

The Pine-Oak Rusts: How Forest Tree Species Connect

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Abstract

The pine-oak rust fungi, which live out their lives as pathogens on pines and oaks, have multiple spore states and complex life cycles. Because they can be severe pathogens of pines, much of what we know about them depends on how damaging they are to management of pine forests for timber, recreation, and ecosystem values. Widely distributed in North America, they are often difficult to identify on their oak hosts, and thus the distributions and frequencies of many species are not well known, especially in urban and rural forest settings. Although they are usually minor pathogens on oaks, changing climates could alter that relationship.

Life is full of connections through which species' natural histories are expressed and enriched: shared habitats, social interactions, and gender relationships are a few among many. Some connections, however, are difficult to appreciate because they are unpleasant to us, especially if they impact us negatively: predator-prey or host-pathogen relationships, for example, can evoke fear or disgust. Our sympathies inherently lie with the animal victim or plant host, and we often dismiss or actively despise the predator or pathogen.

Yet, if we examine nature closely, we discover that ecosystems cannot prosper without disease and death. We define health for ourselves as never being sick and living a long, full life. But, for ecosystems, life-death, predator-prey, and host-pathogen relationships are essential to the health of the system. A forest without tree-killing insects or pathogens would soon be so crowded that it would become uninhabitable to most plants, animals, and other organisms, a strangled, overstocked desert.

Many fungi are benign to plants, while others help decompose and recycle dead plant matter. Some are essential to plant growth; for example, mycorrhizal fungi facilitate nutrient uptake through plant-root symbioses. Many other fungi are parasitic. The pine-oak **rust**¹ fungi fall into the latter category (Figure 1, Table 1). They usually have multiple spore states (Table 2), and their life cycles are often complex (Hedgcock and Siggers, 1949). They are wholly parasitic, that is they require a living host throughout all stages of their lives (technically, they are called

¹ These fungi are called "rusts" because two of their most prominent spore stages (aeciospores and urediniospores) are yellow-orange, orange, or red-orange in color, and, when aggregated on a plant leaf, stem, or cone, appear rust-like from a distance. Examination of the underside of an oak leaf with a hand lens will reveal the individual spores; for viewing oak leaves in the field, a 2"-diameter, 3.5X double-lens magnifier provides a wide and flat field that allows rapid and convenient scanning of leaf surfaces. For information on how to obtain one, contact the author.

Table 1. Pine-Oak rust species, their principal oak and pine hosts, and their geographic distributions.

Rust genus, species, and special form (f. sp.)	Common name	Principal oak hosts	Principal pine hosts	Reported distribution
<i>Cronartium quercuum</i> f. sp. <i>banksianae</i>	Eastern gall rust (galls globose)	North of fusiform rust range: dwarf chinkapin, bur, chestnut, pin, northern pin, & northern red oak; within fusiform rust range: see species list below	Jack pine	NE U.S. into Ontario, Canada
<i>C. quercuum</i> f. sp. <i>echinatae</i>			Shortleaf pine	New Jersey to Texas
<i>C. quercuum</i> f. sp. <i>virginianae</i>			Virginia pine	New Jersey to Alabama
<i>C. quercuum</i> f. sp. <i>pusiforme</i>	Fusiform rust (galls spindle-shaped, tapering at each end)	Cherrybark, bluejack, laurel, water, & willow oak; also, black, blackjack, southern live, post, southern red, scarlet, shingle, Shumard, turkey, & white oak	Loblolly, slash, longleaf, pond, & pitch pine; (shortleaf pine is highly resistant)	SE U.S. (Maryland to Florida, Arkansas, & Texas)
<i>C. strobilinum</i>	Southeastern cone rust	Bluejack, burr, Chapman, chestnut, laurel, dwarf live, southern live, myrtle, post, running, turkey, water, white, & swamp white oak	Longleaf, slash, & South Florida slash pine	North Carolina to Louisiana
<i>C. conigenum</i>	Southwestern cone rust	Mexican blue, Dunn, Emory, gray, canyon live, netleaf, silverleaf, & Arizona white oak	Chihuahua, Apache, Cuban, ponderosa, & other pines	So. Arizona to Mexico & Central America
<i>Cronartium</i> sp.	Oak leaf rust	Coast live & California black oak	None known	California coast, rarely inland
<i>Cronartium</i> sp.	Tanoak leaf rust	Tanoak (<i>Lithocarpus</i> sp.)	None known	California coast

Table 2. Pine-Oak rust fungus spore states, where they are borne, and what they infect.

Spore states	Borne in (fungal organs)	Borne on (host)	Infect (host)
Spermatia & receptive hyphae ^a	Spermogonia	Pine branch, stem, or cone	(Non-infective) ^b
Aeciospores	Aecia	Pine branch, stem, or cone	Oak leaf
Urediniospores	Uredinia	Oak leaf	Oak leaf
Teliospores (aggregated in telial columns)	Telia (emerge from or around uredinia)	Oak leaf	(Non-infective) ^c
Basidiospores	Basidia	Telial column on oak leaf	Pine needle, shoot, or young cone

^a *Hyphae* are thread-like filaments that grow around and within infected plant cells and absorb nutrients to support the growth of the rust fungus.

^b *Spermatia* and *receptive hyphae* are contained in a *spermogonium* that is filled with nectar to attract insects, which carry the *spermatia* to compatible *spermogonia*, where the *spermatia* fertilize the *receptive hyphae*, leading to development of *aecia* and *aeciospores*.

^c Each *teliospore* germinates in place in the *telial column* to produce a short, hypha-like *basidium* that bears four *basidiospores*, which are discharged when the *basidium* matures.

obligate parasites, or biotrophs). If the host dies, the rust fungus dies. Under such constraints, these fungi are adapted to not kill their hosts until they have reproduced (i.e., formed and released spores), after which the host may sooner or later succumb to infection and the disease it causes.

Although closely related to the fungi that form the mushrooms that abundantly fruit on the forest floor in fall and spring—and to the wood rot fungi that produce **conks**² upon the stems and branches of rotted trees and are usually associated with wounds—the rust fungi are aggressive pathogens, attacking trees that are healthy, fast-growing, and not necessarily compromised by insects, decay, climate, or adverse soil or site conditions.

²Generally firm, conspicuous, often large fruiting bodies of decay or stem-rot fungi in which spores are produced.

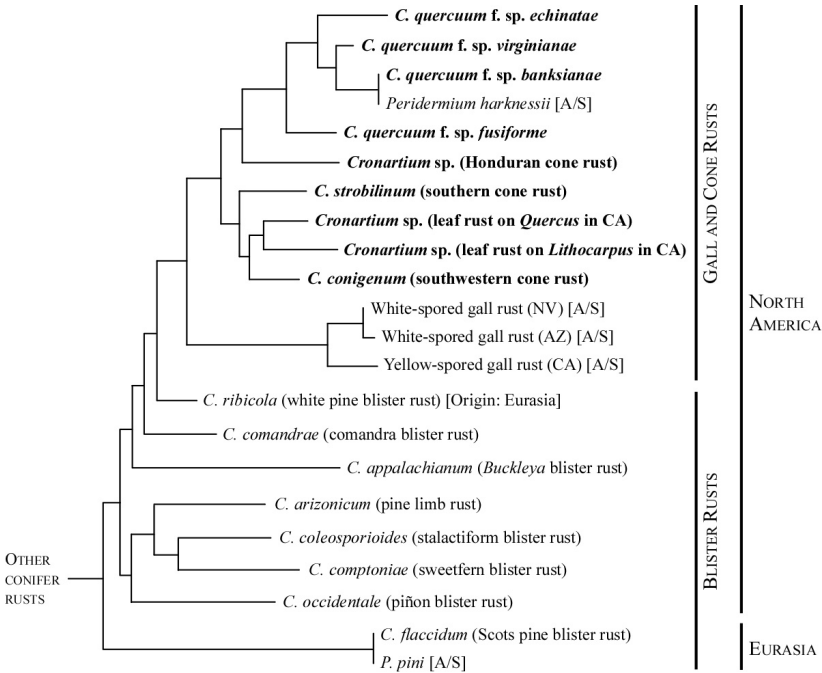


Figure 1. *Cronartium* phylogeny based upon nucleotide sequences of the internal transcribed spacer (ITS) region of the nuclear ribosomal DNA (tree modified from Vogler and Bruns, 1998). Among the North American gall and cone rusts, the species highlighted in bold are known to infect oak leaves and, except for the two *Cronartium* spp. from California, complete their life cycles by infecting pines. Gall rust species in non-bold text (*Peridermium harknessii*, and white-spored and yellow-spored gall rusts) infect from pine-to-pine only. The North American blister rusts in the lower half of the tree alternate between pines and woody and herbaceous species in several Angiosperm families. [A/S, autoecious/short-cycled pine-to-pine rust fungi.]



Figure 2. Underside of a *Quercus agrifolia* (Coast live oak) leaf from Marin Co., CA, showing scattered appearance of minute uredinia emitting orange urediniospores, and associated brown telial columns. Urediniospores infect other oak leaves, building up infection and increasing the potential distribution of the pathogen, while basidiospores (produced from the aggregated teliospores) infect pines. Although the fungal structures are best observed with a hand lens, the contrast between the green leaf and the bright, orange urediniospores would be clearly evident if the photograph were in color.

The pine-oak rust fungi provide a parasitic connection between the natural histories of pines and oaks. These fungi are members of the rust genus *Cronartium*, **heteroecious**³ rusts and their derivatives that spend part of their lives infecting oak leaves (Figure 2) and part infecting pine stems (Figure 3), branches, or cones (Figure 4). The relative degree of parasitism the rust fungi exhibit on their alternate hosts when they occur together helps regulate and modify the local abundance and distribution of pines and oaks.

The severity of damage the pine-oak rust fungi cause is correlated with the type of tissue infected and colonized. Only leaves are infected on oaks, and if infection is especially extensive or damaging on any single oak leaf, that leaf may be shed, effectively eliminating the pathogen. Although pines are infected through needles or succulent shoots, the rust will eventually form a gall in perennial woody tissue, whether branch or stem, which can lead to deformity and death of the infected part. Multiple infections on branches and stems severely inhibit tree growth, often resulting in stunting and premature death of the entire tree.

When a cone is infected by either *Cronartium strobilinum* or *C. conigenum* (Table 2), the cone swells to at least twice the size of an uninfected cone (Figure 4), and, because the hyphae of the rust fungus entirely colonize the infected cone, no

³ A **heteroecious** pathogen uses more than one host during its life cycle; within the *Cronartium* group of rust fungi there are also some that are **autoecious**, i.e., that require only one host during their life cycle (Figure 1).

seed are produced. Instead, aeciospores are produced in abundance on the infected cone surface in late spring, from which they are released and infect oak leaves. Although cone rust fungi destroy all infected cones, they do not directly impact the woody growth of the host tree.

Ranked by severity to the affected host, the gall rusts cause the greatest damage, deforming pine branches and stems and negatively impacting host growth, while the cone rusts, discounting destruction of the seed crop, cause insignificant damage to their hosts. Oak leaf infections generally cause negligible damage to oak, although infection-caused leaf-cast can be intermittently severe.

Where rust-susceptible pine species grow in forests that are heavily mixed with oaks, rust effects on pine growth and form can be severe, thereby maintaining a relatively high abundance of oaks, where otherwise uninfected pines might overtop the hardwoods and limit their ability to thrive. Conversely, non-host pines or other conifers that inhabit or invade an oak forest may eventually dominate the oaks because they are not susceptible to infection. Converting portions of an oak-dominated habitat to single-species cultivation of a rust-susceptible pine can be disastrous, since the planted pines may succumb to a pine-oak rust disease that they would otherwise escape if planted at a distance from oak habitat.

A phylogeny or family-tree of some of the major North American pine-rust fungi is shown in Figure 1 (based upon Vogler et al., 1996; Vogler and Bruns, 1998). Perhaps the best-known of these is *Cronartium ribicola*, cause of the white pine blister rust disease that was introduced from Asia via Europe around the turn of the 20th Century, and which alternates between members of the genus *Ribes* (gooseberries and currants) and the white, or five-needled pines. An invasive exotic, *C. ribicola* spread across North America in just a few decades, and severely affected commercial production of eastern white pine (*Pinus strobus*) in the north-eastern U.S. and Canada, and western white pine (*P. monticola*) and sugar pine (*P. lambertiana*) in the northwestern and Pacific States and Provinces. Today it continues to spread into the habitats of the other white pines in the U.S.; at present, only Great Basin bristlecone pine (*P. longaeva*, the oldest living tree species on earth) is still free of blister rust infection in the wild.

The upper half of Figure 1 depicts the closely related group of gall and cone rust fungi. The pine-oak and oak-oak⁴ rusts are illustrated in bold; their common names, their principal oak and pine hosts, and their known distributions are shown in Table 1. The other species not in bold (*Peridermium harknessii* and yellow- and white-spored gall rust, labeled “A/S”) are autoecious pine-pine rust fungi that infect directly from pine-to-pine, without alternating to oak leaves, and thus, despite their likely derivation from pine-oak ancestors, have no current connections to oaks.

These examples of life-cycle and host complexities are common among the rust fungi, whereby a heteroecious, full-cycled species gives rise to autoecious, short-cycled derivatives that live on either one or the other of the hosts of the ancestor without having to cycle back to the former alternate host. One difference between the oak-to-oak and the pine-to-pine derivatives, however, is significant. The oak-to-oak derivatives that reside on live oaks may continue to cycle from oak leaf to oak leaf without infecting a pine (either because that pine host species is no

⁴ By oak-oak rust fungi, I refer to those that have no known pine host. They produce spore states (**basidiospores**, Table 2) that ostensibly could infect a pine, but no pine host is known. They also produce spore states (**urediniospores**, Table 2) that serve to reinfect oak leaves.

longer in the vicinity, or has been eliminated), because live oaks retain some leaves throughout the year, and thus the spore stages (urediniospores, Table 2) that infect oak leaves can be present at any time of year. However, since these derivatives also continue to produce pine-infecting spores (basidiospores, Table 2) as well, they theoretically retain the ability to infect the former pine host or hosts, which could occur if those pine species were to be reintroduced by humans, or they were to migrate back under an altered climatic regime.

For the pine-to-pine species, however, this flexibility has been lost. The spore stages produced on pines (aeciospores, Table 2) that used to infect oak leaves have been genetically modified in such a way that they now infect pine stem tissue and not oak leaves, and thus their ability to infect anything but pine (usually through succulent, actively-expanding stem tissue) has been lost. In short, the pine-to-pine rusts appear to have evolved into a bottleneck that they can't get out of, while the oak-to-oak species retain a flexibility that potentially could allow them to regain their heteroecious life style, assuming a suitable pine host or hosts were to be introduced or migrate into the vicinity.



Figure 3. A subglobose to elongate, sporulating *Peridermium harknessii* (western gall rust) gall on lodgepole pine, Yellowstone N.P., WY. Aeciospores are enclosed in peridia (note light-colored, bulbous shapes between bark scales at the upper middle) that emerge in spring and early summer. Gall shown here is intermediate in shape between the globose galls of *Cronartium quercuum* f. sp. *banksianae* and the fusiform galls of *C. quercuum* f. sp. *fusiforme*. In *P. harknessii*, which is a pine-to-pine gall rust, the spores borne in the peridia will infect succulent shoots of nearby lodgepole pines, bypassing oaks. In *C. quercuum*, which is a pine-oak gall rust, spores emerging from the galls will infect oaks.

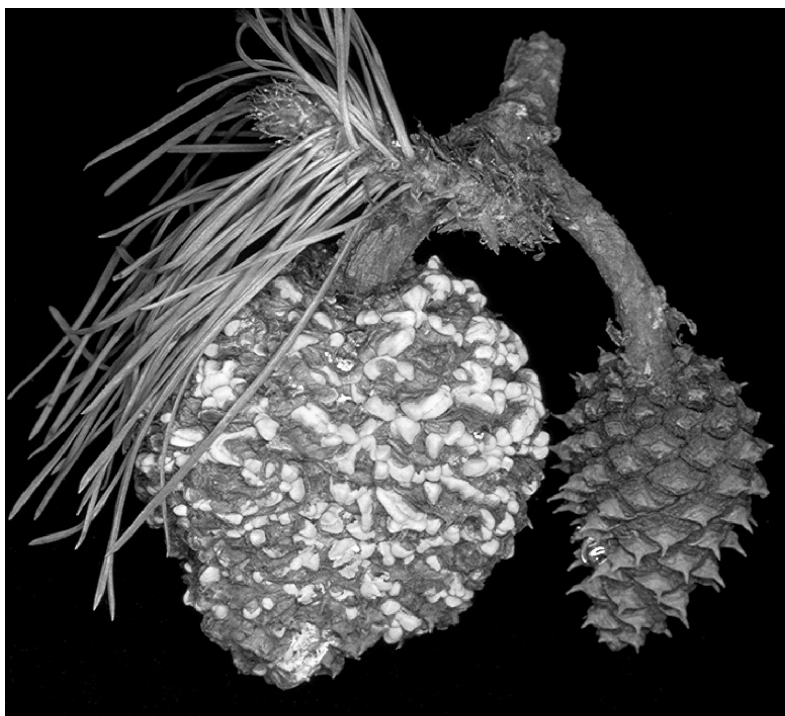


Figure 4. A cone of *Pinus leiophylla* (Chihuahuan pine) infected by *Cronartium conigenum* (on left), Cochise Co., AZ. Infected cones become fully colonized by rust fungus mycelium (masses of hyphae), causing the cone to grow to at least double the size of a normal, uninfected cone (on right). *C. conigenum* spores are borne in peridia that erupt across the surface of the infected cone (note light-colored, bulbous peridia, which have not yet broken open to release aeciospores). When mature, aeciospores will infect nearby susceptible oaks, completing the cycle of infection.

Among the pine-oak rust fungi shown in Table 1, those that adversely affect the growth of pines for timber production are the most intensively studied. For example, fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) has had a major impact upon the economic viability of growing loblolly and slash pine for commercial uses in the southeast, and thus became a major threat to survival of the timber industry. Intensive, long-term, and successful research to develop fusiform-rust resistant loblolly and slash pines has permitted the forest industry to prosper in spite of the fusiform rust pathogen. Much research has also been done on the eastern gall rust, *C. quercuum* f. sp. *banksianae*, on southeastern cone rust, *C. strobilinum*, and on the pine-to-pine western gall rust, *Peridermium harknessii*, all of which affect timber production. The distributions of these four rust species on pine are well established, and the distributions of the three heteroecious species

that also infect oaks are well known within the range of forests where commercial timber harvest occurs.

Less well known are the distributions of the pine-oak rusts outside of forests that are managed for timber production. And, even when these pathogens are thought to damage pines esthetically or are considered threats to pine sustainability in parks and suburban settings, little attention is given to the effects or distributions of the stages of these rusts that infect oaks. As noted earlier, without close examination, the spore stages on oak are cryptic and the damage to oak leaves is usually negligible. Thus, we don't really know how widespread these pine-oak rusts may be outside of forested lands where pines are abundant or cultivated commercially.

Information on distributions of the oak-infecting stages of the heteroecious pine-oak rusts would be useful. Aeciospores are known to spread hundreds of miles from infected pines if the winds are right, and urediniospores can spread infection from oak leaf to oak leaf for many miles, perhaps as far as aeciospores can be transported. Thus, the oak-infecting stages can establish long distances from rust-infected pines. Oak leaf rusts have been found on bur oak (*Quercus macrocarpa*) in South Dakota; they could have come from *C. quercuum* f. sp. *banksianae* infections on jack pine to the north, or from *C. quercuum* f. sp. *fusiforme* on loblolly or slash pine to the south. Other examples are the oak-leaf rusts on coast live oak and tanoak along the central California coast (Table 1); phylogenetically (Figure 1), they appear to be species distinct from the other pine-oak rust fungi, and yet no pine hosts have been found, suggesting they are long separated (both in distance and time) from the pine-infecting species from which they probably derived.

With climates predicted to change dramatically over the coming decades, it is possible that pine-oak rusts will establish elsewhere on live oaks far from infected pine stands. There they could become more common on oak leaves because of altered microclimates, and perhaps become more potent parasites on oaks. However, to make such predictions, we need more baseline data on which pine-oak rusts can be found infecting which oak species and where, especially outside the ranges of their pine hosts. Members of the International Oak Society could contribute substantially to providing observations on distributions and new hosts of these North American native "invasive exotics". Rust-infected oak leaves are readily pressed and dried, and, when properly treated and stored, can be used as sources of fungal DNA for sequencing, through which the species of pine-oak rust can be determined. From these observations and associated sequence data, scientists could begin to map the distributions of these fungi far from their alternate pine hosts. Contact the author if you would like further information on the pine-oak rust fungi, or would like to contribute to this mapping effort.

Acknowledgement

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Detlev R. Vogler is currently a Research Geneticist/Plant Pathologist at the Institute of Forest Genetics, USDA, Forest Service. His research focuses on mechanisms and inheritance of resistance to white pine blister rust in Pacific Coastal white pines, and to western gall rust in Monterey and ponderosa pines; since 2001, he has been studying how forest pathogens affect the diversity, sustainability, and evolution of fire-dominated coniferous forests in Parque Nacional Sierra de San Pedro Martir, Baja Norte, Mexico. With a Forest Service colleague, Brian Geils, he is preparing an extended manuscript on the natural history of the pine stem, branch, and cone rust fungi in North America.



Dr. Detlev Vogler collecting spore samples from an oak-pine rust in central Honduras (May 2002).
photo © Guy Sternberg

Text references

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- Vogler, D. R., and T. D. Bruns. 1998. Phylogenetic relationships among the pine stem rust fungi (*Cronartium* and *Peridermium* spp.). *Mycologia* 90: 244-257.

Suggested readings

- Agrios, G. N. 2004. Plant Pathology. 5th Ed. Academic Press, San Diego, CA. 952 p.
- Authoritative academic introduction to the *Cronartium* rusts as pathogens of pine, from the perspective of practicing forest pathologists and forest managers. Intended as a college-level introductory text in plant pathology, it provides a broad discussion for the general biologist on the science of phytopathology, and on the living organisms and abiotic agents that cause disease in plants. Includes a glossary of phytopathological terms.
- Alexopoulos, C. J., C. W. Mims, and M. Blackwell. 1996. Introductory Mycology. 4th Edition. John Wiley & Sons, New York, NY. 869 p.
- Authoritative academic introduction to the *Cronartium* rusts as fungi, within the context of the larger science of mycology; emphasis on taxonomy, phylogeny, life cycles and spore states, with secondary discussion of these organisms as pathogens. Intended as a college-level introductory text in mycology, it places the pine stem, branch, and cone rusts within the broader context of fungi and related microorganisms. Includes a glossary of mycological terms.
- Sinclair, W. A., and H. H. Lyon. 2005. Diseases of Trees and Shrubs. 2nd Edition. Comstock Publishing Associates, Ithaca, NY. 660 p.
- Information for plant pathologists, foresters, and landscapers who are responsible for the health of trees and forests and who need to know how to recognize and control their pathogens; beautifully illustrated with excellent color photographs. To quote from the dust jacket, "[This book] is a comprehensive pictorial survey of the disorders of forest and shade trees and woody ornamental plants in the United States and Canada. An authoritative reference, it is also a reliable and handy diagnostic tool that will simplify the identification of specific plant diseases by focusing on signs and symptoms that can be seen with the unaided eye or with a hand lens." Extensive glossary, reference list, and index.
- Ziller, W. G. 1974. The Tree Rusts of Western Canada. Publication No. 1329. Environment Canada, Canadian Forestry Service, Ottawa, Canada. 272 p.
- Although long out of print and restricted in geographic scope, this text is a classic in the conifer rust field, well-illustrated and comprehensive, with excellent life-cycle diagrams and glossary. May be available at your local University or College library, or, if you must have a copy, via one of the online used-book services.