

HOST RELATIONSHIP, LIFE CYCLE, AND
SPECIES CONCEPT OF CRONARTIUM and ENDOCRONARTIUM

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INTRODUCTION

Pine stem rusts are probably the most important diseases of pines in the world. Several species of pine stem rusts are considered to be the limiting factors and major concerns in the intensive cultivation of certain pine species. Examples of pine stem rusts that are important in forestry are: several forms of white pine blister rusts in North America and Asia; fusiform rust (Cronartium fusiforme - C. quercuum f.sp. fusiforme) in southern North America; several hard-pine stem rusts (C. comandrae, C. coleosporioides, C. comptoniae, and Endocronartium harknessii) in northern North America; and the C. flaccidum complex (including E. pini) in Europe.

In recent years, several nomenclatural and taxonomical suggestions have been made regarding closely related species (Burdson and Snow 1977, Ito and Uozumi 1976, Wicker and Yokota 1976). In addition, proposals for the taxonomy and nomenclature of species having different life cycles (heteromacrocylic and endocyclic) have been made (Hiratsuka 1968, 1969). There is still, however, no general agreement on the basic taxonomy and nomenclature of several key species complexes and the treatment of species with different life cycles.

The purpose of this paper is to provide an overview of the host relationships, life cycles, and species concepts of pine stem rusts and to discuss several important points where disagreements and problems exist regarding the taxonomy and nomenclature of several species complexes.

KNOWN SPECIES OF PINE STEM RUSTS

According to Peterson (1973) there were 36 validly described Cronartium species, but only 12 species are recognized now as belonging to the genus. Many autoecious species having columnar telia were described as species of Cronartium but now have been transferred to such genera as Crossospora, Cionothrix, Didymopsora, or Dietelia. Although superficially similar in telial morphology, these species are probably not closely related to Cronartium.

Hiratsuka (1969) established a new genus, Endocronartium, for endocyclic species and recognized two species, E. harknessii and E. pini. Two more possible species for inclusion in this genus have been reported: one in Japan on Pinus pumila (Saho and Takahashi 1973) and another in North America on P. jeffreyi (Krebill and Nelson 1970).

Another species, C. keteleeriae, is known to occur as a microcyclic species on needles of the conifer Keteleeria elveyniana from Yunnan, China, but most likely this species does not belong to Cronartium. Preliminary examination suggests that this rust may belong to Cionothrix.

HOST RELATIONSHIP

Because of the obligate parasitism of rust fungi, host relationships are considered important in identification and are very reliable criteria for taxonomy. Differences in host specificity and host range often coincide with distinguishable morphological variations. On the other hand, too much dependence on the host relationship without careful morphological examination results in classifying same or closely related fungi in different taxa.

Plants from eight families belonging to the class Dicotyledoneae are known to be alternate hosts of pine stem rusts (Fig. 1). An interesting family is the Scrophulariaceae (Pedicularis, Castilleja, Melampyrum, etc.) because species of this family are known to be the alternate hosts for the C. ribicola complex (including C. kamtschaticum), C. flaccidum, and C. coleosporioides. A five-needle pine blister rust in Asia was found to infect both Pedicularis and Ribes species (Yi and La 1974, Yokota et al. 1975, La and Yi 1976, Ito and Uozumi 1976, Yokota and Uozumi 1976, Wang 1979, personal communication), although the degrees of reaction of both genera are different between forms. The North American form of C. ribicola with Ribes as the usual alternate host was successfully used to infect Castilleja miniata (Hiratsuka 1976). Those genera (Pedicularis and Castilleja) are also known to be the alternate hosts for the North American C. coleosporioides and European C. flaccidum. The aeciospore morphologies of C. ribicola and C. flaccidum are very similar, and morphological comparisons of all species concerned should be done carefully to arrive at satisfactory taxonomic solutions.

LIFE CYCLE

Most of the pine stem rusts have heteromacrocytic life cycles with spermogonia and aecia on pine hosts and uredinia, telia, and basidia on alternate hosts (Fig. 2). It has been known for a long time that a few pine stem rusts (Peridermium harknessii in North America and P. pini in Europe) do not need alternate hosts to complete their life cycles. According to Hiratsuka et al. (1966) and Hiratsuka (1968), those pine-to-pine species have endocyclic life cycles (Fig. 3). Furthermore, Hiratsuka (1974) established a new genus, Endocronartium, to accommodate the two species.

Two major questions can be raised regarding the above observations and interpretations of the life cycles of the two pine-to-pine rusts and about the suggested nomenclatural treatment in establishing a new genus.

The first question is with regard to the interpretation of the life cycles of pine-to-pine species. Hiratsuka et al. (1966) and Hiratsuka (1968, 1969) concluded that although no basidiospores were produced, Peridermium harknessii and P. pini have endo-type life cycles, probably with nuclear fusion occurring in the spores and subsequent meiosis and septation occurring in the germ tube (Fig. 3). It can be argued, however, that since basidia do not produce basidiospores, the structures should not be called basidia but should be regarded as merely abnormal germ tubes. Accordingly, pine-to-pine rusts can be considered abnormal forms capable of repeating aecial states rather than having endocyclic life cycles.

The second point is that even if those rusts are recognized as having endocyclic life cycles, it is not easy to come up with an acceptable taxonomic and nomenclatural solution to the species. According to Hiratsuka (1969), three possibilities are open for making nomenclatural changes for these endocyclic pine stem rusts: (1) include the two species within the genus Cronartium; (2) recognize the two species as belonging to an existing endo-genus, e.g., Endophyllum; or (3) establish a new genus, as proposed in this paper.

Opinions vary on whether to recognize endo-genera. Some researchers (Cunningham 1930, Laundon 1967) think that endo-species should be included under the parental genera because of the apparent genetic relationships. Others (Arthur 1934, Cummins 1959, Gaumann 1959; Hiratsuka 1973) favor establishing endo-genera. There are two major reasons why some object to the use of endo-genera. First, to recognize endo-genera would place unrelated species into one genus and would create an unnatural classification. Secondly, the spores should not be called teliospores, because they are morphologically aeciospores (although not germinating as such), and deletion of one spore state should not change the genetic affiliation of a fungus (Laundon 1967).

To include the endo-species in their parental genera could cause needless confusion in taxonomy and nomenclature. The parental genera of the endo-species cannot always be predicted, because endo-species are genetically separated from their parental species and the two are on different evolutionary courses. In some cases it would be impossible or highly speculative to assign parental genera because several genera have the same type of aecial state. That no such difficulty is encountered in the two species concerned does not detract from the principle of recognizing endo-genera. To transfer the two peridermioid

species into Endophyllum or other existing endocyclic genera introduces extremely heterogenous species into these genera and is not desirable.

Considering the above, I feel that the establishment of Endocronartium is justified.

Peridermium pini is a type species for the genus Peridermium, so to avoid the confusion of using Peridermium for endocyclic pine stem rusts and creating a new form genus for the other species known as Peridermium, the proposal to conserve the generic name Peridermium with a new type species (Peridermium elatinum) was made (Hiratsuka 1974) and was approved at the 11th International Botanical Congress in 1974.

SPECIES CONCEPT AND NOMENCLATURE

Except for such species as C. comandrae, which is very distinct morphologically from other species, most of the major groups of pine stem rusts have some uncertainty in taxonomy and nomenclature because of the similarity in morphology and lack of definite distinguishing morphological criteria. Species are often divided mainly by alternate host ranges or symptoms on pine hosts rather than by clearly defined morphological features.

Burdsall and Snow (1977) have concluded that C. quercuum and C. fusiforme are nonspecific and consider C. fusiforme to be a synonym of C. quercuum. They could not find significant morphological differences between several forms of pine-oak rusts and proposed four subdivisions based on pine host preference, as follows:

- C. quercuum f. sp. virginiane
- C. quercuum f. sp. banksiana
- C. quercuum f. sp. echinata
- C. quercuum f. sp. fusiforme

Similarly, Ito and Uozumi (1976) and Yokota and Uozumi (1976), dealing with a group of white pine blister rusts in Asia, proposed to reduce C. kamtchaticum to the synonym of C. ribicola and suggested the use of formae specialis (f. sp.), as follows:

- C. ribicola f. sp. ribicola
- C. ribicola f. sp. pedicularis

Wicker and Yokota (1976), dealing with the same group of rusts in Japan, suggested considering these two forms and another with a possible endocyclic life cycle (Endocronartium sp.) to be ecotypes of Cronartium ribicola.

The above-mentioned proposals are based on the assumption that the forms are morphologically indistinguishable and that the only distinguishing features are the host ranges and different host reactions. Although convenient and useful in some situations, the extensive use of f. sp. for subdivisions of major plant-pathogen complexes has some disadvantages and is often undesirable. The International Code of Botanical Nomenclature (Stafleu 1972), which governs the nomenclature of plants (including parasitic fungi), mentions the use of f. sp. in Article 4 (Note), as follows:

In classifying parasites, especially fungi, authors who do not give specific, subspecific or varietal value to taxa characterized from a physiological standpoint but scarcely or not at all from a morphological standpoint may distinguish within the species special forms (*formae specialis*) characterized by their adaptation to different hosts, but the nomenclature of *formae specialis* shall not be governed by the provisions of this Code.

As stated above, f. sp. names are not governed by the code. In other words, f. sp. names have no formal nomenclatural status or authority under the code, based on typification, Latin diagnosis, and principle of priorities. If these forms can be distinguished by morphological features, it is desirable to use subspecific divisions such as subspecies, variety, subvariety, forma, or subforma, which are governed by the code. In both cases mentioned above, not all components of the complexes were studied to make decisions. In the case of the *C. quercuum* - *C. fusiforme* complex no comparison was made with Asian and European forms or several other closely related pine-oak species. In the case of the *C. ribicola* - *C. kamtchaticum* complex no attempt was made to compare it with the North American form and Himalayan form (*Peridermium indicum*), which is reported to have some morphological differences (Coller and Taylor 1927, Peterson 1967). It is important, therefore, to examine the full range of the species complex to arrive at an acceptable nomenclatural and taxonomical decision.

SUMMARY

The host relationships, life cycle variations, and species concepts of pine stem rusts are discussed in terms of taxonomy and nomenclature. The *Cronartium ribicola* - *C. kamtchaticum* complex is examined in terms of two hard-pine stem rusts, *C. coleosporioides* and *C. flaccidum*, on species of *Scrophulariaceae*. The recognition of the pine-to-pine life cycle as endocyclic and the establishment of the genus *Endocronartium* for an autoecious species are discussed. The use of *formae specialis* (f.sp.), as suggested for the *C. ribicola* - *C. kamtchaticum* complex and the *C. quercuum* - *C. fusiforme* complex, is considered a convenient temporary solution, but careful morphological examination of closely related species and forms covering the full host and distribution ranges is recommended to arrive at satisfactory taxonomic and nomenclatural treatments of those groups.

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PINUS

ALTERNATE HOSTS

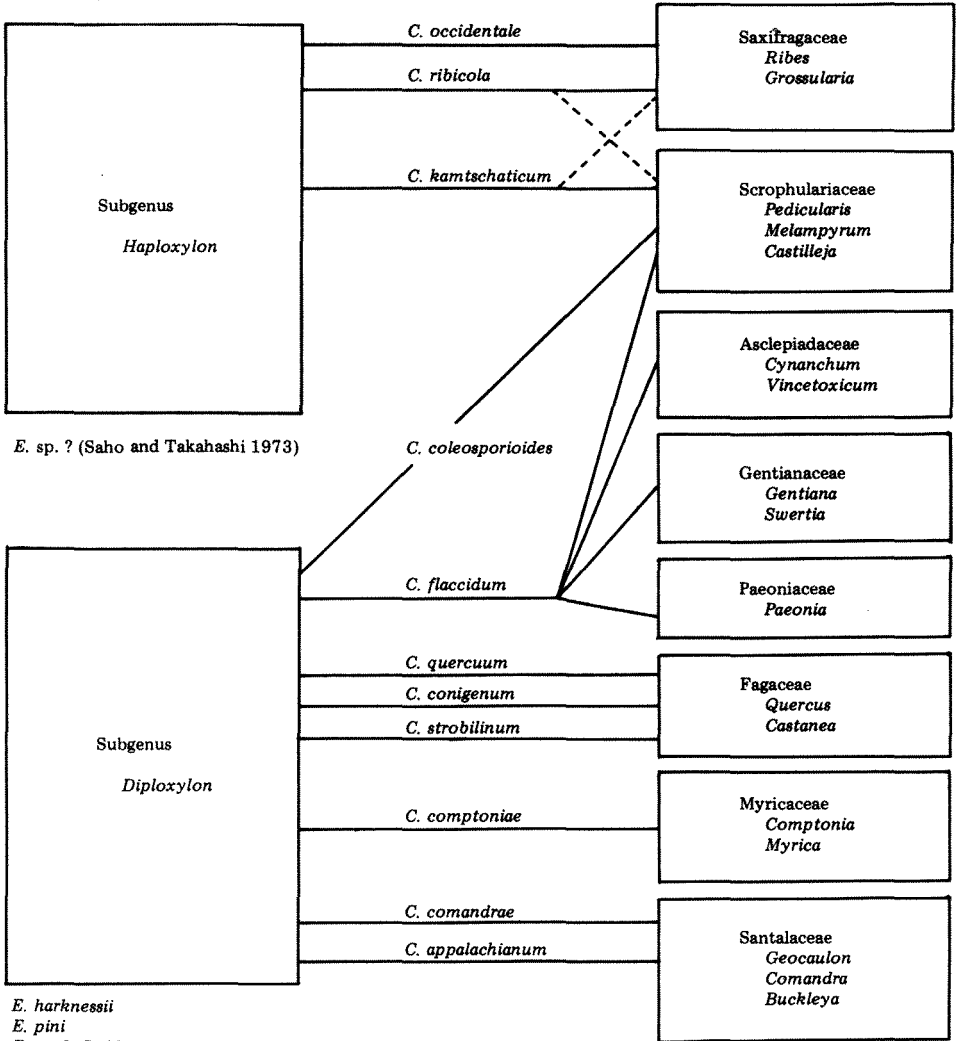


Figure 1. Host relationships of major pine stem rusts.

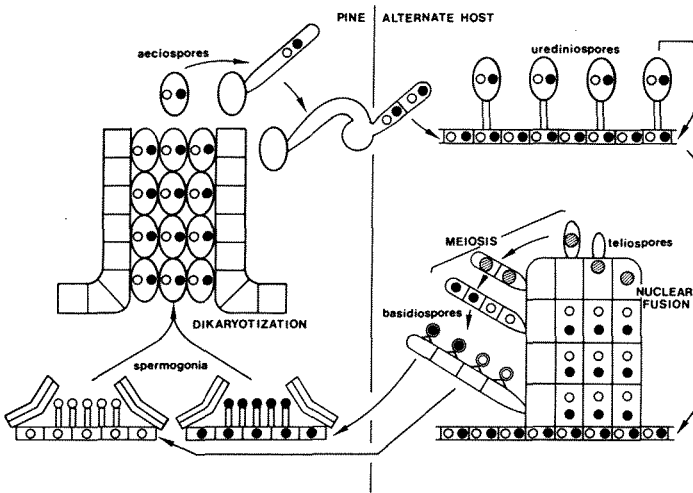


Figure 2. Life cycle of heteroecious pine stem rusts (*Cronartium* spp.).

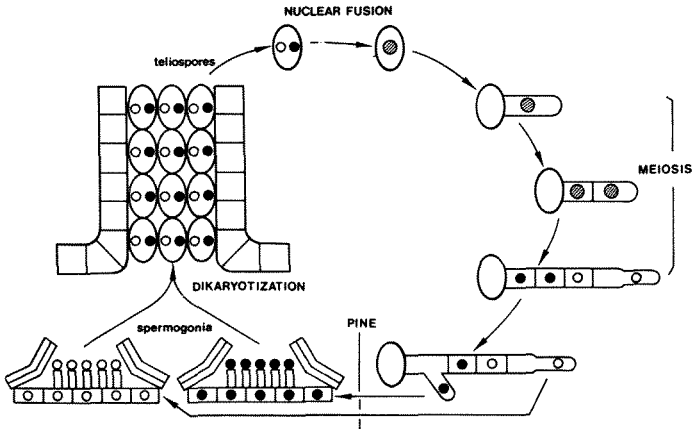


Figure 3. Life cycle of autoecious pine stem rusts (*Endocronartium*).

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