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A COMPARISON OF THE PINE-OAK RUSTS

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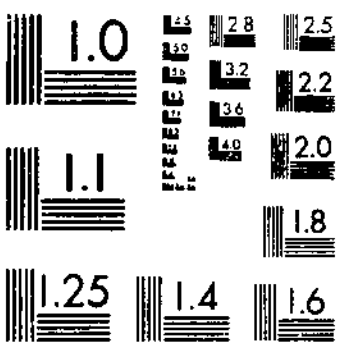

MICROCOPY RESOLUTION TEST CHART
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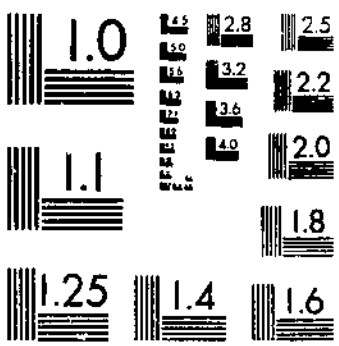

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS-1963-A

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A Comparison of the Pine-Oak Rusts[1]

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CONTENTS

A comprehensive study was begun in 1908 of the host relationships and of a morphologic comparison of five species of pine-oak rust, one of which, *Cronartium fusiforme*, is becoming a serious obstacle to the successful growth of slash and loblolly pine in some localities. In nurseries it has caused large monetary losses and shortages of planting stock. In 1938–39 losses ranged from 10 to 35 percent of the slash and loblolly seedlings. Since 1937 more than 10 million rust-

[1] Submitted for publication November 4, 1948.

[2] The work here reported was done in greenhouses and laboratories of the U. S. Department of Agriculture, at Washington, D. C., from 1908 to 1938, and supplemented by extensive field studies. The senior writer was assisted by Glenn G. Hahn, pathologist, Marie C. Goss, formerly pathologist, Margaret M. Ryan, formerly scientific aide, and N. Rex Hunt, formerly assistant pathologist, of this Division, in the greenhouse and laboratory; and by N. Rex Hunt, E. P. Meinecke, and the late Ellsworth Bethel, formerly assistant pathologist, principal pathologist, and pathologist, respectively, of this Division, in the field work. The junior writer checked the original data, revised the manuscript, and included independent observations of *Cronartium cerebrum* and *C. fusiforme*.

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infected seedlings have been culled. Also, damage to plantations is severe in areas where alternate hosts are abundant and weather conditions are favorable for infection. In studies to develop practicable control measures, it is necessary to distinguish taxonomically between the several species of fungi under consideration.

SUMMARY

This bulletin reports a comprehensive study of host relationships and a morphologic comparison of five pine-oak *Cronartium* species—four native to North America and one to eastern Asia. Considerable confusion exists in the taxonomic literature of this group of economically important fungi. J. C. Arthur, long our leading uredinologist, referred all species of the pine-oak rusts to *C. quercuum*. In disagreement with this classification, the writers consider the four American species—*C. cerebrum*, *C. fusiforme*, *C. conigenum*, and *C. strobilinum*—distinct from each other and from *C. quercuum*.

The geographical distribution of *C. cerebrum* on pine extends in eastern North America from Minnesota eastward through Canada and south to the Gulf of Mexico to eastern Texas. *C. fusiforme* is most prevalent in coastal States from the Eastern Shore of Maryland to Florida and Texas. The distribution of *C. conigenum* is not well defined but is known to occur in the mountains from Arizona through Mexico and Guatemala. *C. strobilinum* is distributed in the Southeast, from eastern North Carolina and Florida west along the Gulf coast to southeastern Louisiana. *C. quercuum* is indigenous to China and Japan and is not known to occur in this country. Host ranges are given.

Field observations suggest that *C. strobilinum* overwinters in the uredial stage on young oak stems, particularly of sprout type, far north of the range of its aecial hosts *Pinus caribaea* and *P. palustris*.

Inoculation of pines with aeciospores of the American species proved that they are heteroecious. No inoculations with *C. quercuum* were made, but this rust also has been reported heteroecious.

As a group, the black oaks were more susceptible than the white oaks to infection by *C. cerebrum* and *C. fusiforme*. On the other hand, species of white oaks were especially susceptible to *C. strobilinum* and slightly more susceptible to *C. conigenum*. The effect of infection by species of *Cronartium* on oak leaves normally is negligible.

Sporidial inoculations were made from telial columns grown from authentic material on oak leaves in the greenhouse, at Washington, D. C. *C. cerebrum* and *C. fusiforme* produced only spheroid and fusiform galls, respectively.

C. cerebrum formed pycnia the first spring after inoculation and aecia in the second. Some seedlings inoculated with *C. fusiforme* showed pycnia late in the fall of the year of inoculation and aecia the following spring. The periodicity of pycnial and aecial fruiting of *C. cerebrum* and *C. fusiforme* was biennial, but the elapsed time for fruiting may be one growing season shorter for *C. fusiforme*. *C. conigenum* also formed pycnia and aecia biennially. In contrast, *C. quercuum* and *C. strobilinum* form them annually.

The season of pycnial fruiting also varies between species. Pycnia of *C. cerebrum* are formed from December to June, *C. fusiforme* from

October to April, *C. quercuum* from December to February, *C. conigenum* in May and June, and *C. strobilinum* in March and April.

Interspecificity was indicated by the results from cross inoculations. *P. virginiana* proved highly susceptible to *C. cerebrum* and resistant to *C. fusiforme* and *C. strobilinum*. Other species of pines infected by *C. cerebrum* and apparently resistant to *C. fusiforme* were *P. banksiana*, *P. densiflora*, *P. echinata*, *P. gerardiana*, *P. glabra*, and *P. pinaster*. *P. clausa* also might be included, as it is infected naturally by *C. cerebrum* and the inoculations with *C. fusiforme* resulted in no infections.

Approximately 35 and 40 percent of the infected pine seedlings died following inoculation with *C. cerebrum* and *C. fusiforme*, respectively. *C. cerebrum* does not spread appreciably from branch to trunk, but remains confined to the original region of infection. The fusiform cankers of *C. fusiforme* often extend from the original point of infection to adjacent trunks and branches. They girdle the tree and are much more lethal than those of *C. cerebrum*.

Pine seedlings, artificially inoculated with *C. conigenum* and *C. strobilinum*, developed small galls near the base of the needles. Under experimental conditions, *C. strobilinum* killed 55 percent of the infected seedlings in 1 year. *C. strobilinum* in the Southeast and *C. conigenum* in the Southwest destroy first-year cones and thereby reduce the amount of pine reproduction.

Study of the comparative morphology of the five species of *Cronartium* revealed both similarities and differences. *C. cerebrum* and *C. fusiforme* are nearest alike, but are distinct in their gall forms. The galls of *C. cerebrum* and *C. quercuum* are always spheroid, those of *C. fusiforme* are always elongated, usually fusiform. The peridia of *C. cerebrum* and *C. fusiforme* are cerebroid, those of *C. quercuum* are irregularly hemispherical. These three species affect woody tissue in nature, while *C. conigenum* and *C. strobilinum* attack only first-year cones. The former has erumpent hemispherical peridia with side walls, the latter has submerged vestigial peridia without side walls. Within species, the different kinds of spores are easily identified by size and shape, but between species comparison of aeciospores or urediospores shows a usual overlapping in range of spore dimensions.

SPECIES OF CRONARTIUM ON PINES AND OAKS AND RELATED GENERA

Of the several species of *Cronartium* described with their pycnial and aecial stages on species of *Pinus* and their uredial and telial stages on species of *Quercus*, *Castanea*, *Castanopsis*, and *Lithocarpus*, the following are recognized as distinct species by the writers:

1. *Cronartium cerebrum* Hedgc. and Long (*1*, *pp. 691–692*; *2*, *3*, *4*, *7*, *9*, *11*, *20*),[3] borne on perennial globoid woody galls, bearing pycnia and aecia with erumpent cerebroid peridia on species of *Pinus* and with uredia and telia on species of *Castanea* and *Quercus* in the eastern United States.

2. *Cronartium fusiforme* Hedgc. and Hunt (*1*, *2*, *3*, *4*, *11*, *20*), borne on perennial fusoid or spindle-shaped woody galls, bearing pycnia and

[3] Italic numbers in parentheses refer to Literature Cited, p. 26.

aecia with erumpent cerebroid peridia on species of *Pinus* and with uredia and telia on species of *Quercus* in the southeastern United States.

3. *Cronartium conigenum* Hedgc. and Hunt (*2, 4, 10, 18*), borne on fleshy swollen cones, bearing pycnia and aecia with erumpent hemispheric peridia on species of *Pinus* and with uredia and telia on species of *Quercus* in Arizona, Mexico, and Central America.

4. *Cronartium strobilinum* Hedgc. and Hahn (*1a, 2, 4, 8*), borne on fleshy swollen cones, with pycnia, submerged aecia, and sunken vestigial peridia on *Pinus caribaea* Morelet and *P. palustris* Mill. and with uredia and telia on species of *Quercus* in the southeastern United States and in Cuba.

5. *Cronartium quercuum* (Berk.) Miyabe (*2, 4, 12, 13, 17, pp. 7–8, 22, 23, 25, 26*), a perennial globoid gall form, bearing pycnia and aecia with erumpent hemispheric peridia, found on pines and on oaks and related genera in Japan and China.

GEOGRAPHICAL DISTRIBUTION AND HOST RANGE OF PINE-OAK RUSTS

Cronartium cerebrum

On Pinaceae, O, I.[4]—From Ontario, Canada, and Maine and Minnesota to Texas and Florida:

Pinus banksiana Lamb. (Canada, Conn., Minn.)
P. caribaea (Fla.)
P. clausa (Engelm.) Vasey (Fla.)
P. echinata Mill. (Fla., Ohio, Pa., Tex.)
P. glabra Walt. (La., Fla.)
P. nigra var *austriaca* (Hoess) Aschers. and Graebn. (N. C.)
P. nigra var. *poiretiana* (Ant.) Aschers. and Graebn. (N. C.)
P. pinaster Ait. (Fla.)
P. ponderosa Laws. (N. C., Wis.)
P. pungens Lamb. (Md., Va.)
P. resinosa Ait. (Mich., Minn.)
P. rigida Mill. (Ga., Maine, N. Y., Ohio)
P. rigida var. *serotina* (Michx.) Loud. (Fla.)
P. sylvestris L. (Canada, Minn., Pa., Va.)
P. taeda L. (Fla., Md., Tex.)
P. thunbergii Parl. (N. C.)
P. virginiana Mill. (Ala., Iowa, N. J., S. C.)

On Fagaceae, II, III:

Castanea dentata (Marsh.) Borkh. (N. C.)
C. pumila (L.) Mill. (N. C.)
Quercus alba L. (Tenn., Va., Wis.)
Q. bicolor Willd. (Va.)
Q. borealis Michx. f. (Canada, Minn., N. H., Va.)
Q. coccinea Muench. (Ga., Md., Minn.)
Q. ilicifolia Wangenh. (Fla., N. J.)
Q. imbricaria Michx. (Md., Va.)
Q. macrocarpa Michx. (Minn.)
Q. marilandica Muench. (N. C., N. J.)
Q. montana Willd. (Ga., Va.)
Q. myrtifolia Willd. (Fla.)
Q. nigra L. (Ala., Del.)
Q. palustris Muench. (Md., Va.)
Q. phellos L. (Md., Va.)
Q. rubra L. (*Q. falcata* Michx.) (Ga., Md.)
Q. stellata Wangenh. (Tenn., Md.)
Q. velutina Lam. (Ga., Md., Minn.)
Q. virginiana var. *fusiformis* (Small) Sarg. (Tex.)

Cronartium fusiforme

On Pinaceae, O, I.—In the southeastern United States from Maryland and Virginia to Florida and Texas:

Pinus caribaea (Fla., S. C., Tex.)
P. palustris (Fla., N. C., Tex.)
P. rigida (N. C.)
P. rigida var. *serotina* (Fla., N. C.)
P. taeda (Fla., Md., Tex.)

[4] The pycnial, aecial, uredial, and telial stages of rusts are represented by O, I, II, and III, respectively.

On Fagaceae, II, III:

Quercus alba (Fla., Miss.)
Q. cinerea Michx. (La., N. C.)
Q. coccinea (N. C.)
Q. imbricaria (La., S. C.)
Q. laurifolia Michx. (La., N. C.)
Q. laevis Walt. (La., S. C.)
Q. marilandica (La., N. C.)
Q. nigra (Fla., N. C., Tex.)
Q. phellos (S. C., Tex.)
Q. rubra (La., N. C.)
Q. shumardii Buckl. (Fla. La.)
Q. stellata (Ga., La.)
Q. stellata var. *margaretta* (Ashe) Sarg. (Fla., La.)
Q. velutina (La., S. C.)
Q. virginiana Mill. (Fla., Miss.)

CRONARTIUM CONIGENUM

On Pinaceae, O, I.—Arizona to Guatemala:

Pinus leiophylla Schiede and Deppe *P. montezumae* Lamb. (Guatemala) (Ariz., Mexico)

On Fagaceae, II, III:

Quercus arizonica Sarg. (Ariz.)
Q. chrysolepis Liebm. (Ariz.)
Q. emoryi Torr. (Ariz.)
Q. grisea Liebm. (Ariz.)
Q. hypoleuca Engelm. (Ariz.)
Q. oblongifolia Torr. (Ariz.)
Q. oocarpa Liebm. (Costa Rica)
Q. pedunculatis Née (Guatemala)
Q. reticulata Humb. and Bonpl. (Ariz.)
Quercus spp. (Mexico and Guatemala)

CRONARTIUM STROBILINUM

On Pinaceae, O, I.—In the southeastern United States from Louisiana to North Carolina:

Pinus caribaea[5] (Fla., Miss.)
P. palustris (Fla., La., N. C.)

On Fagaceae, II, III.—Illinois[6] to Texas, Florida, Virginia, and Cuba:

Quercus alba (Ark., Ill., La., N. C.)
Q. bicolor (N. C.)
Q. chapmani Sarg. (Fla.)
Q. cinerea (N. C., Tex.)
Q. laevis (Miss.)
Q. laurifolia (Fla.)
Q. laurifolia var. *hybrida* Michx. (Fla.)
Q. macrocarpa (Iowa, Kans., Mo.)
Q. montana (Va.)
Q. myrtifolia (Fla.)
Q. nigra (Fla., Tex.)
Q. pumila Walt. (Fla., N. C.)
Q. rolfsii Small (Fla.)
Q. stellata (Fla., N. C., Tex.)
Q. stellata var. *margaretta* (Fla., N. C., Tex.)
Q. virginiana (Cuba, Fla., La., N. C.)
Q. virginiana var. *fusiformis* (Tex.)
Q. virginiana var. *geminata* (Small) Sarg. (Fla., Miss.)
Q. virginiana var. *minima* (Small) Sarg. (Fla., La.)

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[5] *Cronartium strobilinum* was reported by Arthur (*1a*) on the cones of P. *taeda*. The occurrence of the rust on this species of pine was based on specimens collected by P. H. Rolfs, at Lake City, Fla., May 30 and July 10, 1906. The senior writer examined these specimens and found that the host species was *P. caribaea*. The cones of *P. taeda* are never infected by this rust.

[6] A study of the specimens in the herbarium of the Division of Mycology and Disease Survey, Bureau of Plant Industry, Soils, and Agricultural Engineering, showed the following specimens, wrongly determined as *Cronartium quercuum*, to be the uredia of *C. strobilinum*: On *Quercus alba*, two specimens collected near Oregon, Ill., by M. B. Waite, 147, Sept. 9, and 241, Sept. 11, 1889; Rogers, Ark., col. E. Bartholomew, Fungi Columb. 3016, Sept. 25, 1908; Harmon Lake, Miss., col. J. M. White, Seymour and Earle Fungi 214, Aug. 4, 1890; on *Q. macrocarpa*, Manhattan, Kans., col. Kellerman and Swingle, Kansas Fungi 24, Oct. 1886; Stockton, Kans., col. E. Bartholomew, Fungi Columb. 2619, Aug. 31, 1908; Oelwein, Iowa, col. J. C. Gilman, 1437, Sept. 18, 1927; New Haven, Iowa, col. J. C. Gilman, 1456, Sept. 20, 1927; Columbia, Mo., col. B. T. Galloway, 119, Aug. 18, 1886; Columbia, Mo., col. Tracy and Galloway, Sept. 12, 1886; Pickering, Mo., col. E. Bartholomew, Fungi Columb. 2514, Oct. 10, 1907.

CRONARTIUM QUERCUUM

On Pinaceae, O, I.—In China and Japan:

Pinus densiflora Sieb. and Zucc. (Japan)
P. massoniana Lamb. (China)
P. sylvestris (Japan)
P. thunbergii (Japan)

On Fagaceae, II, III:

Castanea crenata Sieb. and Zucc. (China, Japan)
C. mollissima Blume (China, Japan)
Castanopsis cuspidata (Thunb.) Schottky (Japan)
Fagus japonica Maxim. (Japan)
Quercus acuta Thunb. (Japan)
Q. acutissima Carruth. (Japan)
Q. dentata (China, Japan)
Q. glandulifera Blume (Japan)
Q. glauca Thunb. (Japan)
Q. ilex L. (Japan)
Q. mongolica Turcz. (Japan)
Q. mongolica var. *grosseserrata* (Blume) Rehd. and Wils. (Japan)
Q. myrsinaefolia Blume (Japan)
Q. neostuxbergii Koidz. (Japan)
Q. palustris (Japan)
Q. petraea (Mattuschka) Lieblein (*Q. sessiliflora* Salisb.) (Japan)
Q. variabilis Blume (Japan)

METHODS OF INVESTIGATION

The seedlings inoculated were either grown from seed or transplants from nurseries. For best inoculation results pines with young succulent shoots and broadleaf trees with young foliage near the time of their full expansion in growth were preferred to those with slow-growing hardened tissue. Tests with old hardened oak leaves proved them unsuitable for inoculation. Aecia, uredia, and telia were measured with eyepiece and filar micrometers adjusted to a compound microscope. A carefully prepared catalog was kept of date of inoculation, symptoms, date of evident infection, appearance of spore forms, and intensity of infection.

INOCULATION PROCEDURE

If inoculations were made with the spores of more than one species in one day, each was made in a separate compartment or greenhouse. Every possible precaution was taken to insure that the plants were exposed to a single inoculation at one time.

Two similar sets of trees of the same species, each of about the same number, were used in each experiment. One set was inoculated, the other was treated similarly without inoculation and used as a control. The comparative sets of each species of *Cronartium* and their controls were grown in separate compartments under similar conditions of soil, temperature, and light. Self-recording maximum and minimum thermometers and hygrometers were used to record the temperature and moisture conditions in the compartments. As the results from the control sets used were all negative, they are not mentioned here when those from the inoculated plants are given.

Two methods of inoculating pines were used. In one set, chips of galls or masses of loose spores were inserted in a small slit in the phloem under the bark and the wound wrapped with a strip of sterile wet cotton. In the other method, an atomizer was used in spraying needles of shoots with sterile water and the spores were dusted on their surface. In some of these sets the needles were wrapped with wet

sterile cotton strips and in others they were left unwrapped. Immediately after inoculation all inoculated trees were placed for 2 to 4 days in moist chambers in early experiments and in iceless refrigerators (*14*) in later ones. The cotton wrappings were removed in 2 to 4 weeks in case of wound inoculations, and in about 1 week after inoculations made without wounds.

When broadleaf trees were inoculated, the leaves were sprayed with sterile water with an atomizer and spores were dusted or brushed on the under surface. Plants inoculated were immediately placed for 2 to 4 days in a moist chamber in early inoculations and in an iceless refrigerator in later ones. It was found early in the work that leaves dusted with spores on the upper surface were rarely infected.

The period for inoculation of broadleaf and pine trees was lengthened considerably by placing some of the plants in the cooler air outside the greenhouses; others were kept dormant by placing them in cold storage for later use. A second crop of leaves on broadleaf species was obtained by plucking the first crop before it matured. This forced out a new crop of young leaves even in fall or winter, especially with evergreen oaks. No differences were noted in the susceptibility of leaves obtained by the various methods. Repeated defoliation was avoided, lest a weakened growth result.

Spore Treatment and Spore Measurement

Aeciospores received from distant points were at first tested for viability. Later it was found that brightly colored spores were viable when less than a month old. The teliospores are bound together into a telial column by a matrix of a substance containing pectin (*19*). Soaking the telial columns in a hot 4-percent solution of hydrochloric acid dissolved the matrix and separated the teliospores. When stained and mounted in Kaiser's glycerin jelly and erythrosin, they gave slightly swollen dimensions, but the extent of the swelling was determined by an estimation of the distortion. The sporidia used in the inoculations came from young rapidly growing telia.

The spores of the rusts were stained, mounted, and measured, following the methods and formulas of Colley and associates (*5*, *6*) in the study of the aeciospores of *Cronartium ribicola* A. Fisch. and *C. occidentale* Hedgc., Beth., and Hunt. It was essential that the same process for staining and mounting spores should be used in all the spore mounts measured. A uniform method of staining and mounting spores results in equal shrinkage in their size and thus in comparative measurements.

All spores were measured by projection, with the apparatus described by Colley (*5*). The images of the spores were usually projected at 500 to 1,000 diameters on a white field. If magnified to 1,000 diameters they were measured to the nearest micron with a standard white-faced millimeter scale. Wall thickness was measured to approximately tenths of a micromillimeter. The mount was moved across the field by a mechanical stage and spores were selected from a 4-inch circle in the central part of the image in order of their arrangement. Sets of 100 spores were usually measured, but sometimes a smaller or greater number was used.

Method of Weighting Spore Measurements[7]

The problem was to get the most reliable central values for spore dimensions from all the material taken from a single species of host. One hundred spores from each gall had been measured and averaged. For about two-thirds of the localities only one gall was available; for each of the remaining localities, spores from two or more galls were measured. The mean for a locality with more than one gall was obtained by averaging the means for individual galls; the locality means were averaged to obtain a grand mean. The question immediately arose as to how these locality means should be weighted. It is obvious that locality means based on two or more galls are more trustworthy than those based on a single gall and deserve more weight. It is equally obvious, however, that two galls from the same locality do not give as much information on the whole population as would two galls from different localities, so that a two-gall locality mean does not deserve a weight of two. A simple unweighted mean of all the single-gall values, regardless of locality, would not solve the problem, because it would give exactly the same result as if locality means were used and weighted by the number of galls that each represents.

It is evident that the ideal weight of a two-gall mean would be intermediate between one and two. The ideal weight varies inversely with the variance (the squared standard deviation). That is what is obtained in averaging subsamples from a homogenous population by weighting each subsample by the number of individuals it represents. Species are heterogeneous populations, and the variation of means of local subsamples is due in part to variation in the local individuals and in part to differences between localities. The variance within a locality is decreased by measuring a larger number of galls from it, while the variance due to the locality is not at all decreased by increasing the number of galls within the locality.

A rough measure of the variation within localities was obtained by computing the difference between galls of *Cronartium cerebrum*, taken in pairs for all possible pairings from the same locality. There were 49 such pairs, and the differences averaged 0.416μ. As a measure of total variation, 92 pairings were made at random between galls of *C. cerebrum* from different localities and the average difference for these was found to be 0.557μ. The squares of these differences are analogous to the variances that would be obtained by the somewhat more efficient procedure of working from the squared deviations.[8] They are 0.31μ for the total, and 0.173μ within localities. In other words, 56 percent of the total squared differences of single-gall values were due to variation within the locality, leaving 44 percent of the total as the proportion due to the disagreement between localities.

Taking the differences for single galls from different localities as 1.00, the squared differences expected between 2-gall locality means would be $\frac{0.56}{2}+0.44=0.72$. The generalized squared differences for

[7] This section was prepared by Carl Hartley, principal pathologist, Division of Forest Pathology.

[8] The analysis for unequal subsample numbers described by Snedecor (*24, sec. 10.10*) would probably be the best method of comparing variance within and between localities.

locality means based on n galls would be $\frac{0.56}{n}+0.44$. The reciprocals of these values give a single gall weight of 1, a 2-gall locality mean a weight of 1.39; 3, 1.60; 4, 1.72; and 5, 1.81. The weights actually employed were 1.0, 1.4, 1.6, 1.7, 1.8, and 1.9 for locality means based on 1, 2, 3, 4, 5, and 6 galls, respectively. A locality mean based on 100 galls would be given a weight of only 2.2.

The results of the foregoing analysis serve not only to provide a rational basis for weighting in the case in question but also to illustrate the greater efficiency in sampling a widely distributed population if samples are taken from many places. A great increase in the number of measurements made at a single place results in little increase in the reliability of the grand mean where the effect of the locality on spore size is as great as it appears to be in this material.

The method of weighting employed is based on the assumption that the species studied is equally abundant in all localities. This, of course, is never true; but there is ordinarily no quantitative information as to the relative abundance in different localities, so no better procedure seems possible. There is probably some correlation, however, between the number of the galls taken from the localities and the number that existed there. If in collecting or measuring, care was taken to make the number of specimens from each locality correspond roughly with the observed local frequency of the fungus, each locality mean might well be weighted by the number of specimens on which it was based and the simple procedure of averaging all the individual gall mean values without grouping them in locality means would therefore be logical.

INOCULATION RESULTS

Aeciospores on Pines

Experiments by Meinecke (*16*) in inoculating pines with the aeciospores of *Cronartium harknessii* (Moore) Meinecke have shown that this rust may pass directly from pine to pine. It was thought necessary to include in this study inoculations with aeciospores to determine whether reinfection of pine was possible. No infection resulted from extensive inoculations made from 1908 to 1929. The sources of spores and the species of pine inoculated with each species of *Cronartium* are itemized as follows.

Cronartium cerebrum

Twenty-six sets of 19 species or varieties of *Pinus* were inoculated with the aeciospores of *C. cerebrum* from *P. virginiana*, *P. banksiana*, and *P. rigida*. These sets included 252 trees of the following species of *Pinus: caribaea*, *contorta* Dougl., *coulteri* D. Don., *densiflora*, *echinata*, *glabra*, *latifolia* Sarg., *ponderosa*, *ponderosa* var. *scopulorum* Engelm., *radiata* D. Don, *resinosa*, *rigida*, *rigida* var. *serotina*, *sabiniana* Dougl., *strobus* L., *sylvestris*, *taeda*, *thunbergii*, and *virginiana*. Aeciospores were obtained from globose galls, either from artificial inoculations or from natural infections in forests from Michigan to Florida and Texas.

Cronartium fusiforme

Fifteen sets on 124 trees of 12 species of *Pinus* were inoculated with *C. fusiforme*, as follows: *canariensis* C. Sm., *caribaea*, *contorta*, *coulteri*, *latifolia*, *palustris*, *ponderosa* var. *scopulorum*, *radiata*, *rigida*, *sylvestris*, *taeda*, and *virginiana*. The aeciospores were from typical fusiform galls, either from artificial inoculations or from forest trees in Maryland to Florida and Texas.

Cronartium conigenum

Five sets on 16 trees of 5 species of *Pinus* were inoculated with *C. conigenum*, as follows: *caribaea*, *radiata*, *rigida*, *taeda*, and *virginiana*. The aeciospores were obtained from cone galls on *P. leiophylla* from Arizona.

Cronartium strobilinum

One set on first-year cones of 7 trees of *Pinus pinaster* were inoculated with *C. strobilinum*. Cones of other species were not available. The aeciospores were obtained from a cone gall on *P. palustris* from Florida.

Aeciospores on Oaks and Related Genera

Cronartium cerebrum

During the years 1908 to 1930, 86 sets of inoculations with *C. cerebrum* were made from field collections obtained from Michigan to Florida and Texas (table 1). The number of sets of aeciospores used from each species of *Pinus* was as follows: 4 from *banksiana*, 1 *clausa*, 9 *caribaea*, 14 *echinata*, 3 *glabra*, 1 *nigra* var. *poiretiana*, 2 *ponderosa*, 1 *ponderosa* var. *scopulorum*, 3 *pungens*, 3 *resinosa*, 11 *rigida*, 2 *rigida* var. *serotina*, 7 *sylvestris*, 1 *thunbergii*, 7 *taeda*, and 17 *virginiana*. The time elapsing between the date of inoculation and the development of mature uredia of *C. cerebrum* was 9 to 13 days, average 11.

Cronartium fusiforme

Fifty sets of inoculations with *C. fusiforme* were made during the years 1914 to 1931. The number of sets from each species of *Pinus* was: 1 from *caribaea*, 1 *ponderosa*, 1 *rigida*, 2 *rigida* var. *serotina*, and 45 *taeda*. The aeciospores were obtained from typical fusiform galls from artificial inoculations or from galls on forest trees from Maryland to Florida to Texas. Uredia of *C. fusiforme* appeared in 9 to 11 days, average 10.

Cronartium conigenum

Five sets of inoculations were made during the years 1918 to 1923 with aeciospores of *C. conigenum* from cone galls on *Pinus leiophylla* in Arizona. The period for uredial development was 11 to 14 days, average 12.

Cronartium strobilinum

Thirty-eight sets of inoculations with aeciospores of *C. strobilinum* were made between 1918 to 1930. Thirty-five sets were from cone galls on *P. caribaea* and *P. palustris* from Florida and 3 from gall-like

TABLE 1.—*Summation of inoculations with aeciospores of 4 species of Cronartium on Quercus and related genera*

Species inoculated	*C. cerebrum*			*C. fusiforme*			*C. conigenum*			*C. strobilinum*		
	Trees inoculated	Trees bearing—		Trees inoculated	Trees bearing—		Trees inoculated	Trees bearing—		Trees inoculated	Trees bearing—	
		Uredia	Telia		Uredia	Telia		Uredia	Telia		Uredia	Telia
	Number	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*
Castanea:												
alnifolia Nutt.	13	0	0	5	0	0				2	0	0
dentata	42	29	52	10	0	40	3	0	0	9	22	0
mollissima	24	4	25	17	18	59				9	11	0
pumila	17	6	29	2	0	50	1	0	0	7	50	0
sativa Mill.	53	21	58	16	0	75				7	71	0
Castanopsis:												
delavayi Franch.	12	0	0	8	0	0				12	17	0
diversifolia (Kurz) King.	7	0	14	4	0	25				3	0	0
Lithocarpus densiflora (Hook. and Arn.) Rehd.	11	55	64	5	0	20	1	0	0			
Quercus:												
agrifolia Née	38	16	29	21	5	43	5	60	0	7	14	0
alba	84	26	39	24	17	42	2	0	0	19	37	16
bicolor	83	20	69	29	41	90	1	0	0	50	68	14
borealis	239	40	77	66	35	82	11	0	0	26	23	0
cerris L.	22	41	77	9	44	78				6	83	17
coccinea	31	61	87	22	41	45	14	7	0	29	21	0
dentata	27	48	67	4	0	75	1	0	0	8	50	13
douglasii Hook. and Arn.	3	0	67	4	25	75	7	57	0	3	67	67
frainetto Ten.	13	31	85	11	0	91				6	33	33
gambelii Nutt.	66	76	82	18	50	61	12	25	0	35	63	6
imbricaria	20	55	70	4	75	100	3	0	0	5	80	0
kelloggii Newb.	14	79	79	4	50	50	2	0	0	2	50	0
lobata Née	34	76	76	7	57	100	4	0	0	3	33	0
macrocarpa	61	20	74	31	29	87	1	0	0	16	94	13
marilandica	14	64	71	4	25	50				2	0	0
montana	57	30	37	17	18	29	1	100	0	8	38	0
myrtifolia	2	0	50	3	0	100	1	0	0	5	0	0
nigra	2	50	100	1	0	0	2	50	0	2	0	0
palustris	59	32	75	30	11	86	1	100	0	27	33	0
phellos	30	07	73	11	55	64	2	50	0	10	40	0
prinus L. (*Q. michauxii* Nutt.)	9	89	89	8	50	50	1	0	0	1	100	0
robur L.	87	28	69	14	7	86	17	47	0	19	68	21
rubra	9	66	67	8	75	88				14	14	0
stellata	18	38	50	5	0	0	1	0	0	11	91	0
velutina	53	55	70	11	64	82	12	8	0	14	50	0
virginiana	3	0	0	3	0	0				5	100	100
virginiana var. *fusiformis*	30	30	33	10	20	53	6	17	0	14	64	43
virginiana var. *geminata*	3	0	33	3	0	0	1	0	0	3	33	0
Total, all species	1,204			467			113			402		
Average (weighted)		37.2	68.1		26.1	66.0		22.9			47.4	9.2
Total, *Quercus* spp.	1,115			460			108			351		
Average		40.4	72.6		20.7	69.8		21.0			50.1	10.5

growths on needles of inoculated seedlings. Mature uredia developed in 10 to 13 days, average 12.

A summation of the results from all inoculations with aeciospores of the four species of *Cronartium* is given in table 1. The percentages of inoculated trees bearing uredia were 47 for *C. strobilinum*, 37 for *C. cerebrum*, 26 for *C. fusiforme*, and 23 for *C. conigenum*. For telia, the percentages were 68 for *C. cerebrum*, 66 for *C. fusiforme*, 9 for *C. strobilinum*, and 0 for *C. conigenum*. Of infected trees, telia alone were formed from inoculations of *C. cerebrum* on *Castanopsis diversifolia*, *Quercus douglasii*, *Q. myrtifolia*, and *Q. virginiana* var. *geminata*, and from inoculations of *C. fusiforme* on *Castanea dentata*, *C. pumila*,

C. sativa, Castanopsis diversifolia, Lithocarpus densiflora, Quercus dentata, Q. frainetto, and *Q. myrtifolia.*

Urediospores on Oaks and Related Genera

Cronartium cerebrum

Thirty-eight sets of inoculations were made with urediospores of *C. cerebrum* during the years 1908 to 1929. The number of sets from each species of *Quercus* was 23 from *borealis,* 1 *coccinea,* 1 *imbricaria,* 2 *lobata,* 1 *laurifolia,* and 10 *Quercus* spp. Original pine host species were *Pinus echinata, P. taeda,* or *P. virginiana,* and except for 1 set all urediospores came from greenhouse inoculations.

It was not possible to carry inoculations of urediospores of *C. cerebrum* beyond two generations in the greenhouse. The third generation consisted of telia only. Well-developed telia were formed in 20 to 29 days.

Cronartium fusiforme

Fourteen sets of inoculations with *C. fusiforme* were made on species of *Quercus* from 1914 to 1931. The number of sets from each species was 1 each from *borealis, cerris, frainetto,* and *macrocarpa,* 2 each from *bicolor* and *gambelii,* and 3 each from *douglasii* and *phellos.* The original hosts were *P. rigida* var. *serotina* or *P. taeda,* and all urediospores came from greenhouse inoculations.

Inoculations in the greenhouse with the urediospores of *C. fusiforme* could not be carried beyond the second generation. Large telia were formed in 20 to 25 days.

Cronartium conigenum

Ninety sets of inoculations with *C. conigenum* were made on species of *Quercus* during the years 1918 to 1925. One set of 6 trees was inoculated with urediospores from *Q. hypoleuca* collected at Portal, Ariz. The remaining sets were from greenhouse inoculations with urediospores from the following species of *Quercus:* 2 from *alba,* 5 *borealis,* 8 *coccinea,* 3 *douglasii,* 1 *macrocarpa,* 2 *montana,* 4 *palustris,* 6 *robur,* and 58 *Quercus* spp. One set of inoculations was carried through 8 generations of urediospores in the greenhouse and another through 10. The time of telial formation was extremely variable, depending on the season of inoculation. Spring and summer inoculations resulted in successive generations of urediospores, with telia delayed as long as 300 days; in late fall, telia often appeared in about 80 days.

Cronartium strobilinum

One hundred and eighty-seven sets of inoculations with *C. strobilinum* were made during the years 1918 to 1930. Except for 2 sets from *Castanea dentata,* the urediospores were obtained from the following species of *Quercus:* 6 from *alba,* 14 *bicolor,* 2 *borealis,* 6 *dentata,* 6 *douglasii,* 3 *emoryi,* 17 *gambelii,* 12 *macrocarpa,* 3 *montana,* 26 *robur,* 1 *rolfsii,* 3 *stellata,* 2 *velutina,* 34 *virginiana,* 26 *virginiana* var. *fusi-*

formis, 1 *virginiana* var. *geminata*, 1 *virginiana* var. *minima*, and 22 *Quercus* spp. Six sets of urediospores came from Florida and 181 from greenhouse inoculations. One set of inoculations with urediospores was carried through 7 generations in the greenhouse and another through 20 generations. The time of telial appearance after inoculation was essentially similar to that of *Cronartium conigenum*.

A summation of the results from all inoculations with urediospores of the 4 species of *Cronartium* is given in table 2. The percentages of trees bearing uredia from inoculations with urediospores were 66 for *C. strobilinum*, 59 for *C. conigenum*, 48 for *C. cerebrum*, and 29 for *C. fusiforme*. For telia, the percentages were 76 for *C. cerebrum*, 65 for *C. fusiforme*, 12 for *C. strobilinum*, and 5 for *C. conigenum*.

TABLE 2.—*Summation of inoculations with urediospores of 4 species of Cronartium on Quercus and related genera*

Species inoculated	*C. cerebrum*			*C. fusiforme*			*C. conigenum*			*C. strobilinum*		
	Trees inoculated	Trees bearing—		Trees inoculated	Trees bearing—		Trees inoculated	Trees bearing—		Trees inoculated	Trees bearing—	
		Uredia	Telia		Uredia	Telia		Uredia	Telia		Uredia	Telia
	Number	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*
Castanea:												
alnifolia							4	0	0	10	10	0
dentata	3	0	33	2	0	50	22	64	5	30	70	0
mollissima	3	0	33	1	0	100	9	89	11	10	50	0
pumila	1	0	0	4	0	0	13	54	8	14	57	0
sativa	5	0	40				19	47	0	46	46	0
Castanopsis:												
delavayi							2	0	0	10	0	0
diversifolia	1	0	100	1	0	0	2	50	0	12	50	8
Lithocarpus densiflora	2	0	0	3	0	0	3	100	67	6	33	0
Quercus:												
agrifolia	4	25	100				36	64	0	77	70	3
alba	16	25	56	1	0	0	127	33	0	69	74	7
bicolor	11	27	91	7	29	43	22	41	0	79	73	12
borealis	78	58	83	17	6	76	97	65	5	100	25	2
cerris	6	0	100	2	0	50	28	82	4	34	59	12
coccinea	8	13	75	2	100	100	9	44	0	37	10	8
dentata	4	50	100				12	58	0	45	84	0
douglasii	3	100	100	2	100	100	11	82	18	29	76	10
frutetto				1	0	0	23	78	0	29	59	10
gambelii	14	86	93	2	50	50	22	59	0	66	85	2
imbricaria	5	20	100	2	100	100	3	67	0	17	59	12
kelloggii	4	100	100	1	100	100				1	100	0
lobata	5	100	100	1	100	100				3	67	0
macrocarpa	10	10	50	8	0	88	28	71	0	61	85	11
marilandica	3	67	67	1	100	100	5	40	0	4	25	0
montana	6	33	50	1	0	0	28	57	0	48	50	15
myrtifolia				1	0	100	2	50	0	4	0	0
palustris	17	35	82	13	15	85	57	60	7	30	60	5
phellos	10	100	100	3	67	67	9	33	0	9	0	0
prinus	1	0	0	3	100	100				2	0	0
robur	8	13	63	4	25	50	50	74	19	151	81	21
rubra				1	100	100	2	100	50	7	43	14
stellata				1	0	0	7	57	0	7	43	14
velutina	10	100	100	2	100	100	14	57	7	23	35	0
virginiana	1	0	0	2	50	50	3	0	0	23	70	48
virginiana var. *fusiformis*	9	56	56	1	100	100	30	17	0	50	80	44
virginiana var. *geminata*	1	0	0	1	0	0	7	14	0	25	80	32
Total, all species	218			89			630			1,225		
Average (weighted)		47.7	70.1		20.2	65.1		59.5	5.4		65.9	12.4
Total, *Quercus* spp.	233			78			556			1,087		
Average		50.7	78.8		33.3	71.7		59.9	6.2		68.3	13.9

Sporidia on Pines

Cronartium cerebrum

Inoculations were made with sporidia from telial columns grown from authentic material of *C. cerebrum* on oak leaves in the greenhouse. Telia were placed near the base and among the clusters of young needles on young growing shoots of 344 pine seedlings. Of the trees inoculated, 18.6 percent were infected and bore spherical galls within 2 to 3 years at the point of inoculation. On the infected trees, 2 percent of the galls bore pycnia the first year after inoculation and aecia the second year. The first indication of infection was the presence of small yellow-green spots on the needles during the summer after the inoculations. Infection apparently spread through the base of the needles into the shoots.

Inoculations were made on 1,025 trees of 33 species of *Pinus* by inserting telia in slits in the phloem of tender shoots of the current season's growth and wrapping the wounds with wet sterile cotton. Of the trees inoculated, 23 percent bore spherical galls at the point of inoculation. Most of the galls appeared during the summer following inoculation. The first indication of infection was a fusiform swelling that later became spherical. Of the infected trees, 24 percent bore galls with pycnia either the first or second spring after inoculation, with aecia appearing the following spring. More than one-half of the fruiting galls produced pycnia the first and aecia the second spring after inoculation. The rest bore pycnia the second and aecia the third spring. No pycnial or aecial fruiting was noted on galls on 76 percent of the infected trees. The sterility of the galls may have been due to poor conditions of growth in the pots, premature death of the trees from the effect of the rust, or to differences in fungus-host interrelationships.

The first-year cones of 3 species of pine were inoculated by inserting telia in a slit in the epidermal layer and wrapping the wounds with wet cotton. The results were negative with 20 trees of the following species of *Pinus:* 9 *echinata*, 9 *densiflora*, and 2 *virginiana*.

The results from inoculations with sporidia from the telia of *C. cerebrum* (excluding cone inoculations) are given in table 3. Soft pines proved somewhat less susceptible to infection than pitch pines. Inoculation of 33 seedlings of 5 species—*Pinus cembra* L., *P. edulis* Engelm., *P. koraiensis* Sieb. and Zucc., *P. parviflora* Sieb. and Zucc., and *P. strobus*—resulted in 1 nonfruiting gall on *P. cembra* and 4 on *P. edulis*. Of the commercially important pines, *P. virginiana* was highly susceptible to *C. cerebrum*.

Cronartium fusiforme

Thirty-two species of *Pinus* were inoculated with sporidia from telia of *C. fusiforme* during the years 1914 to 1930. Authentic material was used from artificially inoculated trees in the greenhouse.

A total of 184 trees of 12 species were inoculated by placing telia near the base of the axils of the clusters of needles on tender growing shoots. Of the trees inoculated, 51, or 28 percent, were infected and developed fusiform swellings during the first season's growth. Of

TABLE 3.—*Results of inoculating pines with sporidia of Cronartium cerebrum*

Species inoculated	Original source of inoculum						Data on inoculations of trees			Infected trees producing aecia
	P. banksiana	*P. clausa*	*P. echinata*	*P. rigida*	*P. taeda*	*P. virginiana*	Inoculated	Infected	Producing aecia	
Pinus:	Number	Number	Number	Number	Number	Number	Number	Percent	Percent	Percent
banksiana						24	24	29	8	29
bungeana Zucc.					2	9	11	0		
canariensis						39	39	46	0	
caribaea	10		9		4	44	67	1	0	
cembra						2	2	50	0	
contorta					3	21	24	17	4	25
coulteri						21	21	38	5	13
densiflora		20		9		36	65	2	0	
echinata		10	2	18		30	60	7	0	
edulis						20	20	0	0	
gerardiana Wall.						5	5	20	0	
glabra	1			9		9	10	5	0	
halepensis Mill.				18		1	19	68	0	
jeffreyi Grev. and Balf.						10	10	60	0	
koraiensis						1	1	0		
latifolia	3					6	9	11	0	
massoniana						1	1	0		
mugo Turra	2					1	3	33	0	
muricata D. Don		12	2			12	26	31	0	
nigra var. *poiretiana*		9				8	17	24	0	25
palustris	1					2	2	0		
parviflora						2	2	0		
pinaster				9		19	28	11	0	
ponderosa		7				47	54	37	13	35
ponderosa var. *scopulorum*		31			6	56	93	35	4	12
radiata			9	9		62	80	55	0	
resinosa				1	2	13	16	0		
rigida		10		35		29	74	19	3	14
sabiniana						26	26	23	0	
strobus			1			7	8	0		
sylvestris		20				49	69	10	1	14
taeda	5	30	19	36	8	138	236	10	.4	4
thunbergii						20	20	10	0	
virginiana	2	2	16	19	12	177	228	31	16	51
Total trees inoculated	24	151	58	163	37	936	1,369			
Percentage of trees infected								22		
Percentage of trees bearing aecia									4	
Percentage of infected trees bearing aecia										18

the infected trees, 11, or 22 percent, bore galls with pycnia late in the autumn of the year of inoculation and aecia the following spring. The first indication of infection was the appearance of small yellow-green spots on the needles.

Wound inoculations were made on 1,039 trees of 32 species by inserting telia in slits in the phloem of young, tender shoots. Of the trees inoculated, 297, or 28 percent, were infected and later developed fusiform galls at the point of inoculation. Within 5 or 6 months after inoculation, 31 of the infected trees bore galls with pycnia late in autumn and aecia the following spring. Forty-seven trees bore pycnia the spring following inoculation and aecia the spring of the second year. Pycnia and aecia of *C. fusiforme* may develop one growing season earlier than similar stages of *C. cerebrum*. Of the

TABLE 4.—*Results of inoculating pines with sporidia of Cronartium fusiforme*

Species inoculated	Original source of inoculum			Data on inoculations of trees			Infected trees producing aecia
	P. caribaea	*P. rigida*	*P. taeda*	Inoculated	Infected	Producing aecia	
Pinus:	*Number*	*Number*	*Number*	*Number*	*Percent*	*Percent*	*Percent*
banksiana		1	15	16	0		
bungeana			9	9	0		
canariensis			9	9	44	0	
caribaea	2	3	82	87	41	21	50
clausa			4	4	0		
contorta		2	77	79	34	0	
coulteri		2	14	16	38	15	33
densiflora			42	42	0		
echinata			77	77	0		
edulis		3	9	12	0		
gerardiana			1	1	0		
glabra	1		5	6	0		
halepensis		1	19	20	90	0	
jeffreyi			10	10	10	0	
monticola		2		2	0		
mugo		4	4	8	75	0	
muricata		5	10	15	40	0	
pinaster			11	11	0		
pinea L.			12	12	17	0	
ponderosa			42	42	55	31	57
ponderosa var. *scopulorum*		13	58	71	49	10	20
pungens			1	1	0		
radiata		2	56	58	64	3	5
resinosa			63	63	0		
rigida		3	51	54	17	0	
rigida var. *serotina*			21	21	38	0	
sabiniana		3	3	6	50	0	
strobus			18	18	0		
sylvestris			127	127	20	2	8
taeda	4	5	191	200	49	23	46
thunbergii			31	31	10	0	
virginiana		9	86	95	0		
Total trees inoculated	7	58	1,158	1,223			
Percentage of trees infected					38		
Percentage of trees bearing aecia						7	
Percentage of infected trees bearing aecia							26

trees infected and bearing galls, 219, or 74 percent, failed to bear aecia. The reasons for failure are assumed to be the same as those given for *C. cerebrum*.

A summation of the data from the inoculations with sporidia of *C. fusiforme* is given in table 4. *P. taeda* ranked among the highest in percentage of infection and in aecial production. This result substantiates observations that the species is very susceptible to infection. The wide distribution of this pine, its susceptibility, and its great capacity to produce spores make it the most important aecial host of *C. fusiforme*. It is noteworthy that *P. virginiana*, highly susceptible to *C. cerebrum*, proved resistant to *C. fusiforme*. Also, the soft pines—*P. edulis*, *P. monticola* Dougl., and *P. strobus*—were not susceptible.

The following species of *Pinus* not infected by *C. fusiforme* proved susceptible to *C. cerebrum*: *banksiana*, *densiflora*, *echinata*, *edulis*, *gerardiana*, *glabra*, *pinaster*, and *virginiana*.

Cronartium conigenum

Inoculations of *C. conigenum* were made by inserting telia in wounds in the phloem of 47 trees of 17 species of *Pinus:* 5 *caribaea*, 2 *clausa*, 1 *contorta*, 2 *coulteri*, 2 *echinata*, 2 *edulis*, 1 *halepensis*, 1 *massoniana*, 1 *monophylla* Torr. and Frem., 2 *mugo*, 2 *nigra* var. *poiretiana*, 1 *parviflora*, 1 *ponderosa*, 3 *radiata*, 2 *rigida* var. *serotina*, 9 *taeda*, and 10 *virginiana*. The telia were from the following sources: 1 set from *Quercus emoryi* and 3 from *Q. hypoleuca* from Portal, Ariz., 2 sets from *Q. robur* and 2 from *Quercus* spp. grown from artificial inoculations at Washington, D. C. Two seedlings only of *P. caribaea* became infected and developed small galls, one of which bore pycnia in 140 days and the other in 325. Both trees died before aecia were produced.

Cronartium strobilinum

During the years 1919 to 1928, 373 trees of 23 species of *Pinus* were inoculated with sporidia from teliospores of *C. strobilinum* obtained from greenhouse inoculations. The aeciospores originated from cone galls on trees of *P. caribaea* and *P. palustris* in Florida.

First-year cones of all the species available in the greenhouse were inoculated by placing telial columns on the surface of the cones and wrapping them with wet cotton. Cones of the following species of *Pinus* were inoculated: 2 *densiflora*, 2 *pinaster*, and 6 *virginiana*. None of these cones became infected.

Of the 89 pine seedlings 2 to 4 months old inoculated by inserting telial columns in slits in tips of young growing shoots, 17, or 19 percent, were infected and bore pycnia on small galls on the base of the needles in an average of 49 days after inoculation. Sixteen percent bore aecia in an average of 80 days from the time of inoculation. The infected needles assumed an "orange chrome" color [9] and the galls a "Sanford's brown."

Inoculations were made on 274 seedlings of 21 species of pine, 2 to 4 months old, by inserting telial columns in the axils of needles without wounding. Of the trees inoculated, 77, or 28 percent, became infected and bore pycnia in gall-like growths on the base of needles in an average of 60 days. Aecia were formed within an average of 106 days from the time of inoculation.

The results from inoculations with sporidia of *C. strobilinum* are given in table 5. *C. strobilinum*, however, has never been found producing galls on the twigs or needles of young trees. It is hardly possible that such infections could occur, because sporidia are formed at a time when the needles, twigs, and shoots are dormant and not susceptible to infection.

[9] Color in quotes, according to Ridgway (21).

TABLE 5.—*Results of inoculating pines with sporidia of Cronartium strobilinum*

Species inoculated	Original source of inoculum		Data on inoculations of trees			Infected trees producing aecia
	P. caribaea	*P. palustris*	Inoculated	Infected	Trees producing aecia	
Pinus:	*Number*	*Number*	*Number*	*Percent*	*Percent*	*Percent*
canariensis	10	5	15	00	40	67
caribaea	10	55	65	00	68	77
clausa		1	1	0		
contorta	10	15	25	52	24	46
densiflora		2	2	0		
echinata		10	10	0		
halepensis	10		10	30	0	
jeffreyi		5	5	0		
massoniana		1	1	0		
muricata	10	12	22	45	23	50
palustris		9	9	11	0	
pinaster	20	11	31	26	26	100
pinea	10	16	26	38	0	
ponderosa		12	12	25	25	100
ponderosa var. *scopulorum*		4	4	25	0	
quadrifolia Parl		0	0	0		
radiata	10	53	63	33	21	02
sabiniana		2	2	50	50	100
sondereggeri H. H. Chapm. (hybrid)		2	2	0		
sylvestris		7	7	0		
taeda		12	12	33	33	100
thunbergii		24	24	4	0	
virginiana		16	16	0		
Total trees inoculated	90	283	373			
Percentage of trees infected				33		
Percentage of trees bearing aecia					29	
Percentage of infected trees bearing aecia						61

EFFECT OF RUSTS ON INOCULATED AND NATURALLY INFECTED TREES

Inoculations on Pines

Both *Cronartium cerebrum* and *C. fusiforme* were lethal to young pine seedlings in these inoculation tests; about 35 and 40 percent, respectively, of the infected seedlings died within 5 years. Relative infection of species of pine that were susceptible to both fungi is shown in table 6. The percentage of infection caused by *C. fusiforme* was greater for 11 of the 15 species. The much higher susceptibility of *Pinus caribaea* and *P. taeda* to *C. fusiforme* is of particular interest, in view of their commercial importance in the Southeast where both rusts occur naturally.

C. strobilinum caused a surprising amount of mortality among infected seedlings in the greenhouse, killing approximately 55 percent in less than 1 year. Infection trials with this rust were unsuccessful on cones, but produced small galls at the needle bases.

INOCULATIONS ON OAKS

The effect of the uredia and telia of *Cronartium* on the leaves of oak in the greenhouse was slight unless infection was abundant. With heavy infections, the leaves were gradually killed and were shed prematurely, which tended to retard the growth of the trees.

A higher percentage of oaks was infected from inoculations with urediospores than from tests with aeciospores. Thus, the percentages

TABLE 6.—*Relative infection of pines susceptible to both Cronartium cerebrum and C. fusiforme*

Species inoculated	*C. cerebrum*			*C. fusiforme*		
	Inoculated	Infected		Inoculated	Infected	
Pinus:	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
canariensis	30	12	40	0	4	44
caribaea	67	1	1	87	36	41
contorta	24	4	17	70	27	34
coulteri	21	8	38	16	6	38
halepensis	19	13	68	20	18	90
jeffreyi	10	0	00	10	1	10
muricata	26	8	31	15	6	40
ponderosa	54	20	37	42	23	55
ponderosa var. *scopulorum*	93	33	35	71	35	49
radiata	80	44	55	68	37	04
rigida	74	14	19	54	9	17
sabiniana	20	6	23	6	3	50
sylvestris	69	7	10	127	20	20
taeda	230	23	10	200	98	49
thunbergii	20	2	10	31	3	10
Total number of trees	849	201		825	332	
Average percentage of trees infected			23.7			40.2

of trees bearing uredia from inoculations with urediospores and aeciospores in tables 1 and 2 compare as follows: For *C. cerebrum*, 51 and 40; *C. fusiforme*, 33 and 30; *C. conigenum*, 60 and 24; and *C. strobilinum*, 68 and 50. Comparison of the percentage of trees bearing telia indicates a similar relationship. Part of the difference in infection may be due to variations in germinative capacity of the inoculum arising from discrepancy in spore age, handling, and collection method. In the main, the urediospores came from artificial inoculations and were immediately available, while aeciospores came from field collections, some of them sent by mail. On the whole, the lots of urediospores probably had greater germinative capacity than the collections of aeciospores.

Both *C. cerebrum* and *C. fusiforme* infected a proportionately larger number of black oaks than white oaks (table 7). Furthermore, the

TABLE 7.—*Susceptibility of white and black oaks to infection by 4 species of Cronartium*

Species inoculated	White oaks						Black oaks					
	Trees inoculated with—		Aeciospore inoculum		Urediospore inoculum		Trees inoculated with—		Aeciospore inoculum		Urediospore inoculum	
	Aeciospores	Urediospores	Trees with—		Trees with—		Aeciospores	Urediospores	Trees with—		Trees with—	
			Uredia	Telia	Uredia	Telia			Uredia	Telia	Uredia	Telia
Cronartium:	*Number*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*	*Number*	*Number*	*Percent*	*Percent*	*Percent*	*Percent*
cerebrum	539	84	37	01	37	66	477	131	46	78	57	85
fusiforme	179	29	29	04	27	55	165	40	33	78	30	77
conigenum	51	286	31		57	6	49	188	12		61	5
strobilinum	182	677	65	14	77	21	128	235	32	3	28	4

amount of fruiting by each rust was relatively greater on black than on white oaks. For instance, with *C. fusiforme* the percentages of 54 susceptible black oaks, grouped by degree of uredial fruiting, were 44 abundant, 31 medium, 21 sparse, and 4 very sparse. On the other hand, percentages of 52 white oaks grouped on the same basis were 27 abundant, 29 medium, 34 sparse, and 10 very sparse. Species of white oak were especially susceptible to *C. strobilinum* and slightly more to *C. conigenum*.

Naturally Infected Trees

On pine, *Cronartium cerebrum* does not spread appreciably from the original point of infection to adjacent limbs and trunks, but tends to remain confined to galls in the region of the original infection. Bark collars formed above and below the galls delimit their growth. On small trees in the forest and nursery the galls apparently interfere to some extent with conduction and translocation in the part of the tree affected. If a seedling is girdled by a gall it may not live many years and is usually stunted in growth. Galls on side limbs and twigs of pine trees result in the death of some of the infected parts.

The spindle-shaped galls of *C. fusiforme* usually extend rapidly from the original point of infection into adjacent trunks and limbs. They encircle the tree, similar to galls of *C. cerebrum*, but are much more lethal. The galls of *C. fusiforme* commonly have bark collars at their base, which may or may not indicate the downward extension of the gall. Infrequently, collars develop at the upper end of elongated fusiform galls, marking temporarily retarded growth. Larvae of pitch moths, *Dioryctria* spp.,[18] commonly infest the resinous, fungus-infected phloem of fusiform rust cankers. Since much of the tunneling by these larvae tends to girdle the galled part, the effect of heavy insect infestations on single cankers would appear detrimental enough to hasten the death of individual branches or of the tree itself.

In nurseries, Lamb and Sleeth (*15*) reported losses of 15 to 35 percent of slash pine seedlings due to *C. fusiforme*. Two to five percent of longleaf pine seedlings were commonly infected, with several nurseries having as much as 10 to 15 percent infection.

Infection by *C. cerebrum* and *C. fusiforme* on oak leaves normally causes negligible damage. The period for telial production for *C. cerebrum* may vary from February and March in the Gulf States to July and August in Ontario. That for *C. fusiforme* may vary from February in Florida to June in Virginia and Maryland.

C. conigenum is destructive to the first-year cones of *P. leiophylla* in some localities in the mountains in Arizona. It is common around Portal, but a thorough survey of the range of this rust has never been made.

C. strobilinum is detrimental to reproduction in the forest by destroying the first-year cones. During moist seasons in the earlier years of the studies of the disease in Florida, as high as 90 percent of the young cones were destroyed in the region around Palatka. In dry years, the losses were greatly reduced.

[18] Identification by Dr. T. E. Snyder, senior entomologist, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture.

On first-year cones, infection from *C. strobilinum* begins to show the first to the middle of March. Many infected scales may be noted by their "orange chrome" color, which changes to a "Sanford's brown" or "chestnut." In less than 2 months after infection the cones increase in size to that of healthy 1-year cones. During the third and fourth months after infection they become greatly swollen and quadruple in size. The surface of the cone gall ruptures irregularly, and falls away, exposing the layers of aeciospores. At the time of aecial fruiting the cones are often attacked by insects, principally by larvae of *Dioryctria abietella* D. and S., which feed on the spores and parenchymal tissues. The cones dry up, become mummified, and fall to the ground.

Uredial sori of *C. strobilinum* on leaves of *Quercus alba* are easily recognized by the "orange" or "grenadine red" color of the spots on the upper surface of the leaf. The brilliant color is characteristic of the species and sets it apart from all other pine-oak *Cronartium* species. Telia of *C. strobilinum* are found on the leaves of evergreen oaks from December to February in the Gulf States. Neither the uredial nor telial stage causes significant damage to the oaks.

On May 31, 1938, the writers discovered uredia of *C. strobilinum* in the forest southeast of Woodworth, La., on young succulent stems of *Q. stellata*. The rust was too far advanced and abundant to have occurred that season from aeciospore infection. Moreover, cones on *P. palustris*, the only aecial host in the territory, were not affected. The senior writer, later in 1938, found uredia occurring in abundance from southeastern Louisiana to North Carolina on the leaves and succulent stems of the following species of *Quercus: alba, bicolor, stellata*, and *stellata* var. *margaretta*. Very heavy infections were found on *Q. alba* 3 miles southeast of Pilot Mountain, N. C., June 27 and 7 miles southwest of Winston-Salem, N. C., June 29, 1938. These localities were possibly 150 miles from the nearest aecial host. It was too early for such heavy infection from wind-borne aeciospores during the same season.

The occurrence of *C. strobilinum* far north of its aecial hosts, *P. palustris* and *P. caribaea*, is also indicated from collections on *Q. alba* and *Q. macrocarpa* in Illinois, Iowa, and elsewhere.[11] This may be explained by presuming that aeciospores at some time previously were carried great distances north by air currents, infecting succulent woody parts and leaves of oaks. The rust then continued its existence by wintering over on stems, particularly of young sprout type, of its oak hosts.

FRUITING BODIES, FRUITING STRUCTURES, AND SPORES OF SPECIES OF CRONARTIUM

Pycnia, Pycniospores, and Aecia

All species of pine-oak *Cronartium* bear pycnia in flat cavities under the epidermal layer of the galls. At maturity, pycniospores are exuded in sweet, viscid, yellow-tinted drops. A condensed comparison of pycnia and other fruiting stages of five species of *Cronartium* is given in table 8. Measurements of sporidia are not listed.

[11] See footnote 6, p. 5.

TABLE 8.—*Condensed comparison of pycnial, accial, uredial, and telial stages of 5 species of Cronartium*

Items of comparison	*C. cerebrum*	*C. fusiforme*	*C. conigenum*	*C. quercuum*	*C. strobilinum*
Gall:					
Shape	Spherical	Fusiform	Cone gall	Spherical	Cone gall.
Texture	Woody	Woody	Fleshy	Woody	Fleshy.
Collar	Above and below	Below or absent	None	Above and below	None.
Pycnial fruiting:					
Frequency	Biennial	Biennial	Biennial	Annual	Annual.
Season	Dec. to June	Oct. to Apr.	May to June	Dec. to Feb.	Mar. to Apr.
Pycniospores, average size ..... microns	2×4	2×3.8	2×3.5	2×5	1.9×2.8.
Aecial fruiting:					
Frequency	Biennial	Biennial	Biennial	Annual	Annual.
Season	Feb. to July	Feb. to Apr.	June to July	Apr. to May	May to June.
Peridium:					
Mature	Erumpent	Erumpent	Erumpent	Erumpent	Submerged.
Form	Cerebroid	Cerebroid	Hemispherical	Hemispherical	Vestigial.
Apical walls ..... cell layers	3 to 9	2 to 6	2 to 3	2 to 8	1 to 5.
Side walls ..... do	2 to 3	1 to 2	1 to 2	1 to 4	None.
Peridial cells:					
Average size ..... microns	16.8×24.6	15.4×30.2	21.4×54.1	21.9×37.4	14.4×32.8.
Extreme range ..... do	11 to 26×14 to 42	10 to 22×16 to 39	14 to 32×28 to 100	14 to 32×23 to 53	5 to 21×22 to 46.
Average wall diameter ..... do	5.1	4.9	6.0	5.3	3.3.
Aeciospores:					
Average size ..... do	16.4×26.7	15.5×25.1	17.3×31.2	18.0×27.4	15.3×26.0.
Intersextile range [1] ..... do	15 to 18×24 to 29	13 to 18×22 to 28	15 to 20×27 to 35	17 to 20×25 to 30	13 to 17×23 to 29.
Average wall diameter ..... do	3.2	3.3	3.3	2.7	3.2.
Uredial:					
Fruiting season	Feb. to July	Feb. to May	All year	Apr. and May	All year.
Leaf spot color	Yellow to ochraceous	Pale green	Pale green	Pale green	"Orange" to "grenadine red."
Uredia:					
Average size ..... microns	154×191	136×164	166×192	114×132	137×168.
Extreme range ..... do	72 to 252×108 to 324	82 to 208×96 to 360	105 to 262×122 to 360	72 to 198×80 to 216	80 to 216×100 to 360.
Urediospore:					
Average size ..... do	13.8×20.6	13.3×19.1	17.7×24.7	16.4×22.3	14.7×22.4.
Intersextile range [1] ..... do	11 to 15×18 to 24	12 to 15×17 to 21	16 to 20×21 to 28	14 to 18×20 to 25	13 to 17×20 to 26.
Average wall diameter ..... do	2.4	2.0	2.6	2.7	2.3.
Telial fruiting season	Feb. to Aug.	Feb. to June	June to July	Jan. to May	Dec. to Feb.
Telial columns:					
Color	"Walnut brown" to "Vandyke brown."	"Cinnamon-brown" to "Prout's brown."	"Chestnut" to "bay"	"Dresden brown" to "cinnamon-brown."	"Mummy brown" to "black."
Average size ..... microns	97×3,576	104×2,872	117×2,550	90×2,491	108×2,918.
Extreme range ..... do	45 to 200×1,100 to 8,700	60 to 200×600 to 5,000	60 to 220×1,000 to 6,000	60 to 140×1,100 to 4,600	60 to 200×1,000 to 4,400.
Teliospores:					
Average size ..... do	16.2×39.1	14.7×36.4	15.6×34.3	15.9×42.1	14.8×30.5.
Extreme range ..... do	12 to 22×26 to 59	10 to 20×25 to 54	10 to 23×20 to 55	10 to 23×26 to 60	10 to 18×23 to 41.

[1] The intersextile range was obtained from the measurements left after dropping one-sixth of the largest and one-sixth of the smallest spores.

The pycnia of *C. cerebrum* are borne in more or less circular lenticular cavities on the perennial galls 1 to 2 years after infection. The pycniospores are oblong to elliptic and measure on an average $2\mu \times 4\mu$ in size (50 spores) and are borne biennially from December to March in Florida, from March to April around Washington, D. C., and progressively later north to Ontario, Canada. Aecia with cerebroid peridia follow on the same galls 1 year later and are deeper seated in the phloem layer (*11, pl. XI, fig. 1*). Pycnia and aecia then occur on the galls in alternating generations. This was first proved by the senior writer in an unpublished experiment in Takoma Park, Md., with fruiting galls on trees of *Pinus virginiana*.

The pycnia and aecia of *C. fusiforme* resemble those of *C. cerebrum* and agree closely in structure and position on the fusiform galls of this rust. In the greenhouse, the first pycnia are noted on a few trees in the autumn and others in the spring of the year following the inoculation. The pycniospores are oblong to elliptic and average $2\mu \times 3.8\mu$ (40 spores). Some galls produce aecia the spring following inoculation, but are always preceded by pycnia on the same surface the preceding year. They are seated in the phloem several layers of cells deeper than those of the pycnia (*11, pl. XI, fig. 2*). The pycnia and aecia are formed in alternating generations as in *C. cerebrum*. Pycnia were found on galls of *C. fusiforme* at Brooksville, Fla., in December, on *P. caribaea* at Brunswick, Ga., in March, and on *P. taeda* in the southern part of eastern Maryland in April.

Bailey Sleeth and Howard Lamb [12] found pycnia of *C. fusiforme* in several localities in Texas in October 1938. Sleeth collected pycnia on *P. caribaea* at Brooklyn, Miss., October 26, 1938, and on the same host near Elizabeth, La., November 17. In the spring of 1940, the senior writer found about as many trees of *P. taeda* at Brooksville, Fla., were bearing aecia of *C. fusiforme* and *C. cerebrum* as there were others that had borne pycnia the same season, indicating that pycnia and aecia of both species of rust were biennial.

Data on the frequency of pycnia and aecia of *C. conigenum* are incomplete. It appears that the pycnia are formed on the cone galls 1 or 2 years after infection of the cones, and that the erumpent hemispherical peridia break forth from the deeper seated layers of the phloem 1 year later. Some cone galls apparently bear aecia in 2 years and others in 3, indicating that some galls bear pycnia in 1 year and some in 2 years. The pycniospores are ovoid to oblong in shape and average $2\mu \times 3.6\mu$ in diameter (25 spores).

The pycnia of *C. strobilinum* are borne on the current year's crop of cones in Florida in March and April, about 1½ to 3 months after infection. They are formed in irregular, rounded, disk-shaped layers. Aecia are formed later, about 20 cell layers deeper in the phloem. The pycniospores are oblong to ovoid in shape and average $1.9\mu \times 2.8\mu$ in size (60 spores). The aecia are covered on the upper side by a

[12] Formerly pathologists, in the Division of Forest Pathology.

vestigial peridium of 1 to 5 layers of cells (*10, pl. V, fig. C*). This species is the only one in the United States that bears both pycnia and aecia within 4 months from the time of infection.

The pycnia of *C. quercuum*, according to Shirai (*22*), are formed in subepidermal cavities in the phloem of the woody galls and produce pycniospores from December to January. These average $2\mu \times 5\mu$ in size. During the following April and May, aecia form in the same galls 10 to 20 cell layers beneath the pycnial layers. The pycnia and aecia are formed annually within the short period of 5 months. This sets *C. quercuum* apart from *C. cerebrum* and *C. fusiforme*. The senior writer studied a fresh fruiting gall of *C. quercuum* from *P. massoniana* near Nanking, China, collected April 27, 1937, by S. C. Teng. The specimen was a woody spheroid gall with scanty, erumpent, irregularly hemispherical peridia unlike the cerebroid peridia of *C. cerebrum* and *C. fusiforme*.

Peridia and Peridial Cells

The erumpent cerebroid peridium of *Cronartium cerebrum* is the thickest and firmest of all the species of *Cronartium* (table 8). Although the cerebroid peridium of *C. fusiforme* is thinner than that of *C. cerebrum*, it resembles it closely. The erumpent but irregularly hemispherical peridium on cone galls of *C. conigenum* is frail and thin. The erumpent, irregularly hemispherical peridium of *C. quercuum* is rather firm, but not so thick as that of *C. cerebrum*. The submerged vestigial peridium within the cone galls of *C. strobilinum* is fragile, loosely formed, and without side walls.

Uredia and Telial Columns

The measurements of uredia and telial columns, as detailed in table 9 (Appendix) and table 8, were based on many field and greenhouse collections from species of *Castanea, Lithocarpus*, or *Quercus*. The average size of the uredia from field collections, based on the product of the average width by the average length, arranged in order from the largest to the smallest, is *Cronartium conigenum, C. cerebrum, C. strobilinum, C. fusiforme*, and *C. quercuum*.

Study of the data suggested that size of telia, particularly length, would vary directly with telial age. Thus the average length of telia in three collections of *C. fusiforme* early in May 1926 was less than a fourth of that of telia from two collections in June 1938, from the same locality. Phenologic variations might also account for some of this difference. Local meteorological conditions are probably an important factor in telial development. Telia measuring as much as 8.4 and 8.7 mm. in length were obtained in July and September, respectively, from collections of *C. cerebrum* from the mountains of southwestern North Carolina. Mild climatic conditions in sheltered

places in this general region would favor telial longevity and maximum growth. Since many factors affect telial growth, too much significance should not be placed on differences in telial size as reported herein.

Aeciospores, Urediospores, and Teliospores

These spores are classified in table 10 (Appendix) by species of rust and by field or greenhouse collections. Host species are listed by field or greenhouse collection. The fruiting stages of *Cronartium quercuum* were collected on specimens of pines or oaks from China or Japan. No greenhouse inoculations were made with this species.

The average size of the aeciospores from field collections, based on the product of the average width by the average length, arranged in descending order, is *C. conigenum*, *C. quercuum*, *C. cerebrum*, *C. strobilinum*, and *C. fusiforme*. The average size of the aeciospores from greenhouse collections on the same basis is *C. cerebrum*, *C. strobilinum*, and *C. fusiforme*.

The average size of the urediospores from field collections, arranged in descending order, is *C. conigenum*, *C. quercuum*, *C. strobilinum*, *C. cerebrum*, and *C. fusiforme*. The average size of the urediospores from greenhouse collections, excluding *C. quercuum*, is in the same order.

A characteristic of all species of pine-oak *Cronartium* is the progressive maturity of teliospores from the tips of the columns to the bases. The shortest spores, in the tip, are oblong to cylindric or subfusiform, while those formed below the tip are longer and fusiform.

DISCUSSION

There is much need for clarification of the taxonomic position of the pine-oak rusts that were lumped by Arthur (*2*) under *Cronartium quercuum* on the basis of the uredia and telia. In compromise, Weber (*27*), following Arthur's nomenclature with respect to the rusts that cause spherical and fusiform cankers on trunks and branches of pines in Florida, adopted *C. strobilinum* as the binomial for the fungus causing cone galls on two species of pine in that State. Weber indicated that he contributed no evidence that *C. quercuum* was preferable to *C. cerebrum* or *C. fusiforme* as the correct binomial for the branch and stem rusts.

To accept Arthur's grouping of the pine-oak rusts, one must entirely ignore the difference in the forms of aecial fruiting, the fact that the species maintain their distinct aecial forms, and that it is not possible to obtain one aecial form with cultures from another. In the manner and time of fruiting, the species are distinct not only in their pycnia and aecia but also in their uredia and telia.

Apart from these differences, further evidence that the pine-oak rusts are distinct has come from a study of host specificity. This is

particularly evident in localities in the Southeast where host ranges of *C. cerebrum* and *C. fusiforme* overlap. *C. cerebrum* is most common on *Pinus virginiana*, but *C. fusiforme* does not infect this species of pine. In places in Florida *C. cerebrum* is common on *P. clausa* and *P. glabra*, but *C. fusiforme* has never been found on these hosts. The negative results from inoculation of these species of pine with *C. fusiforme* support conclusions from field observation. It is evident that Arthur never had a good set of specimens of *C. quercuum* for study, otherwise he would not have placed a species with annual pycnia and aecia with American species producing pycnia or aecia biennially but in alternate years.[13]

Further evidence for distinguishing *C. cerebrum* and *C. fusiforme* is based on the apparent difference in lethal effect following infection by these rusts under forest conditions. The gross effect of infection by *C. cerebrum* is hyperplastic; the canker is always a swelling formed by abnormal quantitative increase in size and number of cells that go to make the wood. *C. cerebrum* commonly lives for years on large trees with little detriment to the host. On the other hand, *C. fusiforme* commonly forms cankers involving regressive tissue changes and rapid killing of the cambium from the beginning of infection. Such cankers, particularly prevalent on the stems of *P. caribaea*, are characterized by little if any swelling and by abundant flow of pitch over the bark. In time, the wood under the cankered surface becomes exposed, and the trunk, weakened at this point, may break off even before the tree has been girdled by the canker.

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[13] In 1939, Nakamura (*17*) published a good description of *C. quercuum*, which supplements and verifies that by Shirai (*22*). The pycnial layer matures in January and February as a flat layer of pycniospores between the bark and phloem of the fruiting galls. The aeciospores develop in April and May more than 10 cell layers beneath the pycnial layers on the same galls. They are orange-yellow inside and range from 18μ to 24μ×23μ to 30μ in size (*17, pl. IV, fig. 1*). The uredia are of a disk form and range from 100μ to 300μ in flat diameter (*17, pl. IV, fig. 4*). The urediospores range from 10.4μ to 22.4μ×13.5μ to 29.2μ and are echinulate (*17, pl. IV, fig. 2*). The outer wall is colorless, and the contents are orange in color. The telia appear about 5 weeks later. They are reddish brown, threadlike, and 2 to 4 mm. in length. The uredia and telia are borne on species of *Castanopsis, Fagus*, and *Quercus*.

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APPENDIX (TABLES 9 AND 10)

TABLE 9.—*Measurements of field and greenhouse collections of uredia of Cronartium spp.*

Species and source of uredia	Host species [1]	Collections	Uredia	Average size	Extreme range in size
Field collections:	*Number*	*Number*	*Number*	*Microns*	*Microns*
C. cerebrum	4	9	180	154×191	72–252×108–324
C. fusiforme	3	10	200	130×164	82–208× 96–360
C. conigenum	2	4	80	166×192	105–262×122–360
C. quercuum	2	6	120	114×132	72–198× 80–216
C. strobilinum	7	18	360	137×168	80–216×100–360
Greenhouse collections:					
C. cerebrum	9	16	320	151×192	72–252× 85–360
C. fusiforme	12	20	400	140×178	72–288× 80–360
C. conigenum	17	19	190	157×192	100–288×108–360
C. strobilinum	15	33	660	145×171	90–216×108–288

[1] Collections of *C. cerebrum* from the field came from the following species of *Quercus: borealis, coccinea, imbricaria,* and *velutina.* Greenhouse collections included *borealis, coccinea, gambelii, marilandica, palustris, primus, robur, stellata,* and *velutina.*

Field collections of *C. fusiforme* were made from the following species of *Quercus: laurifolia, nigra,* and *phellos;* and greenhouse collections from *alba, bicolor, borealis, coccinea, gambelii, imbricaria, kelloggii, lobata, phellos, primus, shumardii,* and *velutina.*

Field collections of *C. conigenum* were made from *Quercus emoryi* and *Q. hypoleuca,* and greenhouse collections from *Castanea dentata, C. mollissima,* and *C. sativa,* from *Lithocarpus densiflora,* and from the following species of *Quercus: agrifolia, alba, bicolor, borealis, cerris, coccinea, dentata, frainetto, macrocarpa, palustris, robur, sessilifolia,* and *velutina.*

Field collections of *C. quercuum* came from *Castanea crenata* and *Quercus acutissima.*

Field collections of *C. strobilinum* were obtained from species of *Quercus: montana, myrtifolia, pumila, rolfsii, virginiana, virginiana* var. *geminata,* and *virginiana* var. *minima.* Greenhouse collections came from *Castanea dentata* and the following species of *Quercus: alba, bicolor, borealis, cerris, dentata, douglasii, gambelii, imbricaria, lobata, macrocarpa, montana, stellata, virginiana,* and *virginiana* var. *fastiformis.*

TABLE 10.—*Comparison of measurements of spores of Cronartium spp. from field and greenhouse collections*

Species measured and spore collection source	Host[1] species	Collection	Spores measured	Spore wall	Average spore size	Extreme spore range
	Number	*Number*	*Number*	*Microns*	*Microns*	*Microns*
Aeciospores, in field:						
C. cerebrum	7	50	8,000	3.2	16.4×26.7	11–25×16–46
C. fusiforme	3	10	1,400	3.3	15.5×25.1	10–23×15–37
C. conigenum	1	6	1,200	3.3	17.3×31.2	10–25×18–51
C. quercuum	2	4	800	2.7	18.6×27.4	12–20×20–40
C. strobilinum	2	10	1,500	3.2	15.3×26.0	9–23×15–40
Aeciospores, in greenhouse:						
C. cerebrum	2	4	500	2.4	16.6×26.4	12–23×19–34
C. fusiforme	2	4	400	2.3	15.4×24.4	11–21×19–31
C. strobilinum	2	5	250	3.0	15.8×24.9	13–20×17–35
Urediospores, in field:						
C. cerebrum	4	8	1,200	2.4	13.8×20.6	9–21×13–29
C. fusiforme	2	5	500	2.0	13.3×19.1	11–17×14–24
C. conigenum	2	4	1,000	2.6	17.7×24.7	11–25×16–37
C. quercuum	3	4	250	2.7	10.4×22.3	10–25×18–34
C. strobilinum	10	25	3,000	2.3	14.7×22.4	10–21×15–39
Urediospores, in greenhouse:						
C. cerebrum	15	17	2,000	2.2	13.3×19.6	9–20×13–29
C. fusiforme	9	11	1,400	1.8	13.0×18.6	9–18×13–28
C. conigenum	6	8	1,100	2.1	16.5×23.9	10–25×15–38
C. strobilinum	9	14	1,600	2.0	14.4×20.3	9–20×13–38
Teliospores, in field:						
C. conigenum	3	3	300	----------	15.6×34.3	10–23×20–55
C. quercuum	3	3	150	----------	15.9×42.1	12–23×20–60
C. strobilinum	3	4	200	----------	14.8×30.5	10–18×23–41
Teliospores, in greenhouse:						
C. cerebrum	4	5	200	----------	10.2×39.1	12–22×26–59
C. fusiforme	3	5	200	----------	14.7×36.4	10–20×25–54

[1] Field collections of aeciospores of (1) *C. cerebrum*, (2) *C. fusiforme*, (3) *C. conigenum*, (4) *C. quercuum*, and (5) *C. strobilinum* came, respectively, from species of *Pinus*, as follows: (1) *banksiana*, *clausa*, *echinata*, *rigida*, *sylvestris*, *taeda*, and *virginiana*; (2) *caribaea*, *rigida* var. *serotina*, and *taeda*; (3) *leiophylla*; (4) *densiflora* and *thunbergii*; (5) *caribaea* and *palustris*. Aeciospores of (1) *C. cerebrum*, (2) *C. fusiforme*, and (3) *C. strobilinum*, from the greenhouse, came from the following species of *Pinus*: (1) *clausa* and *virginiana*; (2) *ponderosa* and *taeda*; (3) *caribaea* and *radiata*.

Field collections of urediospores of (1) *C. cerebrum*, (2) *C. fusiforme*, (3) *C. conigenum*, (4) *C. quercuum*, and (5) *C. strobilinum* came, respectively, from the following species of *Quercus*: (1) *borealis*, *coccinea*, *imbricaria*, and *velutina*; (2) *laurifolia* and *nigra*; (3) *emoryi* and *hypoleuca*; (4) *acutissima*, *glandulifera*, and *variabilis*; (5) *alba*, *macrocarpa*, *marilandica*, *myrtifolia*, *rolfsii*, *stellata*, *virginiana*, *virginiana* var. *fusiformis*, *virginiana* var. *geminata*, and *virginiana* var. *minima*. Greenhouse collections of urediospores of (1) *C. cerebrum*, (2) *C. fusiforme*, (3) *C. conigenum*, and (4) *C. strobilinum* were obtained, except as otherwise indicated, from the following species of *Quercus*: (1) *agrifolia*, *bicolor*, *borealis*, *cerris*, *coccinea*, *douglasii*, *gambelii*, *macrocarpa*, *marilandica*, *palustris*, *phellos*, *prinus*, *robur*, *rubra*, and *velutina*; (2) *bicolor*, *borealis*, *lobata*, *phellos*, *prinus*, *rubra*, *texana*, *velutina*, and *virginiana*; (3) *borealis*, *cerris*, *montana*, *robur*, *Castanea dentata*, and *C. sativa*; (4) *bicolor*, *borealis*, *gambelii*, *macrocarpa*, *montana*, *robur*, *virginiana* var. *fusiformis*, and *virginiana* var. *geminata*, and *Castanea dentata*.

Collections of teliospores of (1) *C. conigenum*, (2) *C. quercuum*, and (3) *C. strobilinum* made in the field came, respectively, from species of *Quercus*, as follows: (1) *arizonica*, *emoryi*, and *hypoleuca*; (2) *acutissima*, *dentata*, and *glandulifera*; (3) *pumila*, *virginiana* var. *geminata*, and *virginiana* var. *minima*. Greenhouse collections of teliospores of (1) *C. cerebrum* and (2) *C. fusiforme* came, respectively, from species of *Quercus*, as follows: (1) *bicolor*, *borealis*, *palustris*, and *velutina*; (2) *bicolor*, *borealis*, and *macrocarpa*.

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