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INTRODUCTION

The fungus *Wallrothiella arceuthobii* [1] has the distinction of causing the only disease of the leafless mistletoes so far described. Comparatively few botanists have seen this interesting fungus either in nature or in museums, and all reference to it has been omitted from works dealing strictly with plant diseases. The fungus was apparently never collected again from the region where it was originally discovered, and no record exists of preserved material from the place of its second discovery. The discovery of the fungus by the writer in the Northwest adds a new interest to its study, especially since it is found to be so abundant as to have some economic significance.

Owing to the fact that the fungus has only been reported twice and from widely separated stations, its literature is very meager. It was originally discovered by Peck,[2] who published a short account of it under the following name and description:

> *Sphaeria arceuthobii*, n. sp.
>
> Perithecia small, densely caespitose, oblong or cylindrical, very obtuse, shining black; asci subclavate, fugacious; spores crowded, globose, colorless, .00016″ in diameter.
>
> Capsules of *Arceuthobium pusillum*. Forestburgh. Sept. (Plate I, figs. 10–14).
>
> It forms little black tufts, crowning the fruit at the tips of the stems and branches. I have not seen it on the staminate plant. I am not fully satisfied that the generic reference is correct, as the perithecia seem to be mouthless. It is interesting to observe the extent to which parasitism prevails. The Arceuthobium is a parasite on the spruce, this fungus is parasitic on the Arceuthobium, and in a few instances a third parasite, a minute white mold, was seen on the perithecia of the fungus.

The second discovery of the fungus was by Wheeler [3] in the Upper Peninsula of Michigan, who reports it as follows:

> I found that the mistletoe was also attacked by a fungous parasite, which must have a tendency to check the spread of this pest. Each fruit is attacked at its apex by the fungus *Wallrothiella arceuthobii*, Peck, and, of course, destroyed.

Both Peck and Wheeler published some excellent drawings of the fungus, from which a very good idea of the character of the disease may be obtained.

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[1] If the system of classification of Engler and Prantl is employed, the fungus would be referred to Rosellinia. (Engler, Adolf, and Prantl, K. A. E. Die natürlichen Pflanzenfamilien. T. 1, Abt. 1, p. 394, 400, 404, fig. 258, A, B. Leipzig, 1897.)

[2] Peck, C. H. Report of the botanist. *In* 27th Ann. Rpt. N. Y. State Mus. Nat. Hist. 1873, p. 111, pl. 1, fig. 10–14. 1875.

[3] Wheeler, C. F. The geology and botany of the Upper Peninsula experiment farm. *In* Mich. Agr. Exp. Sta. Bul. 186, p. 27–28, 4 pl. 1900.

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HOSTS

The interest arising from the remarkable habit of this fungus of attacking and destroying the immature fruits of *Razoumofskya pusilla* (Peck) Kuntze (*Arceuthobium pusillum* Peck) on the eastern black spruce (*Picea mariana*) has led the writer to search most diligently for it on western species of Razoumofskya. The fungus was not found in any region of the Great Lakes States, although the mistletoe of the spruce was abundant and much material was examined. In the West the search has been more successful. The fungus was first collected on *Razoumofskya douglasii* Englm. (Pl. LV, fig. 1) in the vicinity of Como Lake in the Bitterroot Mountains, Montana. The only tree found bearing infected plants stood in a clump of "left-overs" on a cutting area of the Latchem Lumber Co. The mistletoe is so very abundant in this region and suppresses the Douglas fir (*Pseudotsuga taxifolia*) to such an extent that this tree, according to Supervisor White, of the Bitterroot National Forest, is sometimes omitted altogether from the estimate of the prospective cut. Practically the same conditions prevail throughout the entire Bitterroot and Missoula River Valleys and adjacent regions. It has always been a rule of the writer, in regions of a heavy infection by *R. douglasii*, to look for the small, closely related mistletoe designated by Engelmann "*Razoumofskya douglasii*, var. *abietina*," on *Abies grandis* and *A. lasiocarpa*. Experience has shown that this mistletoe is more likely to occur when its hosts are in the vicinity of the Douglas-fir mistletoe. Whatever conclusions may be drawn from this as to the probable relationship of the mistletoe on *Abies* spp. with the one on *Pseudotsuga* spp., the surmises as to the presence of the former were correct in the present instance.

The mistletoe was discovered once on *A. grandis* by the large spreading or upright brooms. The tree, standing not more than 100 feet from a Douglas fir which supported three immense brooms of *R. douglasii*,[1] was felled and the mistletoe plants carefully examined. A few of the plants, which were pistillate, were found to be infected by *W. arceuthobii* (Pl. LV, fig. 2). On another portion of the same area the fungus was discovered on a few plants (Pl. LV, fig. 3) growing deep within a large broom on *A. lasiocarpa*. Two other mistletoe-infected trees of this species were cut, all that were found in the region, but the parasite was not attacked by the fungus. A search in other sections of the Bitterroot Valley resulted in finding the mistletoe on the grand and alpine firs, but the fungus was not present. At the head of Rattlesnake Creek, a small stream flowing into the Missoula River at Missoula, the fungus was discovered on a small mistletoe (Pl. LV, fig. 4) growing on *Picea engelmanni*. This is the first report of a mistletoe occurring on a spruce in the North-

[1] The brooms caused by this mistletoe are sometimes very large and frequently cause the death of the entire crown above. The infections of no other mistletoe initiate greater and more frequent brooming than do those of *R. douglasii*. For this reason it is one of the most serious parasites of the entire genus.

west. It is apparently the same as that described by Engelmann on spruce from the Sierra Blanca Mountains in northern Arizona under the name "*R. douglasii*, var. *microcarpa*." A single collection of what is apparently the same mistletoe on spruce was made from a recently fallen tree on a cutting area near Laclede, Idaho. The parasite was, however, in a healthy condition. The Douglas-fir mistletoe was found in each of the two last-named regions. The fungus material in all the foregoing cases was very scanty. It is believed, however, that a more protracted search will result in finding the fungus more abundantly on the Douglas-fir mistletoe.

In order to test the ability of the fungus to attack other mistletoes, infected plants of *R. douglasii* were bound in contact with pistillate plants of *R. americana*, the mistletoe of the lodgepole pine (*Pinus murrayana*). To prevent accident, the experiments were protected by binding cheesecloth loosely about the stem supporting the mistletoe, completely inclosing the plants but not interfering with their vital functions. In all, four such experiments were made during the month of October, 1913. Since pollination had already taken place in the early spring, it was inferred that the fruits of the lodgepole-pine mistletoe would mature normally if infection did not occur. In order to have fully mature plants on the same stem for purposes of comparison, small tufts just below the inclosed ones were shielded by a circular piece of thick white cloth tied just above the tuft and hanging down in the form of a loose umbrella. This would not prohibit the circulating spores from coming up under the shield, provided they escaped from the cheesecloth net, but would lessen the chances of inoculation. Furthermore, owing to ascending air currents, spores of fungi usually travel upward or at least not directly downward when starting from an elevated point. Other experiments were initiated on the lodgepole-pine mistletoe by crushing in water a number of mature perithecia and thoroughly spraying the mixture containing spores over a few pistillate plants. To prevent the plants being knocked off during the winter, they were also protected by cheesecloth. These experiments were visited in the latter part of November, 1914. The results were positive. As shown in Plate LV, figure 5, not only had the fruits of the lodgepole-pine mistletoe which were inclosed with the infected plants from the Douglas fir become infected but very thoroughly so. Every fruit bore at its apex the little shiny black tufts of the perithecia of the fungus. One fruit shown to the right in the middle figure of the sprayed plants seemed to have escaped early infection and to have attained nearly a normal size, but, nevertheless, succumbed to the parasite. The tufts of mistletoe just below the infected ones, which were shielded from above, did not become infected and produced normal mature seeds, which were being expelled at the time the experiments were discontinued. The perithecia of the fungus on

R. americana contained mature spores; hence, the life cycle of the fungus in the seed capsule is complete in the fall of the second year coincident with the time required for the ripening of the seeds of the host.

Soon after the conclusion of the experiments, a swamp area in the Kaniksu National Forest, Idaho, scatteringly timbered by lodgepole pine, was visited. The trees were heavily infected with the mistletoes characteristic of this tree. A close examination of the mistletoe plants showed them to be uniformly attacked by the fungus throughout the entire area. So abundant was the fungus that very few of the pistillate plants on any of the trees had escaped attack. This area has been a fruitful source of investigation and a number of important facts have been gathered.

SIGNIFICANCE OF THE FUNGUS TO THE TAXONOMY OF ITS HOSTS

The hosts of *W. arceuthobii*, so far as known at present, are as follows:

Razoumofskya pusilla (Peck) Kuntze on *Picea mariana.*
R. americana (Nutt.) Kuntze on *Pinus contorta.*
R. douglasii (Engelm.) Kuntze on *Pseudotsuga taxifolia.*
R. douglasii, var. *abietina* Engelm., on *Abies grandis* and *A. lasiocarpa.*
R. douglasii, var. *microcarpa* Engelm., on *Picea engelmanni.*

A glance at the foregoing list shows a very interesting association of mistletoes. The form on *A. lasiocarpa* (Pl. LV, fig. 3), as known to the writer, in point of morphology, color, and the time of maturity of pollen and seed, coincides with the form on *A. grandis* (Pl. LV, fig. 2). The mistletoe on *Picea engelmanni* is slightly smaller, often very much so (Pl. LV, fig. 4), but its other characteristics are the same. Comparing these mistletoes with *R. douglasii* and *R. pusilla*, there is at once a marked similarity among all five. They do not vary widely in form and color of the stems. There is some variation in point of distribution of the individual plants on the branch, whether aggregated or appearing singly. Any one mistletoe, however, may exhibit both or either condition. The staminate flowers of all five are a deep rich purple. No other species of the genus possesses this character to such a marked degree. All five bloom at the same time in the same latitude and exposure, and the seeds ripen and are expelled in the same month.

The question naturally arises, What is the true taxonomic position of these mistletoes? Engelmann recognized the close affinities of the small forms on spruce and fir to *R. douglasii* and named them varieties of that species. The isolated and infrequent occurrence of these small mistletoes on spruce and fir in the West should throw some light on their probable relationships. If they are specifically distinct, they should show greater activity in attacking their hosts. As it is, a single tree will bear a few plants (broom formation) and the most diligent search on the same host for miles around will not reveal a second infection. The discovery of *W. arceuthobii* on those forms or species of the same genus in the West which are most similar to the eastern-spruce mistletoe may have some bearing on the taxonomic position of this group of mistletoes. The occurrence of the fungus on *R. americana*, a very definitely associated and characteristic species with no affinity whatever with the mistletoes of the Pseudotsuga-Abies-Picea group, indicates a cosmopolitan character for the disease. To determine this point, the fungus has been introduced into clumps of the yellow-pine and larch mistletoes. These experiments are now under way.

MORPHOLOGY

Photographs of *W. arceuthobii* have not been published. For this reason detail enlargements from the original negatives of infected and uninfected fruits of *R. americana* are reproduced in Plate LVI, figures 1 and 2. Reproductions of photographs of the fungus (natural size) on all its western hosts, so far as known, are likewise shown (Pl. LV, fig. 1–5). These illustrations indicate very clearly the interesting habitat of the fungus. A study of the enlargements (Pl. LVI, fig. 2) shows the shiny black perithecia densely crowded at the apex of the fruit. Varying numbers, sometimes as many as 40 or more, have been counted springing from the brownish black stroma within the seed capsule. The general shape of the perithecia is that of an oblong cylinder. Usually, however, they are slightly enlarged at the free ends and very abruptly rounded. The hyphæ composing that part of the stroma from which the perithecia take their origin are densely compacted, brown or black, with thick walls. Deeper within the capsule, the brown color is not so conspicuous, although the mycelium is generally brownish. The outer walls of the perithecia are uniformly smooth; very rarely a 4- to 6-celled projection is present. The crowded condition of the perithecia often gives them the appearance of being partially embedded in the stroma. The wall between two perithecia when densely crowded may be very thin and appears to be occasionally ruptured on the escape of the spores from the asci. The asci show considerable variation in shape, owing principally to their crowded condition, but when free are uniformly pear- or club-shaped, with fairly long pedicels. Probably in no other species of the order is the early disappearance of the wall of the ascus so characteristic. Before the spores have reached maturity or at least before they have assumed the normal color of mature spores, the ascus wall disappears. The ascus is probably ruptured at the apex by the pressure of the developing spores within. That a considerable pressure must be exerted against the walls of the ascus is shown by the fact that the spores when free are normally spherical, but within the ascus they are often bluntly angular. They often persist in clumps after their escape from the ascus. The asci vary but very little in size. The measurements (Zeiss filar micrometer with No. 12 compensating ocular and 8 mm. n. a. 0.65 apochromatic objective) show a close uniformity to those of the type material. The measurements of the asci from fresh material range as follows: 22.3, 22.8, 24, 24.4, 24.8, 25.2μ in length. Evidently considerable shrinkage takes place in stained material, the stained asci measuring 16.5, 16.9, 19.8, 21.9μ in length. The average breadth of the ascus is 3μ. The ascus contains eight unicellular, globose, thick-walled spores. The spores are at first hyaline, but nearing maturity they assume a very conspicuous brown-black color. The color of the mature spores is assumed after their escape from the ascus. The preliminary color changes may, however, take place within the ascus. Prof. Peck, in his original description, states that the spores are hyaline; still he represents, in his illustration (Pl. LV, fig. 14), four mature spores which are black. The change from a hyaline to the pronounced brown or black color was evidently recognized, since "an ascus containing young spores" is represented, after which "four mature spores" that are black are represented. An examination of some of the type material kindly sent the writer by Mr. H. D. House shows the spores in all stages of development and varying from hyaline to black. The dimensions of the spores in the type material are found to agree with the measurements of the spores in the western fungus, which range as follows: Unstained and out of ascus, 3.7, 4.5, 4.9, 5.3, 5.8, 6.2μ; stained, 4.1, 4.5, 4.9, 5.3, 6.2μ. Previous accounts give the diameter of the spores as "about 4μ." The paraphyses are filamentous, short, and very inconspicuous.

All the asci of a single perithecium do not mature their spores together; instead, at the time mature spores are escaping from the perithecium, young asci showing early stages of spore differentiation are discernible. There is consequently a gradual dissemination of the spores, governed to an extent by the humidity of the atmosphere. The opening through which the spores escape is directly at the apex and is formed by the free ends of the thick-walled hypha composing the walls of the perithecium. The cells composing the tips of these hyphæ seem to possess certain hygroscopic properties, as they are observed to bend in or out on the addition or absence of moisture.

BIOLOGY

In what manner the spores of *W. arceuthobii* are conveyed to the pistillate flower of the mistletoe in nature the writer is not in a position to state definitely. Since isolated infections occur promiscously on different branches of the same tree or on different trees in the same locality, it is evident that the wind is the chief factor in spore dissemination. A fact observed among the infected plants on lodgepole pine of the swamp area previously mentioned supports this view. The area lay with its long axis in the direction of the prevailing winds of the Priest River Valley. An examination of the trees bearing infected plants showed that they were more or less in line with each other and extended in the direction of the most constant winds. On either side of the most heavily infected area the trees did not support infected plants, although the mistletoe was abundant. Furthermore, large compact brooms always bore the greater number of infected plants on the windward side.

The writer has recently determined that insects to a certainty play a rôle in the pollination of these mistletoes. Hymenopterous insects are chiefly in evidence, but those of other orders are also known to promote pollination. During 1914 grasshoppers in great numbers came out of the Hangman Creek Valley near Spokane and fed upon blooming staminate plants of the large mistletoe growing in profusion on yellow pine of the bench lands. These insects seemed to select only the flowers of the staminate plants for food; but, swarming over the pistillate plants, they deposited some of the pollen that adhered to their bodies. It is as easily possible that the spores of the mistletoe fungus are in a minor degree transported in a like manner. Rain dropping from infected to uninfected plants or running down the pendent branches and dropping off at the tips of the mistletoe plants is probably a factor in distributing the disease on any one tree or broom. It so happened at the field station that a number of newly collected infected capsules were left overnight and a portion of the following day on a glass slide under the microscope. An examination of the slide showed that a number of spores had been expelled and lay in a ring about ½ mm. away from the apex of the perithecium. Evidently there is a slight expulsion of the spores under favorable conditions. This came as a surprise, as the stiff ends of the hyphæ forming the perithecial wall seem to open with difficulty. A number of perithecia collected from fallen capsules in the spring still contained numerous spores. The early disappearance of the ascus within the perithecium precludes any expulsion from this source. The force must arise from the continual maturing and crowding of the spores toward the outward end of the perithecium. Under favorable conditions this pressure may become sufficient to force the spores out through the aperture. It has already been indicated that a pressure seems to exist within the perithecium. This force, though weak, may still be sufficient to cause the spores to land on capsules of the same plant that escaped previous infection.

The spores of the fungus are beginning to ripen and to be expelled from the perithecia in the latitude of northern Idaho about the end of November and are capable of germinating immediately. The method of penetration of the germ tube of the spore into the developing fruit of its host has not as yet been observed. Since a considerable period elapses between pollination and the time actual fertilization takes place in the host, it is quite possible that the germination of the fungus spore coincides with the advance of the pollen tube toward the embryo sac. This would enable the germ tube of the spore to travel toward the ovule of its host by a line of least resistance. In early spring, or at the time actual fertilization of the mistletoe takes place, those tissues destined to become the seed are, in infected plants, observed to be completely filled or destroyed by the mycelium of the fungus. After infection, the young seed capsule never increases much in size and is entirely dominated by the parasite. The diseased capsules usually fall away during late winter and early spring, which allows time for the infection of the pistillate plants. The drain on the vigor of the mistletoe plant, if all the young capsules are infected, is such that it may also succumb and fall. If only one or two capsules of the plant are infected, it will remain intact, maturing the uninfected fruit of the season and fruiting again the following year. Usually, however, the infection of all the fruits of a mistletoe colony or of all the plants of a broom is so complete that few or no seeds mature.

ECOLOGY

All collections so far made of the fungus have not been at an elevation much greater than 3,600 feet, although its hosts may range well up toward the timber line. This indicates a preference for the conditions of the lower levels, where it is not so much exposed to fluctuations of warmth and moisture. The latter factor is probably of greater influence. Until the fungus is found elsewhere it may be said to prefer the North Temperate regions. Forestburg, N. Y., its first known station, is about on a line with the Upper Peninsula of Michigan, the region of its second discovery, and northern Idaho, where it was last found. This is its geographical and climatic range at present. Developing either on exposed or shaded plants, the fungus seems to favor those growing in shaded positions, such as the inner parts of brooms. Absence of direct sunlight may promote development, but, after the capsule becomes infected, direct sunlight can not have much influence on the maturing of the fungus. The germination of the spores would probably be promoted by an absence of direct sunlight. Warm fall rains, such as occur in northern Idaho, are undoubtedly very favorable to the development and spread of the disease, since in this region the fungus has been found most abundant. In damp river bottoms or on the borders of swamp areas the lodgepole-pine mistletoe, which frequently occurs in profusion in such a habitat, is very likely to be attacked by the fungus. Prof. Peck [1] does not record the conditions under which the fungus was growing at Forestburg, N. Y., but presumably it was a region of considerable humidity. The Upper Peninsula of Michigan, where Prof. Wheeler collected the fungus, is a region of numerous swamps and abundant atmospheric moisture. In view of the fact that the fungus is parasitic on the rather succulent capsule of the mistletoe, atmospheric humidity should not greatly interfere with its life functions, except probably in the initial stages of spore germination. The fungus should thrive on the larch

[1] Peck, C. H. Op. cit.

mistletoe, provided it is susceptible to attack, owing to the usually damp condition of the compact moss-covered brooms. It remains to be seen under just what conditions the fungus will propagate itself. To this end it is being introduced into mistletoe regions of all types of exposure.

The ease with which the fungus seems to infect its host leads the writer to believe that it may be of some economic importance in the control of certain species of mistletoe, at least for small areas. For a mistletoe species to propagate itself, it must produce seeds abundantly, in order to insure the infection of the young growing forest. The proportion of mistletoe seeds actually causing infection to the total number produced is very small indeed. Some fall to the ground; some fall on plants not susceptible; most of them fall on parts of the host too old to be penetrated by the young root of the seed. With the exception of a few rare instances, where infections have been known to occur on wound tissue of mature parts of trees, the writer has not yet found either in nature or by actual inoculation a seed taking effect on any part of its host other than the more tender shoots or their equivalents in tenderness of bark and then only when the primary sinker found its way to a leaf scar, leaf scale, or other more vulnerable irregularities of the substratum. Again, the seed must fall in such a position that the protruding root may directly find its way under a leaf scale or be sheltered by the thick bunch of needles at each node of growth or at the base of a leaf or leaf sheath; otherwise it may fail of its purpose. The seed may germinate and expend its stored materials in the production of a primary root of half an inch or more, but before the growing point can penetrate the stem, provided it is in such a position as to be drawn toward it, the young hypocotyl is exhausted. Very few seeds cause an infection when not very favorably located or directly through the smooth epidermis possessing a suberized layer.

With the exception of the small forms mentioned in this paper most of the members of the genus are prolific seed producers. If so few seeds find a vulnerable point on their hosts even with an abundant production of seed, so much less will the chances of infection be if the seed production is lessened. An estimate of the number of seed that should have been produced by the lodgepole-pine mistletoe on a small broom was about 400. Not a single mistletoe seed on this broom had reached maturity. All were attacked by the fungus. The biologic control of organic agents destructive to plant life is in most cases a thing very much in the realm of fancy. It seems, however, that a fungus of the nature of *W. arceuthobii* may be introduced into mistletoe regions possessing certain climatic conditions with the prospect of reducing the seed production of these parasites, and thus reducing the damage caused by the mistletoe.

SUMMARY

Wallrothiella arceuthobii, a fungous parasite on the false mistletoes of conifers, is reported for the first time in the West.

This fungus, first collected by Prof. Peck in New York and again by Prof. Wheeler in the Upper Peninsula of Michigan, was considered a very rare species until it was found to be of common occurrence in parts of Montana and Idaho.

Several new facts pertaining to the morphology and general behavior of the fungus are established.

Its host range has been greatly extended.

The significant fact that the fungus is found in the West on those forms of species of the same genus which are most similar to the eastern black-spruce mistletoe, its host in the East, is thought to have some bearing on the taxonomic position of this particular group of mistletoes.

Its parasitism on the false mistletoes is found to be of great significance in the control of these parasites, which are so destructive to many western conifers.

PLATE LV

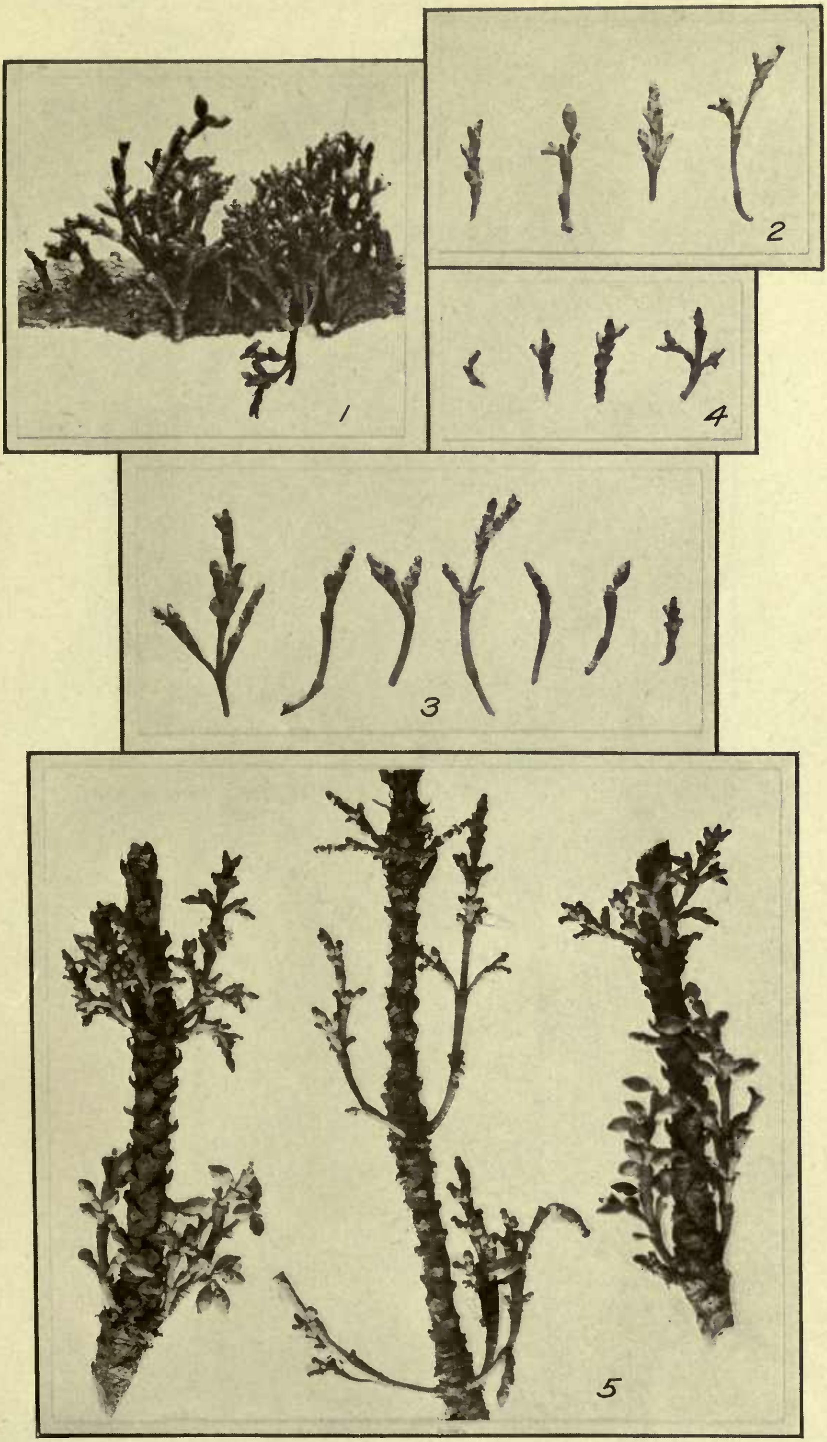
Fig. 1.—*Razoumofskya douglasii* on *Pseudotsuga taxifolia*, infected with *Wallrothiella arceuthobii*. Note that two capsules escaped infection. Natural size.

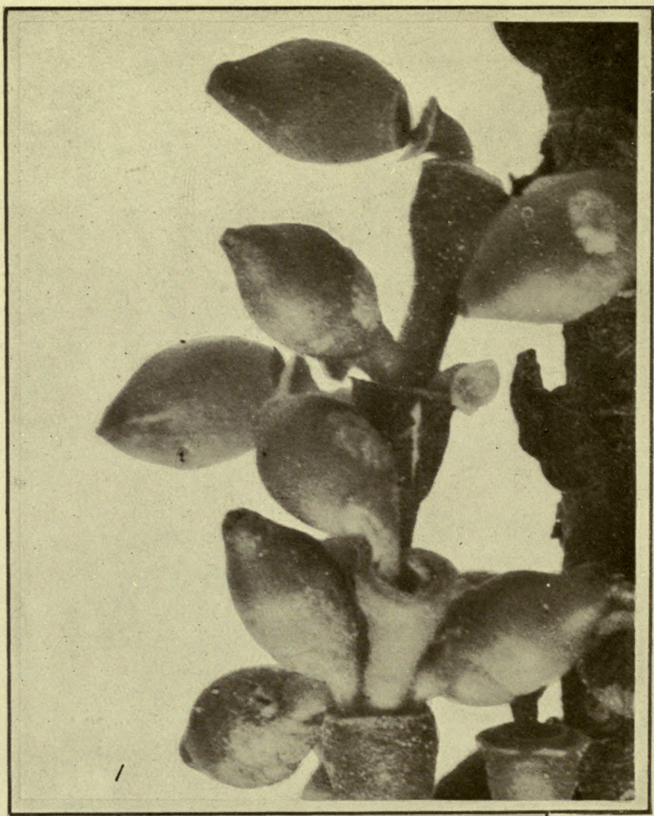
Fig. 2.—*R. douglasii*, var. *abietina*, on *Abies grandis*, infected with *W. arceuthobii*. Natural size.

Fig. 3.—*R. douglasii*, var. *abietina*, on *Abies lasiocarpa*, infected with *W. arceuthobii*. Natural size.

Fig. 4.—*R. douglasii*, var. *microcarpa*, on *Picea engelmanni*, infected with *W. arceuthobii*. Natural size.

Fig. 5.—Left and right figures showing infection of *R. americana* with *W. arceuthobii* by infected plants of *R. douglasii*. The plants at lower part of figures are normal and fully mature. The middle figure shows infection of *R. americana* by spraying upon the plants a mixture containing spores of *W. arceuthobii*. Natural size.





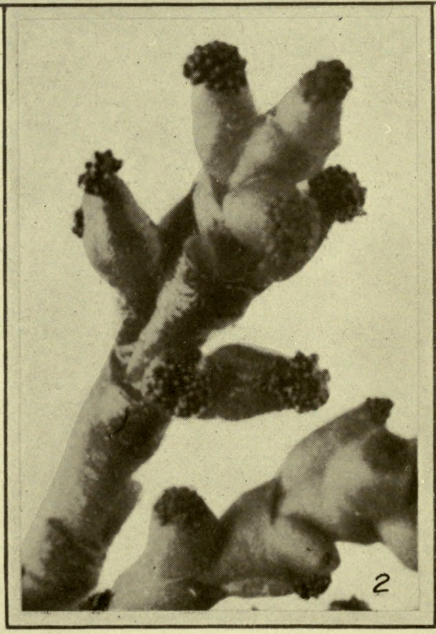


PLATE LVI

Fig. 1.—Enlargement of the normal fruits of *Razoumofskya americana* shown in Plate LV, figure 5.

Fig. 2.—Enlargement of the diseased fruits of *R. americana* infected with *Wallrothiella arceuthobii* shown in Plate LV, figure 5. Both plants are enlarged to the same scale and show the proportionate size of infected and normal mature fruits.

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