COMPARATIVE SUSCEPTIBILITY OF ONION VARIETIES AND OF SPECIES OF ALLIUM TO UROCYSTIS CEPULAE

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INTRODUCTION

Most pathogenic fungi show a distinct variation in their ability to infect different varieties of their host plant. Such a difference in varietal susceptibility is usually the starting point for the breeding or selection of resistant varieties, which is the most effectual method for the control of plant diseases. With respect to onion smut, however, it has never been shown that there is any difference in the susceptibility of the numerous varieties under cultivation; in fact, no very comprehensive variety tests with this objective in view have been conducted. Walker and Jones (12) tested a few varieties, and Whitehead (13, p. 449) in England tested 21 varieties of onions and 11 varieties of leeks (Allium porrum), but none showed resistance. Nevertheless, since there were numerous other varieties which had not been tested, so far as was known to the writer, it appeared worth while to collect seed of as many varieties as could be obtained and test them comparatively in the hope that some of them might show a degree of resistance which should warrant crossing and selection work.

The genus Allium, to which the cultivated onion belongs, is a large genus of some 250 species which are widely distributed over the earth. Urocystis cepulae was first reported on Allium cepa (4, 8) in 1857, in eastern Massachusetts. As early as 1881 (7) it was also reported on A. porrum (leek), in France. Cotton (3) reported it as more serious on this species than on onion in England. Clinton (2, p. 451) reported it as occurring on A. nevadense in the far West of the United States. Quite recently Zillig (14, p. 57) has also reported infection of A. fistulosum L., A. globosum Red., and A. odorum L. Thus this fungus has been found on five species of the genus besides A. cepa.

A more thorough knowledge of the extent of its host range is desirable for at least three reasons:

1. It might give us a clue to the origin of onion smut. This disease seems to have been noticed for the first time on onions in New England about the middle of the last century. Where it came from and where it had passed the preceding centuries, nobody seems to know. There is the strong probability that it came from some native American susceptible Allium; yet, with the exception of

1 Received for publication October 22, 1924; issued, September, 1925.
2 Reference is made by number (italic) to "Literature cited," p. 286.
3 After this paper had been forwarded by the writer for publication, a letter was received from Doctor Zillig stating that he had also been able to infect A. cyaneum Reg., A. flavum L., A. huteri Sund., A. hymenorrhizum Ledeb., and A. obliquum L.
Allium nevadense in the far West, no American Allium is known to be susceptible, so far as the writer is aware. If it were found that some one of our New England Alliums is subject to this disease, then an explanation of its origin would be easy.

(2) It would help settle the question of a possible relationship between Urocystis cepulae and some of the other species of Urocystis which occur on other species of Allium.

(3) In a genus as large as Allium, it is probable that there are some resistant species which may be crossed with A. cepa and that from the hybrid progeny of which a desirable smut-resistant onion might be developed. The initial step is to determine how resistant the different species are, if they are resistant at all.

**EXPERIMENTS WITH ONION VARIETIES**

From the catalogues of American seed houses, 25 onion varieties which seemed to be distinct were selected. Seed of 29 European varieties were obtained from H. Zillig, of the Biologische Reichsanstalt für Land-und Forstwirtschaft, at Trier, Germany, who also was investigating the same phase of onion smut and who kindly sent seed of each of the varieties which he was trying. Three hundred seeds of each of the 54 varieties thus obtained were planted April 25, 1924, in soil which was known to be very heavily infested with smut. When the seedlings came up there was seen to be considerable variation in the percentage of germination. Smut had appeared on all of the varieties after three weeks. All plants, irrespective of infection, were counted on May 30 to determine the percentage of germination, and at that time smut infection was estimated at about 75 per cent on all varieties and none offered evidence of being strikingly more resistant than others. The smutted ones had already begun to die and continued to drop off throughout the summer. On August 11, all the remaining plants were pulled and counted, and the percentage of infection was determined by comparing the number of healthy plants at that time with the number which had germinated on May 30.

The results are presented in Table I. They do not indicate that there is any important degree of resistance in any of the 54 varieties tried. Neither does the theory of some onion growers, that the red varieties are more resistant, find any support in these results. The pigmentation factor shows no relation to the resistance factor. There are, however, still other varieties which have not been tested, and it is possible that some more resistant variety may be found among them. It is therefore important that this line of work should be continued.
American varieties:
- Australian Brown
- Bermudia Yellow
- Crystal white
- Early Barletta
- Early Neapolitan Marzaljola
- Early Yellow Cracker
- Extra Early Rutgers
- Extra Early Yellow
- Giant White Italian Tripoli
- Isbell’s Early White Sugar Ball
- Isbell’s Evergreen Red Globe
- Large Red Wethersfield
- Mammoth Silver King
- Ohio Yellow Globe
- Prizetaker
- Red Italian Tripoli
- Southport Red Globe
- Southport White Globe
- White Adriatic Barletta
- White Bunch
- White Dutch or Strassburg

European varieties:
- Blassrote hollandische
- Blut rote Ulmer
- Bornaer Riesen
- Bronzekugel
- Braunzwiecher schwarzrote
- Calbena Lobkowskiste
- Eisenkopf
- Erfurter blassrote
- Franzoschische oder spanische weisse
- Gelbe Bürn
- Hollandische blutrote plattunde harte
- Hollandische gelbe plattunde harte
- Hollandische silberweisse plattunde harte

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EXPERIMENTS WITH OTHER SPECIES OF ALLIUM

During the last three years the writer has been attempting to determine the susceptibility of all species of Allium of which viable seed could be obtained. The seeds were planted in soil known to be heavily infested with the smut fungus and when the seedlings came up the percentage and severity of infection were recorded weekly until the plants were well grown and there seemed no more probability of new infections. Progress of the investigation has been slow on account of the difficulty of securing viable seed. Letters sent to the American seed houses and botanical gardens where one might expect
to find seed of wild species netted two or three species which did not germinate. Somewhat better success was had in Europe and most of the seed which the writer has obtained came from Kew Gardens, Haage & Schmidt, of Erfurt, Germany, H. Zillig, of Trier, Germany, and Vilmorin–Andrieux & Co., at Paris. Only last summer did the writer succeed in getting seed (or bulblets) of all the three native New England species of Allium. Allium seed seems to lose its vitality very rapidly, and seed more than a year or two old frequently can not be made to germinate. The writer thinks it is possible, of course, that he has not been able always to provide in the plots the special conditions which may be necessary to bring some species to germination. Altogether seed of about 100 species has been tried and the seed of only 39 have germinated.

In the course of this work it has been observed that there are gradations in the severity of infection. On this basis all the species may be divided into the following classes:

Class 1. Most susceptible class. Sori first appear in the cotyledons and may of the plants die at this time. Those which survive may slough off the disease, or lesions may appear in the successive true leaves, ending in the final death of the plant before it forms seeds.

Class 2. Less susceptible than class 1. Smut sori occur only in the cotyledons, and many plants die in this stage, but if they survive no lesions appear in the true leaves.

Class 3. Species barely susceptible in that smut sori may be found in the cotyledons, but the plants are not killed in this or later stages and no sori appear in the true leaves.

Class 4: Entirely resistant species in which smut lesions have not been observed in any of the parts.

In infested soil from the same field three different plantings were made. Nineteen species were planted May 1, 1923 in flats kept out of doors; 40 species in a greenhouse bench on October 11, 1923; and 64 species in an outdoor bed on April 25, 1924. Some species were tested in all three plantings, some in two, and some in only one, depending on the supply of seed and the need of further testing. In cases where fewer than 100 plants came up this fact is mentioned in the following notes on the individual species.

CLASS 1

Allium Cepa L., to which all our varieties of cultivated onions belong, is typical of Class 1. All infection seems to take place through the cotyledon. A large percentage of infected plants die in this stage. If no sori occur in the cotyledon, none will be found in the true leaves which follow. Sometimes, even when the cotyledon is affected, the fungus fails to gain entrance into the growing point and no lesions will be found in the following leaves. In the latter case, the bulb and seed are developed normally. More often, however, the parasite gets into the growing point and each successive leaf will have spore sori, in which case the leaves are short, distorted, and brittle, and the dwarfed plants die in various stages of development throughout the summer. Some of them form bulbs as large as an inch in diameter with longitudinal black spore pustules in the outer scales, but they usually rot before they are harvested. It is doubtful whether a plant which has spores in the first leaf ever recovers. In the soil
which was used for the comparative susceptibility experiments, 80 to 100 per cent of the seedlings which appeared died before harvest.

*Allium fistulosum* L. (Welsh onion). This onion reacts in every way like *A. cepa*, except that the percentage of infection is not so high. In the first planting 50 per cent were infected, 5 per cent in the second, and 25 per cent in the third. Infected plants succumbed in various stages of development. This species is a robust, rapid grower, and lives through the winter out of doors. There was no difficulty in getting a high percentage of the seed to germinate. Zillig also found this species susceptible.

*Allium ascalonicum* L. (Shallot). Only one planting was made, and about 100 strong plants started growth. Ninety per cent had smut in the cotyledons, and those which did not die in this stage had smut in the successive leaves and died throughout the summer, just as did *A. cepa*.

*Allium hookeri* Thwaites. In the first planting 10 per cent were infected. In the second planting 95 per cent were infected, and the majority of the plants died at an early stage. Sori were found in the fourth and fifth leaves, but no smutted plant reached maturity. This species seemed just as susceptible as *A. cepa*.

*Allium libani* Boiss. In the first planting 50 per cent had smut, and in the second 95 per cent of the cotyledons had it. A large percentage of the plants died in that stage. Only a few showed smut in the later stages, and none of the diseased ones developed to maturity.

*Allium senescens* var. *giganteum*. About 100 plants started growth from the one sowing made. Smut lesions were in the cotyledons of almost all of them, and many died in this stage. Lesions also occurred in the early true leaves. By the middle of the summer only 15 plants had survived, but they were free from smut. This appears to be a very susceptible variety and is remarkably different in this respect from the rest of the species (if, indeed, this is only a variety of the form listed below as *A. senescens*, the seed of which was received under the name of *A. fallax*).

*Allium nutans* Sund. Although a large number of plants came up, they all died before the first leaf was fully developed, and all were found to be full of smut lesions. This species appears to be so susceptible that it never gets much past the cotyledon stage in an infested soil.

*Allium flavum* L. There was 95 per cent infection in the cotyledons of the hundreds of plants of this species, and a heavy mortality at this stage. Sori were found in young leaves of some which continued to live, but no smutted plants were found later in the summer. The mortality seems to be all in the young stages.

*Allium schoenoprasum* L. (chives), is much more resistant than *A. cepa*. Infection occurred in only about 2 to 5 per cent of the cotyledons. Later in the summer sori were found in the leaves. Affected plants did not divide and produce tufts of shoots as did the healthy ones. All infected ones died before the end of the summer.

*Allium schoenoprasum* var. *sibiricum* L. Only two plants came up when this seed was planted. One of the two had smut sori on it.

*Allium nutans* L. This is a very susceptible species. Two plantings were made, and some hundreds of seedlings came up. Ninety
per cent of these seedlings had smut in the cotyledon, and most of them died in this stage, but a few continued to develop and had smut sori in the true leaves up to the fourth or fifth leaf, but no sori were found on any plant that was more mature. This species almost falls in class 2.

**Allium neapolitanum** Cyr. Not more than 1 per cent of the hundreds of seedlings which grew from one planting showed smut. Lesions were found, however, in the first true leaf. Hence this species is placed in class 1, although it appears to be very resistant.

**CLASS 2**

**Allium porrum** L. (leek). In England this species is said to be attacked more severely than *A. cepa* (3, p. 170). Zillig also was able to infect it, but neither he nor Cotton described the effect of the disease on the plants. Malbranche (?) stated in 1881 that 20 per cent of the *porrettes* (young leeks) in certain gardens in Rouen were attacked, and that the disease had established itself in the blades and especially the bases of the leaves. The writer made two plantings and had no difficulty in raising hundreds of plants to maturity. The first planting showed 15 per cent of infection in the cotyledons, and the second 10 per cent, but only a very few of the plants died. The writer has searched in vain for sori in the true leaves of the plants. The damage caused by the parasite here is negligible. These observations are surely at variance with those of Malbranche and other European investigators. Apparently the disease is more serious on leeks in Europe than in America.

**Allium angulosum** L. From the one planting made several hundred seedlings were obtained. Ninety-five per cent of the cotyledons had smut, and more than half of the plants died in this stage. Those which survived, however, showed no trace of smut in the leaves. This seems to be an extremely susceptible species, but the mortality is all in the early cotyledon stage.

**Allium nigrum** L. Considerable interest is attached to this species because of its relation to *A. magicum*, on which Passerini collected a smut which he named *Urocystis magica*. (In the past there has been considerable discussion as to whether *U. magica* is identical with *U. cepulae*. If it is, the onion smut fungus may well be of European origin. *A. magicum* is either a variety or a synonym of *A. nigrum*, according to the authority one wishes to follow.) One sowing was made, but the germination was poor; only about 30 seedlings grew. One-third of these had smut in the cotyledon, but none was observed in the later leaves, although all the plants were grown to full maturity and produced blossoms and seeds. The original specimens of *U. magica*, collected by Passerini and examined by the writer in the Harvard herbarium, were on very large leaves. The fact that the large leaves of *A. nigrum* have not been observed to become infected would indicate that the fungus Passerini collected and named was not identical with *U. cepulae*. More thorough infection tests should be made, however, the writer believes.

**Allium pulchellum** G. Don. Three plants came up and died of smut in the cotyledon stage.

**Allium sikkimense** Baker. Only two plants came up. One showed smut lesions and soon died.
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CLASS 3

*Allium volthyicum* Bess. Two plantings were made. Ten per cent of those of the first planting had smut in the cotyledons, and 50 per cent of the second planting had it. No lesions were observed in the true leaves.

*Allium polyphyllum* Kar. and Kir. Two plantings were made, but the germination was poor. Only six plants were obtained. Smut lesions occurred in the cotyledons of half of them, and some died later, but the writer is not sure that the smut killed them. Further tests might place this species in class 1 or 2.

*Allium scorodoprasum* L. Same general condition as for the preceding. Only a few plants came up, but some of them had lesions in the cotyledons.

*Allium obliquum* L. Of several hundred plants which came up 90 per cent had infected cotyledons, but the later leaves showed no sori.

*Allium senescens* L. (*A. fallax* Schult). Out of about 150 seedlings from the first planting, smut lesions were found in only five cotyledons. In a second planting, 2 per cent of the cotyledons had smut. No lesions were observed in any of the leaves, and it was not observed that any of those which had smut in the cotyledons died. Apparently here is a very resistant species, but not immune.

*Allium ampeloprasum* L. Only a few seedlings were obtained. About half of them had sori in the cotyledons.

*Allium darwasicum* Reg. Only 14 seedlings resulted from the one planting made. Three or four of them had smut lesions in the cotyledons.

*Allium montanum* Sib. and Sm. Twenty seedlings grew from the one planting. Two of them had infection in the cotyledons, but no infected ones were observed later.

*Allium paradoxum* Don. Of the three plants which came up, one had cotyledons lesions, but no disease was observed in later stages.

*Allium odorum* L. Three plantings with seed from as many different sources were made, and hundreds of plants were grown. No smut was observed in any of them. The results were at variance with those reported by Zillig, who was able to infect this species. Subsequent to the third planting, Zillig kindly sent some seed which he obtained from the Botanic Gardens in München. When plants grew from these, about 10 per cent had lesions in the cotyledons, this suggesting the possibility that in this species we may have varieties or strains which differ in their susceptibility to the smut organism.

*Allium recurvatum* Rydb. Of the 50 plants which came up, one-half had smut in the cotyledons, but no lesions were observed later on the true leaves. Although many of these plants died in a young stage, it was not evident that the smut was the cause.

CLASS 4

*Allium oreoprasum* Shr. Two plantings were made, and hundreds of seedlings grew, but no smut sori appeared on any of the parts at any time. As far as these trials showed, this species is perfectly immune.

*Allium moly* L. Only one planting with this species was made. The germination was poor, and only a dozen plants were obtained;
none of them showed infection in any stage. Although the writer has had these plants growing for two years, none of them has produced seed.

*Allium heldreichii* Boiss. Only three plants came up, and none of them was infected.

*Allium macranthum* Baker. About 50 plants were obtained from the single planting. No lesion was found at any time on any of them.

*Allium subhirsutum* L. About 100 plants came up. No smut was observed in them at any stage.

*Allium roseum* L. A very few plants came up and soon died, but no smut was observed. The writer is of the opinion that further tests should be made with this species.

**EXPERIMENTS WITH SPECIES WHICH REPRODUCE BY BULBLETS**

It has long been known that when onions are started from sets (small bulbs) they are entirely free from smut. In a previous publication, the writer has shown that all infection of onions takes place through the cotyledons (1). As there are no cotyledons when a plant starts from a bulblet, it is easy to understand why onions from sets are immune. There are many species of *Allium* which never produce seeds but reproduce by small bulblets which form in dense heads in a position much like the seed clusters of seed-bearing species. There are other species which produce both bulblets and seeds, and all gradations may be found between these two methods of reproduction. The most common native wild onion in New England (*Allium canadense*) reproduces by bulblets only. Although the writer has found plants which were producing flowers and seemed to be setting seed, he has never found that the seed matured in this section of the country. Bulblets of this species have been planted and many plants grown to maturity, but no smut has been found at any time. The results were the same using bulblets of *A. roseum*. The writer has not been able to obtain viable bulblets of other species, but there is every reason to believe that the results would not be different. Probably none of the bulblet-producing species are ever infected. In view of the widespread tendency toward the bulbiferous habit throughout the genus *Allium*, it is an interesting speculation as to the influence which the smut fungus may have had in eliminating the seminiferous strains and forcing by natural selection the development of bulbiferous species.

**EXPERIMENTS WITH THE WINTERBECK ONION**

Some seed labeled "Winterbeck Zwiebel" were received from Haag & Schmidt, Erfurt, Germany. The writer is not sure whether this should be considered a distinct species or only a variety of *Allium cepa*. It comes up more quickly than the common onion, and grows more rapidly, but does not develop a large bulb, and the bulb divides more readily, somewhat with the same general habit as the Welsh onion and the multiplier (or Egyptian) onion. Unlike the latter, however, it does not produce a head of bulblets but reproduces entirely by seeds which form in heads, as in the case of the common onion. It is a stronger grower and more hardy than the common onion, less susceptible to damping-off and thrips. It is
regarded as all but immune to smut. Not more than 2 or 3 per cent showed smut in the cotyledons, and no smut was seen in any later stage. In fact, smut is an entirely negligible factor. This seems to be the logical parent species for the breeding of a smut-resistant onion by crossing.

THE RELATION OF UROCYSTIS CEPULAE TO OTHER SPECIES OF UROCYSTIS ON ALLIUM

As far as the writer is aware, no Urocystis other than *Urocystis cepulae* has ever been found on the cultivated onion. Investigators who have found the disease agree as to the remarkable constancy of characters of this species so that not even a variety has been suggested. On other species of Allium, however, four other species of Urocystis have been found, and from the first description of the species up to the present mycologists and pathologists have discussed the relationship of these other species of Urocystis to *U. cepulae* without reaching any agreement. Some have considered all five forms as distinct species, some would unite them all under one species, i.e., regard the onion smut fungus as a variety of or identical with some of the others. Various other combinations are proposed. Not until all of these species have been cultured and studied and cross inoculations made on all host species concerned will this question be definitely settled; but it is hoped that the inoculation experiments just described and supplemented by examination of exsiccati of the pathogenes may contribute something to its solution. Let us examine briefly the other four species.

*Urocystis magica* Pass. was named by Passerini from specimens which he collected on *Allium magicum* at Parma, Italy, in 1875, and distributed in Rabenhorst's *Fungi europaei* as No. 2100 and in von Thuemen's *Mycotheca Universalis* as No. 223. The writer knows of no record that the fungus has ever been collected again on that host in Italy or elsewhere. All subsequent literature merely refers to the original description or consists of observations on studies of Passerini's original collection. It is remarkable that a fungus which was so abundant that it could be furnished in plentiful supply for distribution in two exsiccati should never have been collected again. The writer had occasion to study specimens of both of these exsiccati in the Harvard University herbarium. The long (some of them more than an inch) raised sori were on broad flat leaves. *A. magicum* is considered by most phanerogamic authorities as a synonym or a variety of *A. nigrum* L. This latter species, however, does not have flat leaves, but linear, terete leaves. Apparently, then, the plant on which Passerini collected the parasite was not *A. nigrum* but some other species. The spore balls contained a single spherical, or short, oval, brown central cell surrounded by hemispherical accessory cells. Only rarely did the writer find two fertile cells in a spore ball, and these were not attached by their surfaces, but were held together because surrounded by a common layer of sterile cells. In shape, color, and arrangement of all parts these spores could not be distinguished from those of *U. cepulae*. There is, however, a constant difference in size; the spores of *U. magica* were larger. Fifty spores from each species were measured under identically the same conditions. The central cell of *U. magica*, mounted in lactophenol, measured 14.27 by 15.55 μ as compared with 11.04 by 11.75 μ for *U.
The diameter of the entire spore ball of *U. magica* was 22.19 μ, while that of *U. cepulae* was 16.15 μ. All dimensions are somewhat greater when the spores are measured in a potassium hydroxide solution or when free. When the spores have been kept in a dry state for a long time, the accessory cells collapse but become distended again when treated with a weak solution of potassium hydroxide. Farlow (5, p. 114) considered *U. magica* as identical with *U. cepulae*. Schroeter and Winter (Die Pilze, p. 121, 1884) agree with Farlow and unite all the forms discussed here under *Urocystis colchici* Schlecht. Thaxter (11, p. 144) and Clinton (2, p. 451), on the other hand, point to the differences in the size of the spores as sufficient reason for considering the two species distinct. If by any chance the host plant of *U. magica* was really *A. nigrum*, the fact that the writer was unable to cause infection except on the tiny cotyledons, while in the exsiccati the fungus is on large leaves, seems to the writer another argument against the identity of the two. The constant difference in the size of the spores as observed by all investigators, and the difference in host plants, seem to be sufficient reasons for regarding *U. cepulae* as a species distinct from *U. magica*.

Another species of *Urocystis* has been reported on *Allium rotundum* in Europe by various investigators, and has usually been referred to *U. colchici* Schlecht., a common species there, occurring on a long list of Liliaceae. Some authors give to the form which occurs on Allium the rank of a variety, *forma Allii* under *U. colchici* because of certain morphological differences. The writer made a study of a specimen of *forma Allii* (Fückel Fungi rhenani No. 2217) collected by Fückel in Austria on *Allium rotundum*. All characters and dimensions were so nearly identical with those of *U. magica*, which were studied at the same time, that, from a morphological standpoint, no reason could be found for considering the two as distinct. These two forms are also doubtfully united by Liro (6) in his recent excellent monograph of the genus Tuburcinia.

After the variety on *Allium rotundum* has been removed from *Urocystis colchici*, the species as it occurs on other hosts is easily distinguished from *U. cepulae* because the spore balls commonly are attached in glomerules of 3 to 5 or more, and a single spore ball may have 2 to 3 fertile cells. All dimensions are also larger than those of *U. cepulae*.

Rostrup (9, p. 153) found a species of *Urocystis* on *Allium ascalonicum* in Denmark, in 1890, and referred it to *U. cepulae*. Liro, however (6, p. 50), refers it to his newly described species *U. ferruginea* which differs sharply from *U. cepulae* in the red brown color of the spore powder, and in the angular spores attached in groups of six or more. The writer has not had an opportunity to examine this species, but, judging from the description given by Liro, there would seem to be no question as to its distinctness and no occasion for confusing it with *U. cepulae*.

In 1911, Schellenberg (10, p. 14) described the species *Urocystis allii* from a specimen collected in Switzerland in 1902 on *Allium subhirsutum* and distributed in von Thumen’s Mycotheca universalis as No. 1219. Although in morphological characters it seems to resemble *U. cepulae* even more closely than does *U. magica*, both Schellenberg and Liro consider it as distinct. As previously mentioned in this paper, *A. subhirsutum* L. was found by the writer to be entirely immune to *U. cepulae*, which is regarded as evidence con-
firming the distinctness of the two species of Urocystis. Another collection of a Urocystis on *A. oleraceum* L. was also referred to this same species by Schellenberg.

**ORIGIN OF THE ONION SMUT**

What bearing have the facts set forth in this paper on the problem of the origin of onion smut? The writer believes that there are good morphological and biological reasons for considering the smut fungus as a distinct species from any of the Urocystes found on European species of *Allium*. It should also be pointed out in this connection that even if it should be found that some one of the European species named in recent years was identical with *Urocystis cepulae*, this would not indicate a European origin for the disease. It seems to the writer that it would be much more logical in that case to conclude that the fungus was first on onion and passed from the onion over to the other species where it was collected. In fact, in view of the wide host range which the writer has demonstrated for the onion smut organism, it would seem remarkable if it should not be taken some time by some collector on another species. During the 50 years that it has been in Europe it has had abundant opportunity to spread to other hosts.

In brief, in the writer's opinion, there is not the least evidence that the disease is of Old World origin. On the contrary, there is excellent circumstantial evidence that it did not exist there on any species previous to its discovery in America. Onions have been grown and used by every civilized people in the Old World at least since the building of the pyramids. In all that time onion smut must have come in contact with every disease which occurred on other species of *Allium* indigenous to the countries where they grew. Smut is by no means an inconspicuous disease, and if it had been present in the Old World it very likely would have been mentioned before 1872.

Some of the susceptible species mentioned in this paper are native to the New World, and probably further search will add to the list of our indigenous susceptible ones. Some one or more of these was probably the original host. Possibly it was a native of the far West in this country, like the susceptible *Allium nevadense*. For many years after the onion was brought to America smut seems to have been unknown. The writer offers the theory that as the frontier of civilization advanced into the West, taking along with it the onion, the onion came into contact with the organism in its native home, and that the spores could easily have been taken back to New England in the natural course of commerce, with the result that the disease first became prominent in a great intensive onion center, such as eastern Massachusetts was at that time, rather than in the isolated gardens of the pioneers. It may be significant that smut first appeared within the next decade after the California gold rush of 1849.

**SUMMARY**

None of the 54 varieties of cultivated onions tested showed any considerable resistance to smut.

Out of 39 species of *Allium* tested, 8 seemed to be immune, and 31 showed varying degrees of susceptibility.
Thirteen species seemed very susceptible, and are in the same class as the common onion.

Smut occurred in the cotyledons of 13 more species, but did not kill the plants or occur in the true leaves.

In five other species it occurred in the cotyledons and killed many of the seedlings in that stage, but did not appear in the true leaves. Smut did not occur in species which reproduce by bulblets.

On this basis one might expect to find among the 250 known species of Allium at least 150 which are susceptible to smut.

Urocystis cepulue is considered by this writer as distinct from all other species of Urocystis which have been reported on other members of the genus Allium.

All the evidence the writer has indicates that this parasite lived originally on some wild American species and thence passed over to the cultivated onion.

LITERATURE CITED


(7) Malbranche.


