

# I - C. The Taxonomy of the Soybean Rusts

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The 18 October 1993 issue of Time Magazine, under the title of *Attack of the rust fungus* reported in a brief paragraph that "...according to a Congressional report...at least 4,500 immigrant species..." including the "...soybean rust fungus, have established themselves on U.S. soil... causing billions of dollars in damage." Time magazine in reality misinterpreted the congressional report (6) which stated only the "potential threat" of the soybean rust fungi if accidentally introduced into the soybean growing regions of the U.S. The Time report was ahead of its time. Now we know that soybean rust is in the U.S. in the State of Hawaii (3). Soybean rust have been known for a longer time in the Caribbean Islands, Mexico, other Latin American countries, Asia and Australia. The occurrence of soybean rust pathogen so close to continental U.S. soybean growing regions is too close to be complacent about these pathogens. Very little is known about other populations of very similar rust pathogens in Africa.

Unfortunately, few American or foreign scientists have studied these rust pathogens and little is known about their exact place of origin, natural history, and true relationships to kindred species.

The scientists, who do the research that makes it possible to actually determine that there exists thousands of "immigrant species" that the Time article mentioned, are the biological taxonomists. They often refer to themselves as biosystematists. These are scientists whose research is focused on determining and comparing the millions of traits of the world's millions of different species of living things so that it is possible to know a relatively few specific traits by which a single species can be identified out of the myriad of possibilities. These scientists discover traits, classify organisms based on traits, name the species, and provide the technology for identification of the earth's species diversity.

Agricultural research is almost exclusively commodity oriented. Obviously agribusinesses that deal in maize, wheat, swine, poultry, or soybeans require research that relates directly to their

commodity. But to solve problems for a specific commodity a much broader body of knowledge is required than just the data that are directly connected to that commodity. In the case of the soybean rusts much of this broader base of knowledge is lacking or only tentative. More basic knowledge of these rusts is required for progress in management of these diseases.

General knowledge of tropical and sub-tropical rust fungi, including such basic things as their natural history, geographic and host ranges, life cycles, and true relationships to kindred species is inadequate to mount long-term, cost effective management procedures for these soybean pathogens if they should be introduced into the continental U.S. Compared to many other diseases that affect basic commodity crops, few U.S. or foreign scientists have studied these rusts that attack soybeans. The classification given below must be considered as a first approximation based on this limited knowledge. The familial, generic, and species definitions included here are in reality scientific hypotheses that require further testing and, as hypotheses, are subject to modification or abandonment as new data are discovered and interpreted, or as older data are reinterpreted. In the case of the rust fungi which are classified as belonging to the fungal order Uredinales, it is the research of the taxonomic uredinologist that must be relied upon to discover and evaluate the traits that go into the hypotheses of classification. It is the taxonomic uredinologist who assigns the scientific names to these species concepts and these names become the key words placed in

indexes and computers that unlock the knowledge that exists about these pathogens to other professionals.

Only recently has research been done that has compared all of the rusts on the legume family that are related to the soybean rusts (5). This work is part of a larger effort to produce a modern classification of all of the rusts of the family Phakopsoraceae. This family of rusts is composed of 12 genera and nearly 200 species worldwide (1). The research on the legume rusts was based on comparison of microscopic morphological traits of approximately 200 herbarium specimens representing populations of these rusts in Asia, Australia, and the New World Tropics. Unfortunately, only six specimens were available from Africa. Two closely related genera were recognized as parasitizing legumes, *Cerotetium* and *Phakopsora*. The spermogonia and aecia stages (when known) and uredinia of these two genera are very similar. Telia differ. Morphological variations in the aecia and uredinia stages are sufficient to have a separate anamorph classification for them (1,5).

*Cerotetium*, which is not known to infect soybeans, has a well developed hymenial layer of sporogenous cells that produce long rows of thin-walled, usually hyaline probasidial cells (teliospores). These cells often only loosely joined, germinate at maturity, without a dormancy period, to produce metabasidia and then basidiospores. In herbarium specimens with mature telial sori stages the outermost layers of probasidial cells may have germinated and collapsed, forming an amorphous area over the younger ungerminated cells. Nearly 20 species of *Cerotetium* are known worldwide. Five of these attack legumes. None of them parasitize soybeans but some *Cerotetium* spp. infect some legume genera that also serve as hosts for the soybean rust fungi.

*Phakopsora*, unlike *Cerotetium*, does not produce a well defined hymenial region of probasidial sporogenous cells. A preliminary study of the telial sorus ontogeny indicates that probasidial cells (teliospores) are derived directly

from transformed hyphal cells. At maturity these teliospores may be irregularly grouped together or grouped in more or less distinct layers. Intergradations between these two kinds of groupings occur in some species. Approximately 80 species of *Phakopsora* are known worldwide with six species on legumes. The two species that infect soybeans are best identified by traits of the telial sori. *Phakopsora pachyrhizi*, the Asian-Australian species, has a telial stage in which the spores are in two to seven layers and the spore walls are pale yellowish-brown, and more or less uniformly about 1  $\mu$  thick, or only slightly thickened up to 3  $\mu$  in the apical walls of the outer-most layer of spores. *Phakopsora meibomia*, the tropical Latin American species, has telia in which the spores are in one to four, rarely five, layers; the spore walls are cinnamon-brown to light chestnut-brown, and 1.5 to 2  $\mu$  thick but with the apical walls of the outermost layer of spores up to 6  $\mu$  thick. The nomenclatural history of these two species is complex and is presented in the paper by Ono *et al.* (5). Because of the few specimens available from Africa, the correct assignment for them remains uncertain.

## HOST RANGE

The host ranges of these two soybean rusts are unusually wide (5). *Phakopsora meibomia* has been reported to produce natural infections on 42 species in 19 genera of legumes, 18 species in 12 additional genera have been artificially infected. *Phakopsora pachyrhizi* has been reported to produce natural infections on 31 species in 17 genera of legumes, and 60 species in 26 additional genera have been artificially infected. Twenty-four species in 19 genera are common hosts for both rust species. Among these many legume hosts, *Pueraria tobata*, (Willd.) Okwi (kudzu), is especially noteworthy because of its vigorous growth and widespread occurrence in the southeastern U. S. In addition many species of the other genera known to be hosts occur throughout the continental U.S. and

perhaps could serve as potential alternative hosts and reservoirs of inoculum that could spread to soybeans.

## DEVELOPMENT OF UREDINIAL SORI

The uredinial stages of the soybean rust fungi are important structures in the disease and life cycle because, under proper conditions, from just a few initial infections in a soybean field or on other cultivated or wild legume hosts, a rapid and damaging epidemic may develop. These minute dome-shaped sori, which measure hardly more than 150 $\mu$  across and 70 $\mu$  deep, are the asexual spore producing organs that produce prodigious numbers of windborne spores that spread the disease. Thus, knowledge of their structural anatomy that enables them to produce these spores is necessary to understand the dynamics of the disease. Additionally, knowledge of these anatomical features, when compared to homologous traits in other rusts, helps form a basis for classification and accurate identification of rust species.

The following account is mainly from unpublished research by Buritica and Hennen. Some information is from Marchetti *et al.* (4), which is the only other published paper on sorus development.

Soybean rust uredinial sori begin as tightly intertwined knots of hyphae, nearly always in abaxial substomatal chambers of soybean leaflets. These knots are the protosori from which the mature spore producing organ develops. The genetic, chemical, and physical interactions between the fungus, host, and environment that controls the initiation and rate and progress of development of these sori are unknown. Without doubt these factors are part of whatever repertoire of tolerance or resistance mechanisms that may exist in soybeans and other hosts.

From the protosori two main parts of the mature sori develop: (i) a bounding basal peridium surmounted by the numerous incurved paraphyses of varying lengths and (ii) the fertile spore producing hymenial tissue layer at the base of the sorus. In a mature sorus the longer outer paraphyses

come together at the apex of the dome-shaped structure but leave a small pore. As the sorus matures it pushes against the host epidermis and becomes partly erumpent with the small pore functioning as the escape route for the spores.

The first tissues to form are the irregular basal peridium from which emerge the incurved, mostly unilaterally and apically thickened one-celled paraphyses of various lengths. Because these bounding structures begin to develop and mature first, they delimit and enclose the growth and regulate the size of the mature sorus.

The hymenial tissue begins development a little later within and at the base of the delimiting structures. The first sporogenous cells and spores to mature are centrally located, while younger ones develop radially around these until the basal hymenium expansion stops at the edge of the peridium. Because of this limitation on the size of the hymenial tissue the original number of spore producing cells is limited. However, it appears as if new sporogenous cells may grow between the older ones and produce new crops of spores.

The microscopic details of spore formation are considered important in many fungi and are aiding in development of better systems of classification of species as well as adding to the basic understanding of their growth and development. We found evidence for a type of spore formation in *P. pachyrhizi* termed percurrent proliferation. This mechanism has been reported in at least five other species of rust fungi as determined by both bright-field and transmission electron microscope studies (2). We conclude from our bright-field microscope studies that it is common in most species of *Phakopsora*.

Percurrent proliferation means that a succession of spores is produced from the same locus at the apex of a sporogenous cell, with each successive spore coming through the interior of the remains of the pedicel or intercalary cell of

the previous spore. The remains of the pedicels or intercalary cells are seen as irregular remnant collarettes on the sporogenous cell. The exact number of collarettes, and thus the number of spores produced by a sporogenous cell, could not be determined by our bright-field microscope technique. This method of multiple spore formation

from a single sporogenous cell along with the fact that new sporogenous cells grow between the older nonfunctional ones helps explain how such a multitude of spores can be produced from the limited hymenial space at the base of the enclosed dome-shaped sori.

## LITERATURE CITED

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