialist, causing the most devastating disease of coffee trees to date and economic losses between 1-2 billion US dollars annually. Coffee rust is particularly devastating because it causes immense socio-economic damage in developing countries (Rhiney et al., 2021). A number of rust species are also found on cultivated legumes with *Phakopsora pachyrhizi,* also known as soybean rust, being the most notorious. This species is able to defoliate soybean fields within only a few days, and in some cases can completely decimate entire plots, leading to 100% economic losses (GOELLNER et al., 2010). Moreover, there are no soybean varieties with resistance available and the fungicide treatment is expensive or not always practicable, making it a challenging fungus to deal with. Collectively, rusts and smuts cause many problems for farmers globally, and likely will continue to destroy crops in the future as global climate continues to change and introduce new conditions for the shift of previously established host ranges.

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