

Inoculation Experiments with *Synchytrium macrosporum*.

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With Plate XXIII.

Synchytrium macrosporum was created as a new species by the author (1956) for a parasite which Long collected on leaves of *Xanthium strumarium* at Austin, Texas in 1901. The type specimen of this fungus is deposited at the New York Botanical Garden, and additional material of Long's collection may be found in the herbarium of Cornell University. This species is a short-cycled member of the subgenus *Pycnochytrium* which causes unusually large composite galls on *Xanthium* and is characterized primarily by its large, brilliantly-yellow resting spores on the leaves of this host. On other organs, however, the spores may vary markedly in size and shape (figs. 2—6).

In 1954 Poole reported a *Synchytrium* species on *Riccinus communis* from Cameron, Texas which causes a red stem-gall disease, and in the same year Dr. Marvin D. Whitehead collected what appears to be the same fungus on the same and a large number of other hosts in the same locality. In personal correspondence he reported its occurrence on *Helenium tenuifolium*, *Nandina domestica*, *Ambrosia psilostachya*, *A. aptera*, *Amaranthus berlandiera*, *Erigeron canadensis*, *Solanum elaeagnifolium*, *Parthenium hysterophorus*, *Iva ciliata*, *Croton monanthogynus*, *Phylla incisa*, *Modiola caroliniana* and *Vigna sinensis* in addition to *Riccinus communis* in nature, and kindly sent me herbarium specimens of his collection on *Riccinus communis*, *Nandina domestica*, *Ambrosia aptera*, *A. psilo-*

*) This study has been supported by a grant from the National Science Foundation. I am very grateful to Dr. M. D. Whitehead for the initial collection of *S. macrosporum* and to Drs. A. T. Guard, J. H. Lefforge, A. A. Lindsey, and G. L. Webster of Purdue University, B. L. Turner of the University of Texas, C. Heimsch of Miami University, and Duncan Clemente, Director of Atkins Garden in Cuba for collections of seeds and identification of host plants.

Part of this study was made in the Botany Department of the University College of the West Indies, Mona, Jamaica and I am pleased to express my sincere thanks to Professor A. D. Skelding and his staff for facilities and assistance during this time. Dr. Edith Robertson and Mrs. C. E. Allwood were particularly helpful in identifying the Jamaican host plants.

stachya, *A. trifida*, *Amaranthus berlandieri* and *Vigna sinensis*. I visited the same locality, Kelly's Nursery, on April 21, 1958, and found the fungus abundantly only on *Ambrosia trifida* and sparsely on *Trifolium repens* and *Sonchus* sp. Due to cultivation of the nursery plants and heavy rainfall in the spring of 1958 only a few of the other weed hosts reported by Whitehead were present in the infected area. However, when I visited the same locality again on May 7, 1959 the fungus was very abundant on *Ambrosia trifida*, *Parthenium hysterophorus*, *Rubus trivialis*, *Oenothera laciniata*, *Vicia faba*, *Torilis japonica*, *Ammi majus*, *Ratibida pinnata* and *Specularia perfoliata*. The *Ambrosia* seedlings and plants up to a foot high were so densely infected that their stems were twice the normal diameter and the leaves were malformed and distorted. However, neither *Sorghum halpense*, *S. vulgare* var. *sudanense*, *Cyperus alternifolia* nor several other grasses and sedges were infected although they were growing among the densely infected plants of *A. trifida*. Also, *Oenothera speciosa* in the same locality was free of infection, but several plants of *O. laciniata* were densely infected.

A study of Whitehead's and my own collections and a comparison of them with Long's specimens lead me to believe that Poole's and Whitehead's fungi are identical with *S. macrosporum*. This belief is based on (1) results of cross inoculation experiments which showed that each of the parasites on *R. communis*, *N. domestica*, *Ambrosia aptera*, *A. psyllostachia*, *A. trifida*, *Amaranthus berlandieri* and *V. sinensis* will infect *Xanthium strumarium* and *X. americanum* and cause the same symptoms as *S. macrosporum*; (2) results from other tests showing that each of the parasites sent to me by Dr. Whitehead will in turn infect *R. communis*, *Ambrosia trifida*, *Amaranthus retroflexus*, *Vigna sinensis* and other hosts; (3) close similarity in type of galls induced by each parasite when transferred to *Xanthium* species; and (4) on the similarity in shape, structure and color of the resting spores and their method of germination. Not only do the resting spores germinate in the manner, but they do so readily and abundantly in approximately the same time. The readiness with which they germinate together with the preliminary discovery that their planospores might infect a large number of different plants led me to undertake a host range study of *S. macrosporum* as well as an investigation of the problem of whether or not the galls induced are constant in size, shape and structure on all hosts and can be used as taxonomic criteria.

The structure and type of the galls induced have been used by several investigators as adjuncts in identifying species of *Synchytrium*, and Cook (1945) in particular believed that such criteria are more reliable than the morphological characteristics of the etiological agents themselves. However, no controlled cross inoculation experi-

ments with a member of the subgenus *Pycnochytrium* have been made so far to determine the validity of this view. Also, with the exception of Rytz's (1932) limited tests on *S. aureum*, no intensive host range studies have been made with such species, and almost nothing is known about the number of hosts which a member of *Pycnochytrium* may infect. The present tendency of most collectors of *Synchytrium* is to create either a new species for each parasite found on a new host, or to identify it as *S. aureum* if it develops only resting spores in fairly large galls. As a consequence, this binomial has become a convenient dumping ground for *Pycnochytrium* species with pigmented resting spores which induce composite galls, and to date *S. aureum* has been reported to occur on 198 species in 123 genera of 34 families of flowering plants. Other collectors, as already noted, have created new species for their fungi with the result that a large number of questionable species have been added to *Pycnochytrium*. Quite likely, a number of these species will be found to be identical when their host ranges and the morphological variations they exhibit become known.

Members of this subgenus are reported to be distinguishable by the size, shape, color and structure of their resting spores, but as I (1953) pointed out previously these characteristics are not always distinctive and sharply-defined. Therefore, it has become necessary to determine whether or not these taxonomic criteria can be supplemented effectively by other differences such as host range, specificity, and host reaction for the purposes of identification and classification.

Synchytrium macrosporum is the only member of *Pycnochytrium* that I have found so far which lends itself readily to a study of this nature. In my experience, the resting spores of most species of this subgenus germinate only occasionally and sporadically under laboratory conditions, and it is very difficult to secure enough planospores for extensive inoculation purposes. Those of *S. macrosporum*, on the other hand, germinate in great numbers within a few days or weeks after being immersed in water and, thus, provide an abundant inoculum of planospores for host range studies.

In the present study a germinated spore on *Riccinus communis* was used as a source of planospores. After the preliminary tests had shown that the fungi on the various hosts referred to above were the same species, planospores from one germinated resting spore on *R. communis* was used as the initial inoculum. These were placed on *X. strumarium*, and within three months produced a fairly large number of mature resting spores which germinated readily. Planospores from these spores were used in turn to inoculate other host species, and by such means an abundant supply of resting spores was accumulated. Inasmuch as the initial resting spore from *R. com-*

munis arose from a planospore or zygote, it is obvious that the source of inoculum in these experiments was *monosporic*. As noted earlier, the initial spore on *R. communis* was collected by Whitehead at Cameron, Texas in May, 1954, and the present study was begun in the summer of 1957 when it was 3 years old.

After the supply of spores was built up on numerous hosts, bits of leaves heavily infected with spores were crumbled into a petri dish, flooded with charcoal-treated water, covered, and left either on the laboratory table or placed in a refrigerator for one to four days. Those which were refrigerated usually germinated earlier, but this was not consistently so. In some instances, the spores began to germinate within four days after becoming thoroughly soaked, and germination continued sporadically for three months or more. In this process the spore functions as a prosorus, as shown in figs. 7—11. Its content grows out through a pore in the wall and forms a yellowish-orange vesicle on the surface of the spore (fig. 7, 8). The content of this vesicle then undergoes cleavage (fig. 9, 10) and develops into hundreds of polyhedral sporangia which are held together as a sorus by the wall of the vesicle (fig. 11). These sori may be formed below, above, and occasionally at the side of the spore. In galls whose sheath cells are thick-walled and which do not degenerate readily, the expanding and maturing sorus may burst out of the infected cell and gall at the apical opening, and in such cases it sits like a yellowish-orange sphere on top of the gall. In soft and degenerating galls which expand more readily, the sorus usually remains within the infected cell and gall.

Although it is generally believed that most species of *Pycnochytrium* produce only one generation of resting spores per year, the number probably varies according to the length of the dormant period after maturity, necessary moisture present, and the presence of young susceptible hosts at the time of germination. In *S. macrosporum*, at least, the spores germinate shortly after they are mature if sufficient moisture is present, and I have produced four generations within a year. This is illustrated by the case of *Persea americana* which was inoculated with planospores on January 1, 1958. By February 20 the spores were mature, and on this day dried infected portions of the leaves were crumbled into a petri dish and covered with charcoal-treated water. The spore began to germinate on February 27 and by March 9 planospores were formed. Thus, the life cycle from planospores to planospores was completed in 68 days. In *Molucella laevis* which has a cup-like calyx that holds water for a long time, the mature spores germinated in the living calyx when the plants were watered frequently.

The resting spores of *S. macrosporum* retain their viability for several years, and this may be a contributing factor to its abundance

in nature. This longevity is indicated by the fact that the spores were already three years old when these experiments were begun and is substantiated by results obtained from germination tests under laboratory conditions. Cultures containing 100 resting spores were set up as described above in May of each year from 1957 to 1960, and records were kept of the number which germinated. The results in percentages are as follows: 1957—75%; 1958—59%; 1959—16%; 1960—2%. It's to be noted that the percentages of germination dropped rapidly after 1957, but even after 6 years of storage in the herbarium a few of the spores were still viable.

The sporangia from germinated spores of *S. macrosporum* do not form planospores at once but may remain dormant in the sorus for one to more than two months at room temperature and conditions. If fresh charcoal-treated water is added to the culture after the spores have germinated sporogenesis may occur to some extent. However, in these experiments it was found by repeated tests that the sori must be dissected apart and mounted under a cover glass before sporogenesis occurs. In such mounts planospores were formed within $\frac{3}{4}$ to 3 hours depending on the age of the culture. Sori which were dissected in a drop of water on a slide and set aside without the addition of a cover slip failed to form planospores over a period of 12 to 18 hours. At the end of these periods cover slips added, and sporogenesis occurred in $\frac{3}{4}$ to 1— $\frac{1}{2}$ hours.

The dormancy of the sori and sporangia under laboratory conditions enables one to maintain a stock culture for 1 to 3 months or more and to have an abundance of planospores for inoculation purposes when they are needed. So far it has not been necessary to keep the cultures sterile. The sori and sporangia mature and are capable of producing viable planospores even though the dead host tissue may be densely invaded and overgrown by filamentous fungi.

The sori usually contain from 400 to 850 sporangia, and each of these produce 200 or more planospores (fig. 12). In some large sporangia as many as 600 planospores may be produced. Assuming that all sporangia in a sorus undergo sporogenesis and form planospores, I estimate that a germinated resting spore may give rise to from 80,000 to 170,000 or more planospores. In the present study five fairly uniform-sized sori were used in making single mounts, and in some of these I estimated that $\frac{1}{2}$ million planospores were present.

In preparation for inoculation the emerging leaves of mature plants and seedlings were first swabbed with a dilution of "Tween 88" and then rinsed with charcoal-treated water to insure a wet surface on the host for the planospores. Each mount, as described above, was diluted with 5 cc of charcoal-treated water, and a drop of swarming planospores was placed directly on the treated leaf. Then the whole plant was covered with a bell jar or container to

maintain a high humidity. In cases of large plants which could not be covered with a bell jar, a wet pad of absorbent cotton was placed around the inoculated leaf to provide sufficient moisture for infection. Inoculations were continued for several days until infection occurred or until it became evident that the species were resistant or immune. The same procedure was employed in inoculating the gametophytes and sporophytes of mosses and ferns. Fern gametophytes were grown on agar plates and soil in closed chambers and periodically flooded with a suspension of planospores. In addition, small thalli of *Riccia fluitans*, *Marchantia polymorpha*, *Azolla caroliniana*, *Salvinia rotundifolia* and gemmae of *M. polymorpha* were placed on slides, flooded periodically with drops of planospores and maintained in moist chambers. The same procedure was employed with *Vaucheria glomerata*, *Oedogonium* sp., *Cladophora* sp., *Hydrodictyon africanum*, *Closterium didymotocom*, *Spirogyra* sp., *S. praetensis*, and small plants of *Lemna minor*, which remained healthy and vigorous under such conditions. In the case of the aquatic Phycomyces, small bits of hemp seed infected with the respective fungi were transferred to drops of planospores on slides without cover-glasses and maintained in moist chambers. Additional drops of planospores were added periodically to such cultures.

In susceptible hosts, infection occurs usually in 6 to 18 hours. Within a fortnight the incipient galls may become visible to the unaided eye, but this time varies with the growth rate of the host plants. In 2 to 4 months the spores and galls usually attain maturity and will germinate. In the present experiment all inoculated host leaves were studied carefully with a stereoscopic microscope for evidence of infection and host reaction. Portions of infected leaves were fixed in killing solution, embedded, sectioned, and stained to determine the variations in the size, shape and structure of the galls and spores. At the same time herbarium specimens of most infected plants were preserved. These voucher herbarium specimens and sections of susceptible species are deposited in the Purdue University herbarium where they are available to any investigator who wishes to study them. However, in many instances the galls were immature when collected, and with drying they became shriveled and shrunken. Accordingly, such herbarium specimens are not typical of their appearance in the living condition. In instances of limited infection, all of the infected host material was used up in making sections, and no herbarium specimens of such hosts are available.

The present contribution concerns only the results of these inoculations up to the present time. The experiments are being continued and additional results will be reported later. In another paper I shall describe the variations in the type, structure and size of the galls induced on the various susceptible hosts and discuss their value as

taxonomic criteria. In the results tabulated below the plus and minus signs indicate success or failure of infection. The bold numbers show the number of individuals of a species inoculated, and those in parentheses indicate the number of times each individual plant was inoculated with a drop of planospores. In some species, for instance, 5 to 10 or more seedlings were inoculated 4 to 6 or more times, which means that as many as 20 to 60 separate inoculations were made on one host species. In this manner more than 45,000 separate inoculations were made on the plants listed below over a period of four years. Seedlings were used in the majority of cases, but for some hosts only "mature" plants were available for inoculation. In the case of trees and large shrubs, use of the word "mature" relates to their postseedling or sapling stages. Wherever such mature plants were used they are indicated as such in the results; unless so indicated the host plants were in the seeding stages. Also, the degree of infection is indicated after the name of each susceptible species. The categories of sparse, fair good and dense infection used here are largely arbitrary and may be subject to personal interpretation. Therefore, it is essential to indicate how I have used them: sparse means 2 to 10 galls per host; fair, 10 to 20 galls; good, 20 to 100 or more galls; and dense means a generalized infection of the inoculated area which may include a whole leaf, several leaves, petioles and stem. In this category the infection may be so abundant that the leaves, petioles and stems may be thickened, malformed, distorted, or stunted, and in such instances the composite galls are frequently compound (K a r l i n g, 1955). In several species infection occurred, but the incipient galls and parasites aborted at various stages of development, and such reactions also are indicated after the species name wherever they occurred.

Phycomycota.

Blastocladiaceae

Allomyces arbuscula —, 13 (8)

Saprolegniaceae

Achlya sp. —, 13, (8)

Aphanomyces laevis —, 13, (8)

Saprolegnia ferax —, 13, (8)

Pythiaceae

Pythium proliferum —, 13, (8)

Chlorophyta.

Chlorococcaceae

Hydrodictyon africanum —, 6, (12) . . .

Oedogoniaceae

Oedogonium sp. —, 13, (8)

Cladophoraceae

Cladophora sp. —, 13, (8)

Zygnemataceae

Closterium didymotocum —, 100, (8)

Spirogyra praetensis —, 40, (10)

Spirogyra sp. —, 40, (10)

Heterosiphonaceae

Vaucheria sessilis —, 20, (20)

Hepatophyta.

Ricciaceae

Riccia sp. —, 4, (6), gametophyte

R. fluitans —, 4, (6), gametophyte

Marchantiaceae

Marchantia polymorpha —, 4, (8), large gametophyte

M. polymorpha —, 80, (12), gemmae

Bryophyta.

Polytrichaceae

Polytrichum commune —, 30, (12), gametophyte

Mniaceae

Mnium cuspidatum —, 30, (12) gametophyte

Microphylophyta.

Selaginaceae

Selaginella browni —, 4, (6), gametophyte

S. pallescens —, 4, (6), gametophyte

Pteridophyta.

Polypodiaceae

Cystopteris gracilis —, 6, (6), emerging fronds

Nephrolepis bostoniensis —, 6, (12), emerging fronds

Marsileaceae

Marsilea mucronata —, 8, (8), emerging leaves

Salviniaceae

Salvinia rotundifolia —, 12, (8)

Azolla caroliniana —, 12, (8)

Ginkophyta.

Ginkovaceae

Ginko biloba +, 11, (6), sparse infection, parasite and galls aborted, emerging leaves of sapling

G. biloba, +, 3, (8), good infection, parasite and galls aborted, seedlings

Coniferophyta.

Taxaceae

Taxus cuspidata +, 12, (6), dense infection

Pinaceae

Pinus sylvestris —, 8, (10)

Anthophyta.

Monocotyledons

Alismaceae

Sagittaria latifolia +, 2, (5), sparse infection

Echinodorus rostratus +, 3, (4), sparse infection

Pontederiaceae

Eichornia cassipes —, 1, (6)

Pontederia cordata —, 1, (5)

Bromeliaceae

Ananas comosus +, 3, (8), good infection

Bromelia pingium +, 2, (10), good infection

Liliaceae

Asparagus officinalis —, 35, (12)

Erythronium albidum +, 4, (4), good infection

Ornithogalum umbellatum +, 5, (15), fair infection

Smilacina racemosa +, 2, (3), very dense infection, leaves distorted

Smilax hispida +, 2, (2), very dense infection, leaves greatly distorted

S. balbisiana +, 2, (20), sparse infection, 4 galls on a leaf

Tulipa gesneriana +, 4, (4), dense infection, leaves curled and mal-formed

Uvularia graniflora +, 2, (6), sparse infection

Agavaceae

Agave americana +, 4, (10), fair infection, galls and parasites aborted

Commelinaceae

Commelina nudiflora —, 8, (8), emerging leaves of mature plant

Rhoeo discolor +, 3, (4), dense infection

Tradescantia fluminensis +, 5, (4), dense infection

T. virginica +, 5, (2), fair infection

Amaryllidaceae

Aloe arborescens —, 5, (10), emerging leaves of mature plant

A. striata —, 4, (8), emerging leaves of mature plant

Amaryllis sp. —, 2, (6), emerging leaves of mature plant

Brodea coronaria —, 2, (8) emerging leaves of mature plant

Dioscoreaceae

Dioscorea bulbifera +, 4, (10), sparse infection

Iridaceae

Aristaea compressa +, 6, (15), good infection, most galls and parasites aborted

Crocus sativus +, 8, (5), dense infection

Orchidaceae

Dendrobium moschatum +, 2, (6), good infection

Casuarinaceae

Casuarina equisetifolia +, 3, (5). good infection of cotyledons

Araceae

Alocasia macrorrhiza +, 2, (3), good, scattered infection

Arisaema triphyllum +, 1, (4), sparse infection

A. draconitum +, 4, (6), good infection of stem

Diffenbachia amoena +, 1, (4), dense infection

Philodendron wendlani +, 4, (4), sparse infection

P. oxycardium +, 4, (4), sparse infection

Pistia stratiotes +, 3, (6), sparse infection, galls and parasites aborted

Symplocarpus foetidus +, 3, (5), dense infection

Gramineae

Lacryma jobi +, 15, (25), fair infection, galls and parasites aborted

Zea mays +, 6, (4), good infection

Musaceae

Musa ballisiana, +, 8, (6), good infection

M. paradisiaca var. *sapientum* —, 1, (10), unfolding leaf of young sucker

Zingiberaceae

Zingiber zerumbet +, 3, (5), sparse, scattered infection

Cannaceae

Canna indica +, 3, (5), sparse infection on mature plant

Potamogetonaceae

Potamogeton vaseyi —, 3, (5), mature plant

Dicotyledons

Saururaceae

Saururus cernuus +, 1, (8), mature plant, sparse infection, galls and parasites aborted

Salicaceae

Populus deltoides +, 5, (5), sparse scattered infection

Salix nigra +, 5, (6), good infection

Juglandaceae

Carya ovalis +, 3, (12), sparse infection, galls and parasited aborted

Myricaceae

Myrica microcarpa +, 3, (5), fair infection

Betulaceae

Betula lutea +, 5, (6), good infection

B. papyrifera +, 4, (10), fair infection

Carpinus caroliniana +, 3, (6), good infection

Fagaceae

Castanea dentata +, 1, (6), sparse infection

Quercus alba +, 2, (6), sparse infection, galls and parasites aborted

Q. palustris +, 1, (5), sparse infection

Q. rubra +, 1, (5), sparse infection

Ulmaceae

Celtis laevigata +, 4, (4), dense infection, leaves and petioles greatly distorted

Ulmus americana —, 8, (15)

Moraceae

Brosimum alicastrum +, 2, (4), fair infection

Broussonetia papyrifera +, 6, (6), good infection, leaves slightly distorted

Chlorophora tinctoria +, 20, (6), good infection

Morus nigra +, 6, (3), good infection

Piperaceae

Peperomia obtusifolia +, 4, (5), fair infection

P. sandersi +, 4, (5), fair infection

Urticaceae

Boehmeria nivea +, 20, (8), fair infection

Fleurya aestuans +, 3, (6), sparse infection, mature plant

Pellionia daveauana +, 6, (8), good infection

Pilea microphylla +, 3, (8), sparse infection

Urtica chamaedryoides +, 8, (10), sparse infection

U. dioica +, 10, (4), dense infection, leaves of mature plant distorted

Cannabinaceae

Cannabibus sativus +, 8, (6), good infection

Humulus lupulus +, 4, (6), dense infection

Aristolochiaceae

Aristolochia triangularis +, 15, (8), good infection

Asarum canadense +, 6, (4), fair infection

Polygonaceae

- Antigonon leptopus* +, 20, (6), dense infection
Coccolobis uvifera +, 2, (6), sparse infection
Fagopyrum cymosum +, 5, (6), dense infection
Polygonum convolvulus +, 8, (12), sparse infection
P. cuspidatum +, 4, (6), fair infection
P. persicaria +, 12, (12), sparse infection
P. scandens +, 12, (12), sparse infection
Rumex acetosa —, 4, (16), mature plant
R. acetosa +, 5, (6), seedlings, sparse infection
R. crispus +, 8, (6), good infection
R. mexicanus +, 8, (6), good infection
Triplaris surinamensis +, 1, (4), sparse infection of small sapling leaves

Chenopodiaceae

- Atriplex hastata* +, 5, (3), good infection
A. nummularia +, 3, (15), sparse infection
Beta vulgaris +, 8, (3), fair infection
B. vulgaris var. *cicla* +, 5, (6), dense infection
Chenopodium album +, 6, (8), dense infection, leaves distorted
C. ambrosioides +, 8, (6), fair infection
Kochia childsii +, 12, (6), good infection
Spinacia oleracea +, 15, (4), dense infection, leaves distorted

Droseraceae

- Dionea muscipula* +, 4, (8), sparse infection, mature plant
Drosera rotundifolia —, 4, (15), mature plant

Caryophyllaceae

- Arenaria serpyllifolia* +, 8, (2), dense infection
Cerastium vulgatum +, 8, (6), fair infection
C. tomentosum +, 12, (8), sparse infection
Dianthus armeria —, 6, (10)
D. barbatus +, 8, (6), good infection
Drymaria cordata —, 12, (8), mature plant
Gypsophila paniculata +, 10, (8), good infection
Lychnis chalcedonica +, 8, (6), good infection
Saponaria officinalis +, 3, (4), dense infection, leaves distorted
Silene antirrhina +, 6, (8), dense infection
S. armeria +, 8, (8), dense infection

Portulacaceae

- Claytonia virginica* +, 7, (5), fair infection
Portulaca oleracea +, 12, (4), fair infection

Nymphaeaceae

- Nymphaea* sp. —, 10, (8), mature plants

Cercidiphyllaceae

- Cecidiphyllum japonicum* +, 1, (4), dense infection

Trochodendraceae

- Trochodendron aralioides* +, 1, (8), sparse infection

Ranunculaceae

- Aconitum napellus* +, 2, (5), dense infection, leaves greatly distorted
Aguilegia canadensis +, 4, (2), dense infection, mature plant, leaves distorted
Anemone virginica +, 20, (10), fair infection
Caltha palustris +, 3, (4), fair infection
Clematis virginiana +, 3, (4), fair infection, mature plant
C. trifoliata +, 3, (5), fair infection

- Delphinium ajacis* +, 15, (5), good infection
Hepatica acutiloba, +, 5, (4), good infection, mature plant
Ranunculus abortivus +, 4, (22), sparse infection, parasite and galls aborted early
R. anemonaepolis +, 4, (8), sparse infection
R. ficaria +, 6, (15), sparse infection
R. scleratus +, 2, (5), dense infection
Thalictrichum sp. +, 4, (5), dense infection

Berberidaceae

- Berberis thunbergii* +, 12, (5), dense infection, seedlings distorted, several killed
Mahonia aquifolium —, 3, (6)
Nandina domestica +, 5, (4), good infection
Podophyllum peltatum +, 5, (12), sparse infection, galls and parasites aborted

Menispermaceae

- Menispermum canadense* +, 3, (4), good infection, mature plant

Calycanthaceae

- Calycanthus floridus* +, 6, (4), dense infection, leaves greatly distorted

Annonaceae

- Anona cherimoya* +, 6, (8), good infection
A. muricata +, 6, (8), dense infection, leaves distorted
Asimina triloba +, 4, (6), dense infection, leaves distorted
Cananga odorata +, 7, (2), dense infection but most parasites and galls aborted

Dilleniaceae

- Wormea burbigghi* +, 1, (6), good infection
Gustavia augusta +, 2, (8), fair infection

Magnoliaceae

- Liriodendron tulipifera* +, 3, (3), good infection
Magnolia grandiflora +, 2, (4), dense infection
— *stellata* +, 1, (6), dense infection

Crassulaceae

- Crassula arborea* —, 4, (6), mature plant
Kalanchoe crenata +, 3, (6), fair infection
K. laxiflora +, 3, (6), fair infection
Sedum acre —, 5, (8), mature plants

Baselaceae

- Basella alba* +, 5, (3), dense infection, leaves distorted
B. rubra +, 3, (6), fair infection

Amaranthaceae

- Achyranthes aspera* +, 2, (8), dense infection
A. indica +, 6, (5), fair infection
Amaranthus berlandiera +, 12, (5), good infection
A. blitoides +, 2, (5), sparse infection
A. hybridus +, 10, (5), good infection
A. retroflexus +, 5, (10), good infection
A. spinosa +, 5, (5), fair infection
Celosia argentea var. *cristata* +, 10, (4), dense infection, leaves and petioles distorted
Gomphrena decumbens —, 5, (8), mature plant
G. globosus +, 15, (6), good infection

Nyctaginaceae

- Boerhavia paniculata* +, 8, (8), good infection
Bougainvillea spectabilis +, 4, (4), fair infection, mature plants
Mirabilis jalapa, +, 8, (4), very dense infection, plants greatly distorted
M. jalapa +, 5, (4), dense infection, mature plants
Pisonia acuelata, +, 2, (4), good infection

Phytolaccaceae

- Phytolacca americana* +, 5, (4), dense infection, leaves greatly distorted
P. rivinioides +, 5, (4), good infection, mature plants

Azoiaceae

- Mesembryanthemum crinifolium* +, 4, (8), sparse infection
Mollugo verticillata +, 3, (5), dense infection, mature plant
Sesuvium portulacastrum +, 20, (6), good infection

Lauraceae

- Lindera benzoin* +, 2, (8), dense infection, leaves distorted
Persea americana +, 4, (6), dense infection, leaves distorted

Papaveraceae

- Argemone spinosa* +, 5, (8), dense infection
Eschscholtzia californica +, 6, (20), fair infection
Chelidonium majus +, 5, (6), sparse infection
Hunnemannia fumariaefolia +, 6, (4), dense infection
Papaver orientale +, 10, (8), fair infection
Sanguinaria canadensis +, 3, (8), fair infection

Fumariaceae

- Dicentra spectabilis* +, 3, (6), sparse infection

Capparidaceae

- Cleome ciliata* +, 8, (5), fair infection
C. spinosa +, 8, (5), fair infection
Polanisia viscosa +, 10, (5), fair infection

Cruciferae

- Alyssum murale* +, 10, (6), good infection
Arabis alpina +, 15, (4), dense infection
Aubretia deltoidea +, 30, (6), good infection
Berteroa incana +, 20, (6), good infection
Brassica oleracea var. *capitata* +, 20, (4), dense infection
B. oleracea var. *italica* +, 15, (4), dense infection
B. rapa +, 15, (6), dense infection
B. campestris +, 15, (4), dense infection
B. tournefortia +, 15, (6), sparse infection
Cakile lanceolata +, 10, (5), dense infection, leaves distorted
Capsella bursa pastoris +, 30, (6), good infection
Cardamine bulbifera +, 6, (8), sparse infection, mature plant
Dentaria laciniata +, 8, (6), dense infection
Draba reptans +, 12, (10), sparse infection
Hesperis matronalis +, 10, (6), dense infection
Iberis gibraltica +, 15, (4), dense infection, leaves malformed
Lepidium virginicum +, 15, (6), dense infection
Lunaria biennis +, 18, (5), dense infection
Matthiola bicornis +, 30, (10), sparse infection
Nasturtium officinale +, 2, (6), good infection, mature plants
Raphanus sativus +, 15, (4), dense infection
Roripa sessilifolia +, 3, (6), dense infection, mature plant
Thlaspis arvense +, 6, (6), good infection

Moringaceae

Moringa oleifera +, 6, (6), fair infection

Sarraceniaceae

Sarracenia purpurea —, 3, (10), mature plants

Saxifragaceae

Hydrangea quercifolia +, 6, (4), dense infection

Heuchera americana +, 3, (6), sparse infection, mature plants

Mitella diphylla +, 4, (5), dense infection

Philadelphus pubescens —, 6, 15

Tolmiea menziesii +, 1, (6), dense infection, mature plant

Platanaceae

Platanus occidentalis +, 4, (5), sparse infection

Altingiaceae

Liquidambar styraciflua +, 2, (5), dense infection

Hamamelis virginiana +, 1, (5), dense infection

Rosaceae

Amygdalus persica +, 2, (6), fair infection

Chrysobalanus icaco +, 2, (5), dense infection

Cotoneaster nitens +, 1, (6), sparse infection

Duchesnia indica +, 6, (12), sparse infection, mature plants

Eriobotrya japonica +, 2, (15), sparse infection, galls and parasites aborted

Fragaria vesca +, 3, (5), sparse infection, mature plants

Physocarpus opulifolius +, 4, (6), good infection

Potentilla simplex +, 5, (8), fair infection

P. recta —, 2, (6), mature plant

P. rupestris —, 15, (20)

Rosa floribunda +, 1, (4), good infection, mature plant

Rubus trivialis —, 6, (9), mature plant

Leguminosa

Abrus precatorius +, 5, (6), sparse infection

Acacia farnesiana +, 1, (5), fair infection

A. lutea +, 2, (5), fair infection

A. nilotica +, 12, (5), dense infection

A. robusta +, 15, (12), sparse infection

A. tortuosa +, 8, (4), dense infection, seedlings killed

Albizzia julibrissima +, 2, (8), dense infection, seedlings killed

A. lebeck +, 1, (6), dense infection

Alysicarpus rugosus +, 10, (8), dense infection

Amphicarpaea bracteata +, 5, (6), good infection

A. trisperma +, 13, (7), fair infection

Arachis hypogea +, 5, (6), sparse infection

Baptisia australis +, 8, (5), dense infection

Bauhinia galpini +, 12, (4), dense infection

B. saigonensis +, 6, (8), good infection

Caesalpinia coriaria +, 5, (10), sparse infection

C. pulcherrima +, 12, (6), dense infection

Cajanus cajan +, 5, (4), sparse infection

Calpurnia subdecidia +, 7, (8), dense infection

Canavalia altissima +, 8, (4), very dense infection

Cassia absus +, 2, (12), sparse infection

C. alata +, 12, (10), sparse infection

C. appendiculata +, 6, (4), dense infection

C. aristellata +, 1, (8), sparse infection

- C. artemisioides* +, 1, (8), dense infection
C. bicapsularis +, 3, (6), sparse infection
C. bauhiniioides +, 5, (6), sparse infection
C. corymbosa +, 4, (4), good infection
C. desolata +, 1, (4), sparse infection
C. durangensis +, 6, (4), dense infection
C. emarginata +, 1, (8), sparse infection
C. fasciculata var. *rostrata* +, 5, (6), dense infection
C. fasciculata var. *puberalata* +, 5, (6), sparse infection
C. ferruginea +, 4, (6), sparse infection
C. fistula +, 4, (6), dense infection
C. grandis +, 1, (6), sparse infection
C. laevigata +, 3, (5), good infection
C. lindheimeri +, 6, (4), dense infection
C. macrantha +, 1, (6), sparse infection
C. marylandica +, 3, (5), fair infection
C. mimosioides +, 4, (4), dense infection
C. nictitans +, 4, (4), dense infection
C. nodosa +, 6, (5), dense infection
C. patellaria +, 2, (12), fair infection
C. petersiana +, 3, (6), sparse infection
C. roemeriana +, 2, (12), sparse infection
C. rotundifolia +, 2, (8), sparse infection
C. siamea +, 3, (6), dense infection
C. sulcata +, 4, (4), dense infection
C. tora +, 1, (5), dense infection
C. torosa +, 18, (5), fair infection
Centrosema sophera +, 4, (5), good infection
C. virginianum +, 4, (7), dense infection
Cercis canadensis +, 4, (4), fair infection
Crotalaria incana +, 5, (2), dense infection
C. striata +, 6, (6), sparse infection
C. varicosa +, 5, (4), sparse infection
Crotalaria sp. +, 3, (6), dense infection
Dahlbergia ecastophyllum +, 6, (5), dense infection
Delonix regia +, 3, (4), dense infection
Desmanthus virgatus +, 3, (4), dense infection
D. brevipes +, 2, (6), sparse infection
Desmodium glutinosum +, 4, (6), sparse infection
D. salicifolium +, 1, (5), good infection
Dolichos lablab +, 8, (6), sparse infection
Dorycnium rectum +, 8, (6), fair infection
Enterolobium saman +, 8, (6), dense infection
E. cyclocarpon +, 2, (4), dense infection
Erythrina indica +, 2, (8), sparse infection, mature plant
E. vespertilio +, 7, (6), dense infection, leaves greatly distorted
Flemingia strobilifera +, 4, (4), dense infection
Galactia muelleni +, 5, (6), dense infection
Gleditsia triacanthos +, 10, (8), dense infection
Gliricidia sepium +, 1, (6), sparse infection
Glycine soja +, 8, (2), dense infection
Gymnocladia dioica +, 8, (6), fair infection
Hebestigma cubensis +, 4, (6), dense infection, galls and parasites
 aborted

- Indigofera subulata* +, 1, (5), sparse infection
Kennedyia prostrata +, 2, (6), dense infection
Lathyrus odoratus +, 6, (5), dense infection, leaves distorted
Leucaena glauca +, 4, (5), dense infection
Lupinus subcarnosus +, 8, (3), dense infection
Mucuna urens —, 2, (20)
Neptunia pubescens var. *floridana* +, 6, (6), sparse infection
Olneya tesota +, 4, (12), dense infection, galls and parasites aborted
Ormosia monosperma +, 1, (4), dense infection, leaves greatly distorted
Parkia javanica +, 6, (6), good infection
Phaseolus athryoides +, 12, (8), sparse infection, some galls aborted
P. purpurascens —, 6, (12)
P. vulgaris +, 6, (3), dense infection
Peltophorum brasiliensis +, 1, (5), dense infection
P. africanum +, 1, (6), sparse infection
Pisidia piscipula +, 6, (4), good infection
Pithecolobium dulce +, 8, (4), dense infection
Poinciana gillesi +, 3, (4), dense infection
Prosopis pubescens +, 6, (6), good infection
P. glandulosa +, 1, (4), dense infection
Psoralea floribunda +, 3, (6), dense infection which killed seedlings
P. pubescens +, 8, (6), sparse infection
Pterocarpus indicus +, 7, (6), dense infection
P. vidalensis +, 1, (6), dense infection
Robinia pseudacacia +, 6, (6), good infection
Saraca indica +, 6, (6), dense infection of stem
Sesbania benthamiana +, 1, (8), good infection
S. cannabina +, 8, (5), sparse infection
S. drummondii +, 2, (5), dense infection
S. macrocarpa +, 3, (10), dense infection
S. sericea +, 2, (6), fair infection
Sophora japonica +, 4, (8), fair infection
S. secundiflora +, 1, (4), dense infection
Thermopsis caroliniana +, 12, (3), dense infection
Trifolium repens +, 5, (6), sparse infection
Ulex europaeus +, 12, (5), dense infection
Urana cylindacea +, 4, (8), dense infection
Vicia pisiformis +, 1, (4), sparse infection
Vigna sinensis +, 10, (2), dense infection
Wistaria japonica +, 5, (5), dense infection, leaves greatly distorted
- L i n a c e a e**
Linum collinum +, 10, (4), good infection
- T r o p a e o l a c e a e**
Tropaeolum majus +, 6, (3), dense infection, leaves malformed
- L i m n a n t h a c e a e**
Floerkea proserpinacoides +, 6, (5), good infection, mature plant
Limnanthus alba +, 3, (20), sparse infection of flower buds
- Z y g o p h y l l a c e a e**
Kallstroemia maxima +, 2, (6), good infection, mature plant
- O x a l i d a c e a e**
Averrhoa bilimbi +, 15, (8), sparse infection
- R u t a c e a e**
Citrus ichangensis +, 12, (5), dense infection, most galls and parasites aborted

C. nobilis var. *deliciosus* —, 6, (8), mature plant

C. sinensis +, 10, (5), dense infection, most galls and parasites aborted

Dictamnus albus +, 1, (6), dense infection

Severinia buxifolia +, 6, (9), dense infection

Suriaceae

Suriana maritima +, 8, (5), sparse infection

Simarubaceae

Ailanthus altissima +, 6, (5), dense infection, leaves malformed

Meliaceae

Melia azedarach +, 12, (10), sparse infection, galls and parasites aborted

Trichilia hirta +, 6, (6), sparse infection

Erythroxylaceae

Erythroxylum obovatum +, 1, (6), sparse infection

Malpighiaceae

Heterotropis laurifolia +, 6, (6), sparse infection

Malpighia puniceifolia +, 3, (5), dense infection, leaves distorted

Geraniaceae

Geranium maculatum +, 6, (3), good infection

G. pusillum —, 5, (12)

Pelargonium hortorum +, 6, (5), sparse infection, mature plant

P. africanum —, 20, (15)

Euphorbiaceae

Acalypha virginica +, 3, (5), sparse infection

Cnidioscolus stimulosus +, 4, (15), sparse infection, galls and parasites aborted

Croton monanthogynus +, 2, (5), dense infection

Euphorbia colorata +, 6, (8), fair infection

E. hirta +, 4, (6), sparse infection, mature plant

E. maculata +, 6, (4), fair infection

E. marginata —, 6, (8)

E. pulcherrima +, 6, (6), fair infection

E. splendens +, 3, (4), good infection

Hura crepitans —, 3, (15)

Jatropha curcas +, 6, (6), fair infection

J. gossypifolia +, 5, (3), good infection

J. multifida +, 6, (5), sparse infection

J. panduraefolia +, 6, (6), good infection

Phyllanthus acidus +, 5, (8), good infection

P. urenia +, 10, (18), sparse infection, only 3 galls

Poinsettia sp. +, 5, (6), dense infection

Ricinus communis +, 10, (4), dense infection, leaves malformed

Tragia urticifolia +, 10, (6), dense infection, leaves distorted

Buxaceae

Pachysandra terminalis +, 5, (6), dense infection, leaves distorted

Anacardiaceae

Mangifera indica +, 4, (6), sparse infection

Rhus hirta +, 6, (5), good infection

R. toxicodendron —, 2, (8), mature plant

Spondias mombin +, 6, (8), sparse infection, emerging leaf of sapling

S. mombin +, 2, (5), dense infection, seedlings killed

Aquifoliaceae

Ilex opaca +, 1, (5), sparse infection

Staphyleaceae

Staphylea trifoliata +, 3, (4), good infection

Aceraceae

Acer negundo +, 2, (5), fair infection

A. saccharinum +, 2, (5), fair infection

Celastraceae

Celastrus scandens +, 1, (6), dense infection, leaves malformed

Euonymus europaea +, 6, (4), dense infection, leaves malformed

E. fortunei +, 20, (15), dense infection

E. obovata +, 3, (6), fair infection, mature plant

Hippocastanaceae

Aesculus parviflora +, 4, (6), dense infection

Sapindaceae

Blighia sapida +, 5, (6), sparse infection

Koelreuteria formosana +, 10, (8), good infection

K. paniculata +, 5, (6), dense infection, leaves and petioles malformed

Melicocca bijuga +, 4, (6), sparse infection, galls and parasites aborted

Sapindus drummondi +, 2, (6), sparse infection, leaves distorted

S. saponaria +, 2, (6), good infection, leaves distorted

Dodonaeaceae

Dodonaea physocarpa +, 3, (9), good infection

Balsaminaceae

Impatiens balsamina +, 8, (4), dense infection, leaves distorted

I. pallida +, 8, (3), dense infection, leaves distorted

I. sultana +, 8, (3), dense infection, leaves distorted

Rhamnaceae

Ceanothus americanus +, 2, (4), fair infection

Colubrina reclinata +, 5, (12), sparse infection

Vitaceae

Cissus sicyoides +, 10, (8), dense infection, leaves distorted

C. trifoliata +, 3, (4), fair infection, mature plant

Parthenocissus tricuspidata +, 4, (5), dense infection

P. quinquefolia +, 4, (4), dense infection, mature plant

Vitis aestivalis +, 5, (6), dense infection

V. labrusca +, 2, (6), good infection

Tiliaceae

Corchoropsis tomentosa —, 8, (22)

Tilia americana +, 5, (4), good infection

Triumfetta hispida +, 10, (5), fair infection

Malvaceae

Abelmoschus marribat +, 11, (8), sparse infection

Abutilon crispum —, 5, (6)

A. pauciflorum —, 5, (6)

A. theophrastii +, 8, (6), dense infection

Althaea rosea —, 10, (12)

Callirrhoe involucrata , 15, (10), sparse infection of one leaf

C. leocarpa —, 6, (5)

Gossypium arboreum +, 6, (6), dense infection

G. herbaceum +, 6, (6), dense infection

Hibiscus sp. +, 8, (12), good infection

H. aculeatus +, 6, (4), dense infection

H. cannabinus +, 2, (6), good infection, mature plant

H. esculentus +, 8, (4), dense infection

Lavatera alba +, 8, (6), good infection

- L. cretica* +, 20, (5), dense infection
L. thuringiaca +, 2, (8), dense infection
L. trimestris +, 7, (7), good infection
Malachra sp. +, 30, (10), sparse infection
Malva crispa +, 20, (8), sparse infection
M. rotundiflora +, 6, (5), good infection
Malvastrum peruvianum +, 25, (8), good infection
Pavonia hastata +, 1, (8), fair infection
P. spicata +, 1, (4), dense infection
Sida carpinifolia +, 2, (8), fair infection, galls and parasites aborted
S. ciliaris +, 6, (8), fair infection
S. rhombifolia +, 8, (6), fair infection
S. spinosa +, 12, (5), good infection
Thespesia populnea +, 5, (5), dense infection
Urena lobata +, 15, (4), dense infection

T h e a c e a e

- Camellia japonica* +, 4, (6), good infection, galls and parasites aborted

G u t t i f e r a e

- Calophyllum inophyllum* +, 4, (6), good infection
C. kunstleri +, 1, (6), good infection
Mammea americana +, 2, (10), sparse infection, galls and parasites aborted

B o m b a c e a e

- Ceiba pentandra* +, 4, (4), sparse infection
Guazuma ulmifolia —, 12, (20)
Melochia nodiflora +, 6, (20), sparse infection, 5 galls on one leaf
Waltheria americana +, 5, (15), sparse infection, galls and parasites aborted early

H y p e r i c a c e a e

- Ascyrum hypercoides* +, 5, (4), fair infection
Triadenum japonicum +, 5, (6), fair infection

C i s t a c e a e

- Helianthemum mutabile* +, 6, (6), good infection

B i x a c e a e

- Bixa orellana* +, 2, (10), good infection

V i o l a c e a e

- Viola pedata* —, 4, (12)
V. pubescens +, 3, (8), sparse infection, few aborting galls and parasites

P a s s i f l o r a c e a e

- Passiflora quadrangularis* +, 15, (5), good infection

P a p a y a c e a e

- Carica papaya* +, 8, (6), dense infection

F l a c o u r t i a c e a e

- Casearia hirsuta* +, 12, (6), good infection
C. sylvestris +, 12, (6), good infection
Dovyalis hebecarpa +, 8, (9), dense infection
Flacourtia indica +, 15, (10), good infection, galls and parasites aborted
F. jangomas +, 5, (10), dense infection, galls and parasites aborted
Idesia polycarpa +, 10, (12), sparse infection, galls and parasites aborted early

B e g o n i a c e a e

- Begonia semperflorens* +, 4, (6), fair infection, scattered galls on emerging leaves of mature plants

Cactaceae

Harisia gracilis

Mylocerus triangularis +, 5, (8), dense infection

Opuntia compressa +, 1, (5), very dense infection of emerging leaves of mature plant

O. dillenii +, 4, (12), dense infection

O. tuna +, 1, (4), good infection

Lythraceae

Ammania coccinea +, 1, (4), sparse infection

Lagerstroemia indica +, 3, (5), fair infection, mature plant, galls aborted

L. speciosa +, 6, (10), good infection

Lythrum alatum —, 4, (15), emerging leaves of mature plant

L. alatum +, 4, (12), sparse infection, six galls on one leaf

Punicaceae

Punica granatum +, 15, (6), good infection

Combrataceae

Conocarpus erectus +, 5, (8), sparse infection

Terminalia catappa +, 2, (3), sparse infection

T. edulis +, 9, (15), dense infection, galls and parasites aborted

Melastomaceae

Rhexia virginica +, 2, (4), dense infection

Onagraceae

Fuchsia hybrida +, 3, (5), dense infection, leaves and petioles greatly distorted

Guara coccinea +, 6, (6), dense infection, leaves distorted

Jussiaea suffruticosa +, 18, (15), good infection

Oenothera biennis +, 7, (8), sparse infection, galls scattered

O. laciniata +, 8, (6), dense infection

O. speciosa —, 8, (6).

Haloragaceae

Halorrhagis alata +, 10, (8), good infection

H. colensoi +, 7, (7), fair infection

H. masafuerana +, 7, (8), sparse infection

Araliaceae

Acanthopanax sieboldianus +, 1, (3), very dense infection, leaves greatly distorted

Aralia cordata +, 5, (6), sparse infection, mature plant

Fatsia japonica +, 1, (5), dense infection

Hedera helix +, 6, (5), dense infection, leaves greatly distorted, mature plant

Schefflera actinophylla +, 1, (5), fair infection

Umbelliferae

Ammi majus +, 2, (6), good infection

Anethum graveolens +, 20, (6), good infection

Anthriscus cerefolium +, 10, (6), good infection

Carum carvi +, 20, (6), good infection

Chaerophyllum procumbens +, 10, (4), good infection

Coriander sativum +, 30, (6), good infection

Cryptotaenia canadensis +, 3, (4), dense infection, leaves distorted

Daucus carota +, 15, (4), dense infection, leaves and petioles distorted and thickened

Foeniculum vulgare +, 10, (4), dense infection

Hydrocotyle umbellata +, 5, (6), dense infection

H. bonaerense +, 6, (4), dense infection

- Osmorrhiza claytoni* +, 6, (3), dense infection
Pastinaca sativa +, 10, (4), dense infection
Pimpinella anisum +, 10, (4), good infection
Sanicula canadensis +, 15, (4), dense infection, leaves malformed
Thymus vulgaris +, 10, (6), good infection
Trachymene coerulea +, 6, (8), good infection

Ericaceae

- Vaccinium macrocarpum* +, 6, (4), fair infection, galls scattered

Cornaceae

- Cornus canadensis* +, 2, (6), dense infection, leaves distorted

Primulaceae

- Anagallis arvensis* +, 10, (6), dense infection
Cyclamen persicum +, 4, (12), fair infection
Lysimachia nummularia —, 15, (25), mature plants
Primula japonica +, 10, (6), good infection
P. sinensis var. *fimbriata* +, 6, (6), good infection

Plumbaginaceae

- Armeria pseudo-armeria* +, 5, (20), sparse infection, 10 galls on one leaf
Plumbago scandens +, 12, (6), dense infection, leaves malformed

Sapotaceae

- Achras zapota* +, 6, (12), sparse infection

Ebenaceae

- Diospyrus virginiana* +, 6, (4), dense infection, plants greatly distorted

Oleaceae

- Chionanthus virginica* +, 4, (6), dense infection
Forsythia suspensa +, 4, (10), sparse infection, galls and parasites aborted
Fraxinus americana +, 2, (4), fair infection
F. nigra +, 2, (4), fair infection
Ligustrum vulgare +, 6, (8), good infection

Apocynaceae

- Allamanda cathartica* +, 3, (4), sparse infection, mature plant
Apocynum cannabinum +, 1, (4), dense infection, mature plant
Tabernaemontana coronaria var. *flore-pleno* +, 5, (8), dense infection
Vinca rosea +, 12, (6), fair infection

Asclepiadaceae

- Asclepias* sp. +, 8, (4), good infection
A. curassavica +, 15, (6), good infection
A. incarnata —, 10, (8)
A. physocarpa +, 15, (6), dense infection, leaves distorted
A. tuberosa +, 3, (6), dense infection
A. verticillata —, 10, (8)
Calotropis procera +, 10, (4), good infection
Ceropegia palustris +, 2, (8), good infection
Oxypetalum coeruleum +, 15, (5), dense infection,

Convolvulaceae

- Argyria bracteata* +, 4, (6), dense infection
Calonyction muricatum +, 2, (6), fair infection
Convolvulus japonica +, 4, (6), good infection
Dichondria repens +, 7, (8), fair infection, mature plant
Ipomoea battatis —, 4, (6), mature plant
I. carnea +, 3, (6), good infection, mature plant
I. dissecta +, 6, (6), good infection
I. pandurina +, 5, (6), good infection

- I. pes-caprae* +, 4, (6), fair infection
Polymeria distgina +, 3, (8), sparse infection
Quamoclit coccinea +, 3, (8), sparse infection
- Polemoniaceae**
Gilia capitata +, 15, (12), sparse infection
Phlox drummondii +, 4, (8), good infection
P. pilosa —, 4, (8), mature plant
Polemonium coeruleum +, 10, (6), good infection
P. reptans —, 6, (10), mature plant
- Hydrophyllaceae**
Hydrophyllum appendiculatum —, 3, (15), mature plant
Nama jamaicense —, 5, (10), mature plant
Nemophila insignis +, 10, (5), dense infection
Phacelia bipinnatifida +, 10, (4), dense infection
- Boraginaceae**
Borago officinalis +, 15, (6), dense infection
Boureria baccata +, 9, (15), dense infection
Cordia alba +, 10, (5), dense infection, leaves distorted
C. gerascanthus +, 10, (5), dense infection
C. sebestena +, 6, (4), dense infection, leaves greatly distorted
Cyanoglossum officinale +, 10, (5), good infection
Ehretia tenuifolia +, 5, (8), good infection
Heliotropium indicum +, 8, (8), dense infection, leaves distorted
Myosotis alpestris +, 30, (6), good infection
Tournefortia hirsutissima +, 10, (6), fair infection
- Verbenaceae**
Duranta plumieri +, 2, (6), good infection
Lantana trifoliata +, 8, (6), good infection
Phyla incisa +, 1, (6), good infection
P. nodiflora +, 1, (6), good infection
Priva echinata +, 3, (6), fair infection
Tectonia grandis +, 2, (6), sparse infection
Verbena bonaerensis +, 12, (8), good infection
V. alternifolia —, 10, (12)
Vitex cymosa +, 7, (8), good infection
- Labiatae**
Adjugate reptans —, 5, (12), mature plants
Coleus blumei —, 4, (15), mature plants
Glechoma hederacea —, 12, (10), mature plants
Lamium maculatum +, 6, (8), good infection, mature plants
L. purpureum +, 6, (6), good infection
Lavandula officinalis +, 15, (5), dense infection
Leonotis nepetefolia +, 3, (4), good infection, mature plants
Leonurus cardiaca +, 4, (7), sparse infection, mature plants
L. sibiricus +, 8, (6), fair infection
Mentha piperita +, 8, (4), dense infection, mature plants
Molucella laevis +, 8, (6), dense infection, leaves greatly malformed
Marrubium vulgare +, 8, (6), sparse infection
Nepeta cataria —, 6, (12), mature plants
N. cataria —, 15, (15), seedlings
Ocimum sp. —, 12, (15)
Physostegia virginiana +, 20, (6), sparse infection
Prunella vulgaris —, 6, (15), mature plants
P. vulgaris —, 20, (15), seedlings

Salvia splendens +, 20, (5), dense infection

Sideritis candicans +, 12, (10), fair infection

Stachys agraria —, 6, (8), mature plants

S. hispida —, 12, (10)

Thymus vulgaris +, 8, (8), good infection

Gesneriaceae

Columnea allenii +, 4, (8), good infection

Saintpaulia ionantha +, 4, (8), sparse infection, mature plants

Acanthaceae

Eranthemum watti +, 9, (15), good infection

Fittonia argyroneura +, 2, (5), good infection

Hygrophila lancea +, 20, (8), fair infection

Justicia debilis +, 22, (6), dense infection

J. procumbens +, 12, (14), sparse infection, 2 galls on one leaf

Ruellia reptans —, 4, (8), mature plants

R. reptans +, 2, (6), good infection, seedlings

R. tuberosa +, 6, (8), fair infection

Thunbergia alata +, 20, (6), dense infection

Phrymaceae

Phryma leptostachya +, 3, (4), sparse infection

Plantaginaceae

Plantago aristata +, 5, (15), dense infection

P. asiatica +, 12, (6), sparse infection

P. bellardi +, 5, (12), sparse infection

P. coronopus +, 3, (8), sparse infection

P. japonica +, 8, (10), sparse infection

P. lagopus +, 10, (8), fair infection

P. lanceolata —, 15, (12), mature plants

P. lanceolata +, 8, (6), good infection, seedling

P. major +, 5, (8), good infection

P. maritima +, 20, (8), good infection

P. psyllium —, 3, (20)

P. pumila +, 10, (12), sparse infection

P. purshii +, 20, (20), sparse infection

P. rhodosperma +, 15, (8), good infection

P. rugeli +, 12, (8), good infection

P. serraria +, 10, (10), sparse infection

P. virginica +, 15, (8), good infection

P. wrightiana +, 8, (20), sparse infection, 6 galls on one plant

Santalaceae

Comandra ramondioides +, 5, (8), sparse infection

Santalum album +, 4, (4), dense infection

Rubiaceae

Boraria laevis —, 6, (12)

Coffea liberica +, 3, (8), sparse infection

Galium saxatile +, 10, (5), good infection

G. asprellum +, 10, (5), good infection

Guettardia elliptica +, 3, (5), dense infection

Ixora ruscifolia +, 8, (15), good infection

Morinda citrifolia +, 15, (6), dense infection, leaves greatly distorted

M. rojoc +, 2, (8), sparse infection

Pentas lanceolata +, 4, (5), good infection, large outgrowths on stem

Phuopsis stylola +, 15, (10), fair infection

Richardsonia pilosa +, 8, (8), sparse infection

Caprifoliaceae

- Lonicera* sp. +, 2, (6), sparse infection
L. xylosteum +, 6, (5), good infection
Sambucus canadensis +, 4, (10), sparse infection, galls and parasites aborted
Triosteum perfoliatum +, 2, (5), good infection
Virburnum lantana +, 8, (4), good infection

Solanaceae

- Brunfelsia americana* +, 8, (8), sparse infection
Capsicum baccatum +, 20, (6), dense infection
C. frutescens +, 30, (4), dense infection
Cestrum diurnum +, 12, (6), good infection
Datura stramonium +, 3, (6), good infection, leaves locally distorted, mature plant
D. suaveolens +, 2, (8), sparse infection, mature plant
D. suaveolens +, 15, (5), dense infection, seedlings
Lycopersicum esculentum +, 5, (6), good infection
Nicotiana affinis +, 15, (7), dense infection
N. tabacum —, 5, (12), mature plants
Petunia hybrida +, 15, (10), fair infection
Physalis subglabrata +, 8, (6), good infection
Schizanthus pinnatus +, 8, (6), dense infection
Solanum melongena +, 50, (5), good infection
S. nigrum +, 10, (4), good infection
S. rostratum +, 5, (6), good infection
S. torvum +, 40, (8), sparse infection, 3 galls on 2 leaves
S. tuberosum +, 5, (10), sparse infection

Scrophulariaceae

- Afzelia cassioides* +, 1, (5), sparse infection
Castilleja coccinea +, 8, (10), fair infection
Collinsonia canadense —, 15, (20)
Cymbalaria muralis +, 6, (5), dense infection, mature plant leaves greatly distorted
Digitalis purpurea var. *gloxiniaefolia* +, 10, (5), sparse infection
Penstemon barbatus +, 5, (5), sparse infection
Linaria vulgaris +, 6, (5), good infection
Scrophularia marylandica —, 15, (20)
Torena fourieri +, 30, (15), sparse infection
Verbascum thapsus +, 3, (6), sparse infection, galls and parasites aborted
Veronica peregrina var. *typica* —, 5, (10), mature plant
Veronica sp. +, 15, (5), good infection

Bignoniaceae

- Arrabidaea magnifica* +, 6, (8), sparse infection, mature plant, galls and parasites aborted
Bignonia unguis-cati +, 3, (6), fair infection
Catalpa bignonioides —, 5, (12), mature plant
C. bignonioides +, 6, (6), dense infection, seedlings
C. longissima +, 8, (5), good infection
Jacaranda silicifolia +, 12, (6), good infection
Pandorea australis +, 10, (6), dense infection
Parmentiera cereifera +, 15, (25), good infection of one seedling, out of fifteen
Spathodea campanulata +, 10, (6), good infection

Tecoma radicans +, 3, (5), sparse infection, few scattered galls

T. stans +, 2, (8), sparse infection

Barringtoniaceae

Barringtonia speciosa +, 2, (6), sparse infection

Myrtaceae

Eucalyptus camaldulensis +, 2, (6), sparse infection

E. grandis +, 9, (6), fair infection

E. globulus +, 1, (8), sparse infection, galls and parasites aborted

Eugenia buxifolia +, 3, (6), dense infection, leaves distorted

E. jambosa +, 4, (6), dense infection, leaves distorted

E. malaccensis +, 3, (4), dense infection, leaves distorted

Psidium cattleianum +, 20, (10), dense infection

P. guajava +, 12, (6), dense infection

Rhizophoraceae

Rhizophora mangle +, 1, (8), sparse infection, galls and parasites aborted

Valerianaceae

Valerianella eriocarpa —, 2, (15)

V. chenopodifolia —, 6, (15)

V. stenocarpa +, 8, (15), good infection, galls and parasites aborted very early

Dipsacaceae

Scabiosa caucasica +, 10, (5), dense infection

Cucurbitaceae

Benincasa hispida +, 2, (8), dense infection

Citrullus vulgaris +, 10, (4), dense infection, leaves greatly distorted

C. colocynthis +, 2, (6), dense infection

Cucumis anguira +, 7, (4), dense infection, leaves distorted

C. melo +, 8, (4), dense infection, leaves distorted

C. sativus +, 8, (4), dense infection, leaves distorted

Cucurbita foetidissima +, 6, (6), good infection

C. moschata +, 10, (4), dense infection

C. pepo +, 10, (4), dense infection, leaves distorted

Lagenaria siceraria +, 5, (4), dense infection

Momordica balsamina +, 6, (4), dense infection, leaves greatly distorted

Melothria japonica +, 20, (7), fair infection

Campanulaceae

Campanula americana +, 1, (4), dense infection, mature plant

C. carpatica +, 10, (6), good infection

Campanula sp. +, 6, (6), good infection

Platycodon grandiflorum +, 3, (6), good infection

Specularia perfoliata +, 5, (4), dense infection

Lobeliaceae

Lobelia cardinalis +, 15, (5), good infection

Compositae

Achillea sp. +, 6, (12), sparse infection

Ageratum sp. +, 20, (6), sparse infection

Ambrosia aptera +, 6, (6), fair infection

A. eleator —, 3, (6)

A. psilostachys +, 6, (6), good infection

A. trifida +, 6, (6), fair infection

Antennaria plantaginifolia +, 6, (3), fair infection

Anthemis tinctoria +, 20, (8), fair infection

— *cotula* —, 10, (10)

- Arctium lappa* +, 7, (5), fair infection
Bellis perennis +, 15, (5), dense infection
Bidens bipinnata +, 6, (4), dense infection
B. frondosa +, 12, (4), dense infection
Cacalia atriplicifolia +, 5, (6), sparse infection, galls and parasites aborted
Calendula officinalis +, 12, (4), good infection
Calliopsis sp. +, 30, (8), fair infection
Calyptocarpus vialis +, 4, (6), good infection, mature plants
Centaurea cyanus +, 10, (6), dense infection
C. imperialis +, 12, (6), dense infection
Cirsium palustre +, 6, (3), dense infection, mature plant
Chrysanthemum leucanthemum +, 8, (8), good infection
Cynara scolymus +, 15, (6), dense infection
Dahlia pinnata +, 12, (6), dense infection
Doronicum caucasicum +, 5, (6), dense infection
Emilia sonchifolia +, 5, (6), good infection, mature plant
Erigeron annuus +, 4, (6), fair infection, mature plant
E. philadelphicus +, 4, (6), fair infection, mature plant
Eupatorium urticifolium +, 2, (4), dense infection, mature plant
Gaillardia sp. +, 30, (6), good infection
Galinsoga parvifolia +, 5, (4), good infection
Gerbera jamesonii +, 10, (5), dense infection
Haplopappus gracilis —, 5, (10)
H. spinulosus —, 6, (10)
Helichrysum bracteatum +, 15, (5), good infection
Helianthus annuus +, 10, (6), good infection
Hieracium auranthiacum +, 5, (4), dense infection, mature plant
Kleinia articulata +, 4, (5), good infection
Lactuca sativa —, 5, (12), mature plant
L. scariola +, 4, (4), dense infection, leaves distorted, mature plant
Lagascea mollis +, 8, (10), sparse infection, galls and parasites aborted
Liatris scariosa +, 12, (6), good infection
Matricaria capensis +, 1, (5), sparse infection
Prenanthes altissima +, 12, (8), good infection
Pyrethrum roseum —, 20, (15)
Rudbeckia serotina +, 3, (15), sparse infection
R. purpurea +, 10, (4), dense infection
R. laciniata +, 1, (4), dense infection, mature plant
Sanvitalia procumbens +, 10, (6), good infection
Senecio obovatus +, 3, (7), good infection, mature plant
Sonchus asper +, 2, (3), dense infection
Spilanthus urens +, 20, (5), good infection
Synedrella nodiflora +, 4, (4), good infection
Stokesia cyanea +, 15, (5), dense infection
Tagetes tenuifolia +, 10, (4), dense infection
Taraxacum officinale —, 6, (30), mature plant
T. officinale —, 20, (25), seedlings
Tithonia rotundifolia +, 8, (3), dense infection
Veronina cinerea +, 4, (5), good infection, mature plant
Xanthium americanum +, 12, (2), dense infection
X. strumarium +, 5, (3), dense infection, leaves distorted
Zinnia angustifolia +, 30, (3), dense infection

Discussion.

As shown in the results above 811 species and 7 varieties in 576 genera of 166 families were inoculated, and of these 707 species in 509 genera of 141 families became infected in varying degrees of intensity. The number of families successfully infected depends, of course, on whether the *Agavaceae*, *Dodonaeaceae*, *Barringtoniaceae*, etc. are recognized as distinct families. Nonetheless, infection occurred in approximately 86% of the species inoculated. In the various categories *) of infection 165 species were sparsely infected, 91 fairly, 175 goodly, and 255 densely infected. In 27 species the parasites and galls aborted at various stages of development. No infection occurred on ferns, mosses, liverworts, algae and fungi.

A large number of flowering plants also did not become infected although they were inoculated repeatedly with a dense suspension of planospores. However, this does not a priori indicate an inherent immunity or resistance in all negative cases, in my opinion. Leaves of species like *Althaea rosea*, *Verbascum thapsus*, *Plantago psyllum*, etc., with a dense covering of trichomes are difficult to wet thoroughly and thus provide a moist surface and direct contact for the planospores with the epidermis. Leaves of other plants like *Euphorbia marginata*, *Eucalyptus* species, and *Eschscholzia californica* have a thick waxy cuticle which prevents wetting. Although attempts were made to overcome such structural barriers by the use of a wetting agent I think they influenced the success or failure of infection to some degree. The wide range of plants which are susceptible and the inconsistencies in results obtained with the same species at different times lead me to believe that many of the species which remained uninfected would be susceptible to *S. macrosporum* if conditions were optimum and structural barriers were effectively removed.

In species like *Lysimachia nummularia*, *Ajuga reptans*, *Prunella vulgaris* and others, the leaves are readily wettable, and although inoculated a large number of times they did not become infected. Such species, thus, appear to be resistant or immune to *S. macrosporum*.

In most families listed above only one or a few species were available for inoculation, and it is impossible to draw any conclusions about their susceptibility as families. In other families such as the *Urticaceae* (6—6), *Chenopodiaceae* (8—8), *Campanulaceae* (5—5), *Papaveraceae* (6—6), *Acanthaceae* (8—8), *Amaranthaceae* (10—8), *Bignoniaceae* (10—10), and *Ranunculaceae* (13—13), several species were inoculated as indicated by the first number in parenthesis after the family name. The second numeral indicates the number which

*) See a definition of these categories in the introduction.

became infected. In the *Cruciferae* (23—23), *Leguminosae* (91—89), *Euphorbiaceae* (16—14), *Malvaceae* (29—26), *Umbelliferae* (17—17), *Asclepidaceae* (19—17), *Labiatae* (23—12), *Plantaginaceae* (18—16), *Solanaceae* (18—17), and *Compositae* (60—54) a large number of species were available for inoculation. All inoculated species of the *Urticaceae*, *Chenopodiaceae*, *Campanulaceae*, *Papaveraceae*, *Acanthaceae*, *Bignoniaceae*, *Ranunculaceae*, *Cruciferae*, and *Umbelliferae* were infected, and solely on the basis of the limited number of used one might conclude that these families are very susceptible to *S. macrosporum*. In the *Leguminosae*, *Amaranthaceae*, *Euphorbiaceae*, *Asclepidaceae* and *Plantaginaceae* only 2 of the species were uninfected. In the *Solanaceae*, *Malvaceae*, *Compositae* and *Labiatae* 1, 3, 6 and 9 species, respectively, remained uninfected. In most of the other families also the percentages of infection were high. In the *Leguminosae* all 31 species of *Cassia* were susceptible, as well as all but 2 of the 18 species of *Plantago* in the *Plantaginaceae*. The high susceptibility of the *Leguminosae* to *S. macrosporum* is not surprising inasmuch as species of this family are the hosts of a fairly large number of *Synchytrium* species. Despite the positive evidence noted above, however, I do not think definite conclusions on relative family susceptibility can be drawn at this time, because the number of species tested is too small to be very significant.

The degree of abortion of the parasite and galls in the 27 species noted previously varied greatly in different species. In some the parasite and host cell died shortly after infection with the result that only microscopic unicellular dots were visible on the host leaves. In others the parasite attained considerable size before dying, and in such instances fairly distinct and large galls were formed. These species may be regarded, therefore, as susceptible to infection but resistant in varying degrees to the development of the parasite.

The degree of infection varied considerably in the most susceptible families. In the *Plantaginaceae*, for instance, most infections were sparse although some species were inoculated as much as 20 times. In the *Leguminosae*, on the other hand, the majority of infections were dense. Furthermore, the degree of infection in the susceptible species was not correlated with the density or total amount of inoculum used. The latter was kept as uniform as possible, yet the degree of infection varied markedly. Leaves of *Ambrosia trifida*, for instance, which are densely infected in nature, were inoculated 8 times but only 22 galls and resting spores developed. I estimate that more than a million planospores were placed directly on the seedling leaves of this host. Also, it should be noted here that seedling leaves of *Cirsium palustre* and other susceptible species were densely infected on one occasion, but when the experiment was

repeated no infection occurred although the conditions were apparently the same.

Accordingly, the factors involved in successful infection under laboratory and greenhouse conditions are not clearly understood at present. The inconsistencies have led me to consider the possibility that infection might be associated with the sexuality of the etiologic agent. Are the planospores of *Pycnochytrium* species like *S. macrosporum* obligate gametes incapable of parthenogenetic development which must fuse before they can infect a host cell, as *Kusano* (1930) postulated, and are all the resting spores zygotic in origin? Fusion of gametes occurs in *S. macrosporum*, but it is not known whether resting spores develop only from such fusions or from planospores as well. Within 30 minutes to an hour or more after discharge from the sporangia large numbers of planospores aggregate and become quiescent in dense (fig. 14) masses at various places in the mounts. Fusions usually, but not always, occur in such masses to form zygotes (fig. 15—19). The percentage of zygotes formed, however, is not very high under laboratory conditions so far as is known. In four separate mounts of small single sori of 195, 140, 200, and 140 sporangia, which produced approximately 39, 28, 40 and 30 thousand planospores, respectively, only 199, 140, 180, and 150 zygotes were counted — a slight fraction of one per cent. In mounts of several sori such as were used for inoculation, the number of zygotes was considerably higher. Nevertheless, the low percentage of zygotes formed is more in line with the low number of infections, resting spores and galls obtained on numerous hosts in my experiments. To test the suggestion that only zygotes are capable of infection, mounts of several sori with their discharged planospores were allowed to remain under cover slips on slides until zygotes were formed and most of the planospores had degenerated. These were then transferred to the leaves of several species which had been resistant to infection in spite of numerous inoculations of active planospores. Some of these became infected within two weeks, which substantiates to some degree the view that only zygotes are capable of infecting the host. However, the results obtained so far are too meager to warrant definite conclusions. Obviously, if only zygotes are infective fusions must occur abundantly in nature to account for the general and dense infections of the numerous hosts found at Cameron, Texas.

The ubiquity of *S. macrosporum* in host range and the variations which it may exhibit on different hosts have raised the question of its possible identity with *S. aureum*. As noted above *S. aureum* has been reported from most countries in the world and on 198 species in 123 genera of 34 families of flowering plants. It, also, develops only resting spores and has a life cycle similar to that of *S. macrosporum*. Furthermore, its resting spores vary greatly on different

hosts, and it induces marked variations in gall structure. On these grounds the two species might appear to be identical. However, except for Rytz's (1907, 1932) careful study of *S. aureum* in nature in Switzerland and his limited outdoor cross inoculations, the reports of its wide occurrence elsewhere are based on isolated collections, and no controlled experiments have been made with the various collections to determine their host ranges. As related previously, most collectors have identified their collections of *Pycnochytrium*-like species which induce composite galls and develop only resting spores as *S. aureum* without making host range and developmental studies. Until this is done it is not at all certain that the numerous collections labeled *S. aureum* relate to this binomial, and extensive host range studies will probably reveal the presence of biological races in this species. It is significant that *S. macrosporum* did not infect *Lysimachia nummularia* and *Prunella vulgaris* in spite of repeated inoculations. These species are two of the original hosts reported by Schroeter and Schneider (1869) for *S. aureum*.

Synchytrium macrosporum may turn out to be different cytologically from *S. aureum* when the latter species is better known in this respect. As shown in fig. 10, cleavage in the sorus of *S. macrosporum* occurs fairly early before many mitoses have occurred and usually delimits uninucleate segments or "protospores" as in *S. decipiens* (Harper, 1899) and *S. oxalydis* (Karling, 1955). The nuclei then divide rapidly to produce multinucleate sporangia (fig. 11). As noted above, the cytology of *S. aureum* is poorly known, but according to Rytz's (1907) figures most of the cleavage segments are multinucleate. However, it is quite possible that his figure relates to a later stage, and that he did not observe a protospore stage. Studies are now being made on the host range and cytology of an European collection of *S. aureum* to compare it more accurately with *S. macrosporum*.

It is quite possible also that many of the *Pycnochytrium* or short-cycled species, including *S. lepedii*, *S. erigerontis*, *S. lythrii*, *S. sambuci*, *S. parthenocissi*, *S. duchesnae*, *S. corni*, *S. asterum*, *S. cocculi*, *S. cardiospermi*, *S. ellicicola*, *S. liquidambaris*, *S. gonoboli*, *S. carpinii*, *S. clematidis*, *S. bignoniae*, *S. erectites*, *S. polygoni*, *S. callicarpi*, *S. tecomae*, *S. mitchellae*, *S. trachelospermi*, *S. fraxini*, *S. ulmi*, and *S. violae*, which Cook (1949, 1953) reported from Louisiana may be identical with *S. macrosporum* or it with them. I have succeeded in infecting the hosts of all of Cook's species, except those of *S. ulmi* and *S. mitchelli*, with *S. macrosporum* and induced thereby very similar reactions in the hosts. Cook's species occur in fairly close geographical proximity to *S. macrosporum*, and it is quite likely that they extend westward from Louisiana into Texas. It is to be noted, however, that so far none of his species, except *S. erigerontis*, have

been found occurring on the same hosts as *S. macrosporum* in nature. Cook described his species briefly but made no developmental or host range studies. I made a careful study of his herbarium material and his fixed and stained sections of these species and found that they are fairly similar in spore sizes and shapes as well as in the reactions they induce in their respective hosts. At least, the difference which they exhibit are no greater than those of *S. macrosporum* on different hosts. However, the exact identity and relationship of Cook's species with *S. macrosporum* and *S. aureum*, remain to be shown.

Summary.

Synchytrium macrosporum is a member of the subgenus *Pycnochytrium* which develops large resting spores in composite galls and parasitizes a large number of plants in Texas. Under greenhouse conditions it has proven to be ubiquitous in host range. To date 811 species and seven varieties in 576 genera of 166 families of plants, including fungi, algae, liverworts, mosses, ferns gymnosperms and angiosperms from tropical, subtropical, and temperate zones as well as annuals, perennials, shrubs, and trees, have been inoculated with planospores from a monoplanospore stock. Among these, 707 species in 509 genera of 141 families became infected in varying degrees of intensity. No infections occurred in fungi, algae, liverworts, mosses and ferns.

Among the infected plants, 610 species, 371 genera and 75 families are new hosts for *Synchytrium*.

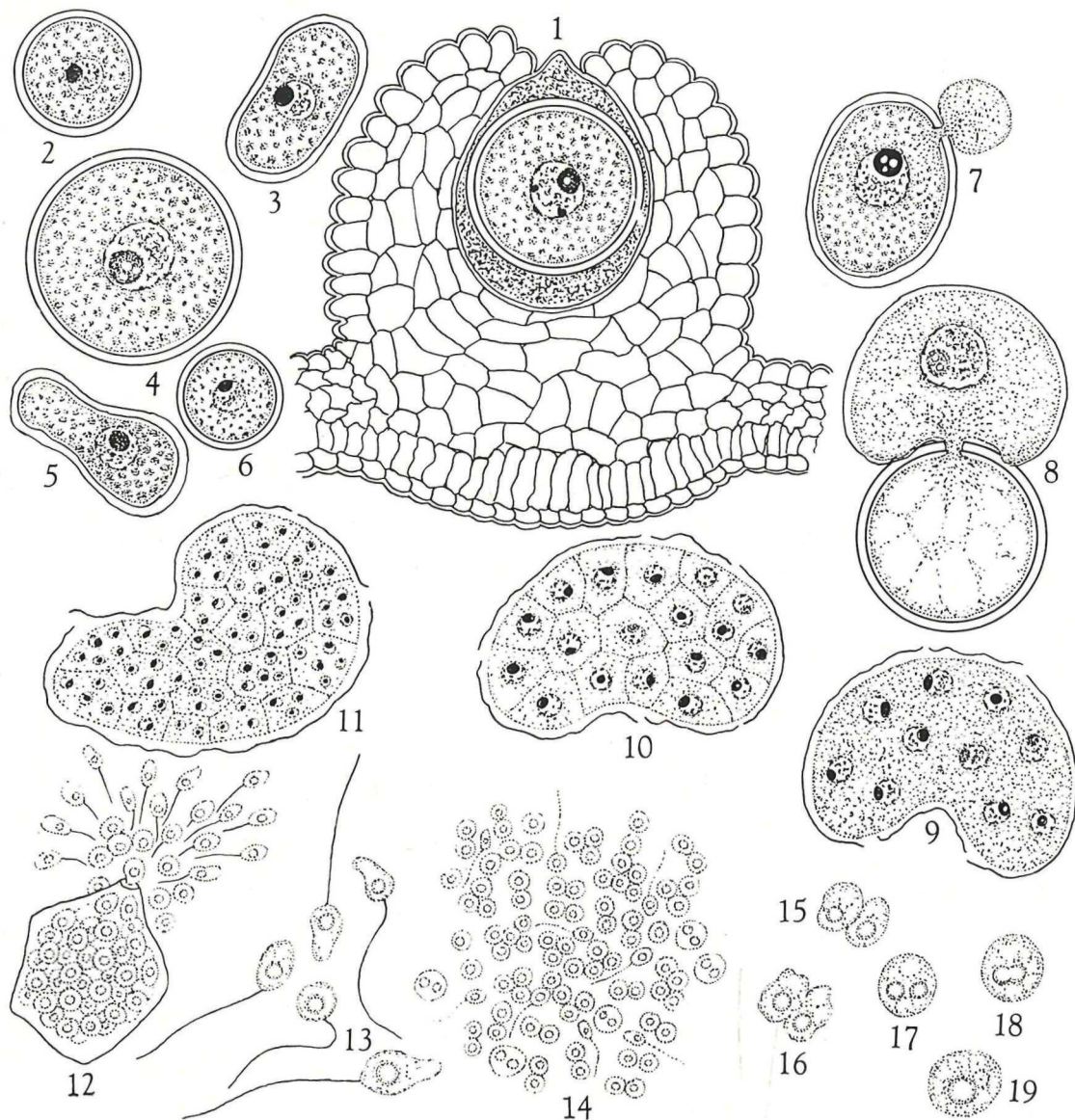
In the various categories of infection 165 species were sparsely infected, 91 fairly, 175 goodly, and 255 densely infected. In 27 of the infected species the parasites and galls aborted at various stages of development.

Among the families in which a large number of species were tested the *Cruciferae*, *Leguminosae*, *Cucurbitaceae*, *Solanaceae* and *Compositae* were most susceptible under the conditions of these experiments.

The degree of infection was not closely correlated with the number of times of inoculation or the total amount of the inoculum. The inconsistencies in results obtained suggest that success of infection might be associated with the sexuality of the etiologic agent.

Bibliography.

- Cook, M. T. 1945 a. Species of *Synchytrium* in Louisiana. I. Description of species found in the vicinity of Baton Rouge. *Mycologia* **37**: 284—294.
— 1945 b. Species of *Synchytrium* in Louisiana. II. Species of Louisiana *Synchytrium*. *Mycologia* **37**: 571—575.



- 1945 c. Species of *Synchytrium* in Louisiana. III. The structure and development of the galls. *Mycologia* 37: 715—740.
 - 1949. Species of *Synchytrium* in Louisiana. V. A new species on *Sambucus canadensis*. *Mycologia* 41: 24—27.
 - 1953. Species of *Synchytrium* in Louisiana. VIII. New species. *Mycologia* 45: 101—114.
- Harper, R. A. 1899. Cell division in sporangia and asci. *Ann. Bot.* 13: 467—525.
- Karling, J. S. 1953. *Micromyces* and *Synchytrium*. *Mycologia* 45: 276—287.
- 1955 a. Prosori in *Synchytrium*. *Bull. Torrey Bot. Club* 82: 218—236.
 - 1955 b. Galls induced by *Synchytrium* and their relation to classification. *Amer. Jour. Bot.* 42: 540—545.
 - 1956. New and unidentified species of *Synchytrium*. — III. *Sydowia* 10: 243—254.
- Kusano, S. 1930. The life history and physiology of *Synchytrium fulgens* Schroet., with special reference to its sexuality. *Jap. Jour. Bot.* 5: 35—132.
- Poole, D. D. 1934. Red stem gall of castorbean caused by *Synchytrium* in Texas. *Pl. Dis. Reporter* 38: 728.
- Rytz, W. 1907. Beiträge zur Kenntnis der Gattung *Synchytrium*. *Centralbl. Bakt. Parasitenk. u. Infekt.* II, 18: 635—655, 799—825.
- 1932. Beiträge zur Kenntnis der Gattung *Synchytrium*. III. Infektionsversuche mit einem *Synchytrium* vom Typus *S. aureum* Schrott. *Deut. Gesell.* 50: 463—471.
- Schroeter, J. and W. G. Schneider. 1869. Übersicht der in Schlesien gefundenen Pilze. *Jahresb. Schles. Gesell.* 47: 140—159.

Explanation of Plate XXIII.

Fig. 1—19. *Synchytrium macrosporum*. Fig. 1. Large composite gall on leaf of *Xanthium strumarium*. Fig. 2—6. Variations in the sizes and shapes of resting spores from different organs of *X. strumarium*. Fig. 7, 8. Germination stages of resting spores. Fig. 9. Multinucleate sorus. Fig. 10. Sorus after cleavage into predominantly uninucleate segments. Fig. 11. Sorus with multinucleate sporangia. Fig. 12. Discharge of planospores. Fig. 13. Planospores. Fig. 14. Aggregation of planospores. Fig. 15—19. Stages in the fusion of gametes to form zygotes.

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Jahr/Year: 1960

Band/Volume: [14](#)

Autor(en)/Author(s): Karling John S.

Artikel/Article: [Inoculation Experiments with Synchytrium macrosporum.
138-169](#)