AECIAL STAGES OF THE LEAF RUSTS OF RYE, PUCCINIA DISPERSA ERIKSS. AND HENN., AND OF BARLEY, P. ANOMALA ROSTR., IN THE UNITED STATES[1]

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INTRODUCTION

In 1918, investigations on the leaf rusts of rye, barley, wheat, corn, and related grasses were begun by this laboratory in cooperation with the Office of Cereal Investigations, United States Department of Agriculture. Since it has been shown by Stakman (*11*)[2] and others that, as in northern Europe, *Puccinia graminis* Pers., the stem rust of wheat, oats, barley, rye, and related grasses, can be controlled in the northern United States by eradicating its alternate host, the common barberry, *Berberis vulgaris* L., it seemed important to determine the aecial hosts of the leaf rusts in this country and the rôle they may perform in propagating these rusts. In a previous paper, the writers (*5*) already have reported on the alternate host of the leaf rust of wheat, *P. triticina* Erikss., and at this time are presenting the results of similar studies on the leaf rusts of rye and barley.

LEAF RUST OF RYE, PUCCINIA DISPERSA

DeBary (*3*) established the fact that *Anchusa arvensis* and *A. officinalis* are aecial hosts of *Puccinia dispersa*. This relationship was determined by inoculating the leaves of Anchusa with the basidiospores of the rust fungus. The resulting infection produced aeciospores which, when applied to the leaves of rye plants, produced infection and subsequent development of urediniospores.

When basidiospores of rye leaf rust were sown on *Berberis vulgaris* L., *Rhamnus frangula* L., *R. cathartica* L., *Ranunculus acris* L., *Ranunculus bulbosus* L., *Leontodon taraxacum* L. (*Taraxacum officinale* Weber), and *Urtica dioica* L., no infection resulted. Nielson (*9*) later obtained infection on rye following inoculation with aeciospores from *Anchusa officinalis*. Plowright (*10*) also obtained aecia on *Anchusa arvensis* by placing rusted rye straw near that host. Eriksson (*4*) was able to infect *Anchusa arvensis* and *A. officinalis* with *Puccinia dispersa* on rye, but obtained no infection on *Myosotis alpestris* F. W. Schmidt, *Symphytum asperum* Lepechin (*S. asperrimum* Donn), and *Pulmonaria officinalis* L. and only pycnia on *Nonnea rosea* Link. Sowings of aeciospores from Anchusa produced uredinia on rye but not on the other inoculated grass hosts. Klebahn (*6*) reports on similar experiments in which aecia were obtained on Anchusa. Uredinia also were obtained on rye when inoculated with aeciospores from Anchusa. In the

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[2] Reference is made by number (italic) to "Literature cited," p. 1126.

United States, Arthur (*1*, *2*) secured infection on *Lycopsis arvensis* L. (*Anchusa arvensis*) with *Puccinia dispersa* from rye. A few pycnia developed in one instance and numerous pycnia and a few aecia in another. He states that—

> It is possible, yet scarcely probable, that the explanation (of this weak development of aecia) lies in the lessened vigor of the American rye rust, which is propagated by repeating spores alone, the aecial hosts being practically wanting in America.

In Europe, the leaf rust of rye is characterized by several workers as having teliospores which develop and germinate during the same season. Eriksson (*4*) especially has emphasized this point and states that in Sweden the teliospores begin to germinate as soon as they mature, that is, about the middle of July, and cease germinating when kept out of doors during the winter. The aecia were produced from the beginning of August to the end of September. Although in Eriksson's experiments the teliospores did not germinate after overwintering in the open, he found they would remain dormant until spring if kept indoors. Most of the other European writers on rusts appear to agree with these statements of Eriksson. DeBary (*3*), however, who originally discovered the connection, states that the teliospores germinated after overwintering. Klebahn (*6*) questions whether this was out of doors, pointing out that DeBary does not state the manner in which they were overwintered. DeBary (*3*), however, does state that aecia are to be found throughout the year from spring to late summer and in mild winters even in January.

GERMINATION OF THE TELIOSPORES

During the winter of 1918–19, a number of collections of telia of the leaf rust of rye were wintered along with those of the leaf rust of wheat and were tested for germination in the spring of 1919. One collection of the leaf rust of rye germinated in April. Since, as stated above, the teliospores of the leaf rust of rye are generally believed to germinate only in the late summer and fall of the year in which they are formed, all the collections of telia of this rust, made in the spring and summer of 1919, were tested for germination beginning July 15, and at intervals of two to four weeks until April 7, 1920.

Each collection was tied in a coarse cheesecloth bag and hung on the east side of a building about 2 feet from the ground All the material was brought into the greenhouse two days before testing and placed on moist sphagnum for that length of time. The test for germination was made by scraping some of the teliospores from the rye leaves and placing them in a hanging drop on the bottom of an inverted Syracuse watch glass. These drops were then examined after 12 hours.

Twenty collections of teliospores obtained from the States of Indiana, Georgia, Delaware, New York, Wisconsin, Minnesota, Nebraska, Kansas, Washington, Oregon, and California were thus wintered and tested. Of these, 15 showed germination at some time during the test. Germination first took place on August 19 in 2 collections, and between that date and November 25, 10 additional collections showed germination. All these collections and 2 others continued, for the most part, to germinate during December. During January, 11 of the 14 still showed some germination. In February there apparently was a sharp falling off in the number of collections showing germination, only six showing germination during that period. In March, another collection was added to the list for the first time. On April 7, when the material was last tested, five cultures still showed germination. One of these five was the collection which germinated on August 19 of the preceding summer. This culture showed germination on 9 consecutive occasions during the winter, another 10, a third 7, a fourth 6, and the other, which first showed germination in April, germinated twice.

These results are the more striking when one considers that the teliospores were subjected to sudden and extreme temperature changes, from low winter temperature to the warm temperature of the greenhouse. They then were placed out of doors and again suddenly subjected to low temperatures and the drying effects of freezing. Such treatment certainly would be expected to be fatal to any except the most hardy spores. This may explain why some of the collections did cease to germinate before spring. From the information now available, it would appear that in this country the teliospores of the leaf rust of rye, as a general rule, are capable of germinating whenever conditions are favorable either in the fall or, surviving the winter, in the spring, or both. The repeated germination of some of the collections would indicate that differences existed among the teliospores as to dormancy, otherwise one would expect all the spores to germinate when germination was first observed.

It is difficult to draw conclusions with reference to a rust of this type in which the telia long remain covered by the epidermis, as the length of time the epidermis remains over the telium may prove to be a factor. It is well known, however, that in some species of rusts, especially short-cycled species of Puccinia, there are to be found in the same telium spores which germinate at once and others which germinate only after a considerable resting period.

What the significance of the difference in action of the collections may be is difficult to say. While most of the collections which germinated in the fall continued to germinate until well into the winter, one showed germination only on September 12, and, although tested 13 times during the winter and spring, gave no more evidences of germination. Four others germinated only up to January 5. On the other hand, one collection gave no germination until March 8, although tested previously 10 times throughout the fall and winter. It is possible that in this country the leaf rust of rye may be made up of different strains differing, among other things, in the length of time which it takes to mature their teliospores and in the ability of these to overwinter. On the other hand, these differences may be due largely to environmental conditions under which the spores developed. These are questions which are difficult to solve as the leaf rust of rye, unlike some of the leaf rusts of native grasses, does not form its teliospores upon seedlings, and the time and care which would be necessary to grow different pure cultures of leaf rust of rye on maturing plants under controlled conditions has made it thus far impracticable to attempt to investigate this phase.

The writers' observations to the effect that all the teliospores of *Puccinia dispersa* necessarily do not germinate in the late summer and fall, but some at least may remain dormant during the winter, support the original statements of DeBary (*3*) as to the germination of the teliospores of this rust after overwintering, which have been somewhat questioned. It always has been difficult to determine how the aecial infection occurring in the fall can figure importantly in the winter survival of the rust. Certainly if the rust should not hibernate in the uredinial stage on the rye plant itself, the autumnal aecia can not be a factor in its survival. On the other hand, under such conditions, those teliospores which remain dormant until the next spring may be of importance in regions where the rust does not overwinter on rye itself and the aecial host is present.

From still another point of view, it is interesting to note the germinative ability of the teliospores of *Puccinia dispersa* subsequent to their winter survival. Eriksson was influenced to separate the leaf rust of wheat as a species, *Puccinia triticina*, from the leaf rust of rye largely because the former, unlike the latter, was unable to infect Anchusa and because the teliospores of the leaf rust of wheat germinated only after overwintering, while those of rye germinated shortly after harvest and did not overwinter. Here it may be pointed out that during the

winter of 1919–20, the authors observed that a number of collections of teliospores of the leaf rust of wheat were germinable in early December and continued to germinate until spring in a manner similar to those of *P. dispersa*. The distinction between these species on the basis of difference in time of germination of their teliospores therefore is not as sharp as it first appeared.

Klebahn (*7*) has shown that teliospores which usually are known to germinate only after the close of the winter season may be made to germinate by alternate drying and wetting. Recently, Maneval (*8*) also has shown for a number of such rusts that the teliospores will germinate if alternately wet and dried or soaked long enough. However, it probably is true that the teliospores of *P. triticina* generally germinate only after hibernation while those of *P. dispersa* usually are capable of germinating in the fall of the same year in which they are formed. However, they may retain this ability throughout the winter. Varying climatic conditions in different years, however, may tend to level such a distinction.

INFECTION OF ANCHUSA

The above collections, on being found germinable, were sown on potted plants of *Anchusa officinalis* grown in the greenhouse from seed obtained from Prof. Ed. Fisher of Berne, Switzerland. Of the 15 collections germinating only 5, however, produced infection. Of these 5, only 2 produced both pycnia and aecia, while the other 3 developed pycnia only. Aeciospores from the 2 plants showing aecia were sown on seedling plants of Rosen rye, producing uredinia typical of *Puccinia dispersa*. The 5 collections which gave infection were obtained from Mt. Vernon, Ind., Madison, Wis., Manhattan, Kans., Kearney, Nebr., and Seattle, Wash. These were the same collections which still showed germinating teliospores on April 7. Each of these collections, however, was sown a number of times without obtaining infection. This was especially true during the fall and winter, most of the infections being obtained in the spring, as happened in both instances of aecial production. Apparently the reason for this was the condition of the Anchusa plants, for they developed little new growth in the greenhouse during the fall and winter, and many of the older leaves died. With the advent of spring, new growth took place and more abundant infection resulted. In consequence, no very definite conclusions can be drawn from the negative results obtained from the other 10 collections as they germinated only at times when the Anchusa plants were in poor condition. It is evident, however, that the teliospores of *P. dispersa* which overwintered were able to infect Anchusa, thus establishing their identity with the species *Puccinia dispersa* as distinguished by Eriksson. But for this fact, the overwintering of the teliospores in the absence of infection of Anchusa would have indicated the possibility of their having belonged to another race or species of leaf rust on rye. By the close of winter, such a small amount of material was left that no attempt was made to inoculate plants of Anchusa in the field.

Although infection was not obtained to any extent in the greenhouse in the fall, mulching of Anchusa plants in the field, where they were in good growing condition, resulted in abundant production of aecia. On August 12, 1922, rye straw from the Agronomy plats, heavily covered with telia of the leaf rust of rye, was used to mulch vigorously growing plants of *Anchusa officinalis*. The summer of 1922 was very dry and no rain fell until August 23. On August 31, numerous yellowish spots containing pycnia were noted scattered over the leaves, petioles, and young flower parts. Aecia appeared in these areas in considerable abundance in about a week (Pl. 1, A). Again, on September 22, shortly following a rain, new infected areas containing pycnia were found scattered over the plants. Aecia also followed in these areas. With the fall rains, infection was more or less

continuous. On November 10, when last observed, the plants were covered with a heavy development of aecia and, even then, many newly-formed pycnia were evident. Although the rusted straw remained as a mulch throughout the winter, and the Anchusa plants produced vigorous growth the following spring, no infection was observed. In the fall of 1923, the same plants again were mulched with rye straw laden with teliospores of *Puccinia dispersa*. No infection resulted. This would indicate that, if its aecial host be present, the leaf rust of rye occasionally may produce its aecia in abundance in this country in late summer and fall just as it does in Europe. Also the indications are that the absence of its aecial host apparently has not destroyed in any way the inherent ability of the rust to produce aecia.

At the time *Anchusa officinalis* was mulched with rye straw, other boraginaceous species in close proximity also were mulched with the same material in order to determine whether the rust might not have still other aecial hosts. These Boraginaceae were *Nonnea rosea* Link, *N. lutea* DC., *Cerinthe minor* L., *C. major* L., *C. alpina* Kit., *Lappula echinata* Gilib. (*Myosotis lappula* L.), *Myosotis palustris* Hill, *M. arvensis* (L.) Hill, *M. alpestris* F. W. Schmidt, *M. virginica* (L.) BSP., *Symphytum asperum* Lepechin (*S. asperrimum* Donn) and *Pulmonaria officinalis* L. All these plants were exposed to infection equally with the plants of *Anchusa officinalis*, but in only one case was there any indication of infection. One plant of *Nonnea rosea* developed a few pycnia but the infection proceeded no further. This additional link in evidence points to the identity of the leaf rust of rye in this country and in Europe, for Eriksson (*4*) in Sweden found that *Myosotis alpestris* and *Symphytum asperrimum* were immune, while pycnia developed on *Nonnea rosea*.

Earlier in July, 1920, a new host for the leaf rust of rye was discovered in *Anchusa capensis* Thunb. This had been planted as a border plant around flower beds near the horticultural greenhouses of Purdue University. The plants showed a fairly heavy development of aecia (Pl. 1, B) the spores of which, when sown on rye, produced typical uredinia of the leaf rust of rye. As this sporulation occurred in advance of the application of the straw mulch, the infection must have started from a small plat of rye to the north, or perhaps from straw contained in the manure used in fertilizing the bed. This seems to be the only record of the occurrence of aecia of the leaf rust of rye in this country except where Anchusa plants had been planted and mulched for the purpose of obtaining the aecia. Flowering specimens of this species of Anchusa were sent to Prof. B. L. Robinson of the Gray Herbarium, Harvard University, who kindly had them compared with an isotype of *Anchusa capensis* and reported that they appeared to be identical.

It is not probable, however, that the aecial hosts of the leaf rust of rye are of much importance in this country at the present time. The aecia, with one exception, as stated above, have only been found where Anchusa plants have been mulched with rye straw for the purpose of producing the aecia. *Lycopsis arvensis*, presumably the *Anchusa arvensis* of northern Europe, occurs in North America from Nova Scotia to Ontario, Minnesota, Pennsylvania, and Virginia. So far as we have been able to determine, aecia of *Puccinia dispersa* have never been collected on this species. Since *Puccinia dispersa* overwinters fairly commonly in the uredinial stage on rye, the rust maintains itself without the aecial stage.

It hardly would appear probable that, were the development of the aecial stage in this country to occur in the fall, as it does in Europe, conditions affecting maintenance of the rust would change to any extent. The rust would have to survive the condition either in the aecial stage on Anchusa or, what is more probable, pass

over to rye and survive in the uredinial stage on that host. As volunteer rye in the eastern United States usually is heavily rusted in the fall, in the absence of Anchusa it seems improbable that the presence of the aecial stage would influence the situation to any extent. If the teliospores commonly retain their germinability until spring, Anchusa species may be of some importance in that they may serve as additional centers for spread of the rust. Our observations are not extensive enough to warrant drawing any conclusions as to this possibility, the general situation in Europe indicating its rare occurrence in the spring, even there.

LEAF RUST OF BARLEY, PUCCINIA ANOMALA

The aecial stage of the leaf rust of barley, *Puccinia anomala* Rostr. (*P. simplex* [Körn.] Erikss. and Henn.), was unknown until Tranzschel (*12*), working in Russia in 1914, sowed teliospores on plants of *Ornithogalum umbellatum* L., *O. narbonense* L., *Muscari botryoides* (L.) Mill., *M. tenuiflorum* Tausch, *Scilla sibirica* Andr., and *Allium angulosum* L. Many aecia developed from this sowing on *Ornithogalum umbellatum* and a smaller number on *O. narbonense*. The other plants remained uninfected. Aeciospores from *O. umbellatum* were sown upon *Hordeum vulgare* L., producing urediniospores and teliospores. We have not been able to find records to show that these results have been repeated elsewhere.

Barley straw, heavily laden with teliospores of the leaf rust of barley, was collected at Washington, D. C., Blacksburg, Va., and Mt. Vernon, Wash., in the summer of 1921. Part of each of these collections was wintered in a similar manner to that described for rye, and part was used to mulch small areas where bulbs of the Star-of-Bethlehem, *Ornithogalum umbellatum*, had been planted. The collections of telia, when brought into the greenhouse on March 24, 1922, were found to germinate and were sown on Star-of-Bethlehem plants growing in pots. Infection was obtained in each case, pycnia appearing April 4, followed by aecia April 18 (Pl. 1, C). From these cultures, aeciospores were sown on barley, producing uredinia typical of *Puccinia anomala*. The groups of plants of Star-of-Bethlehem, mulched in the field with straw of each of these collections, also showed infection, pycnia appearing about April 15, followed by aecia. On May 18, uredinia developed on barley sown near the aecia-bearing Ornithogalum plants.

During the summer of 1922, barley straw bearing telia of *Puccinia anomala* was collected at Lafayette, Ind., and used to mulch *Ornithogalum umbellatum* in the field. On April 17, 1923, pycnia were noted upon these plants, followed on May 5 by aecia.

Puccinia anomala more nearly resembles a Uromyces than a species of Puccinia. The teliospores are for the most part one-celled. Indeed, in some collections considerable search is necessary in order to find the two-celled spores. According to usage, however, the presence of these few two-celled teliospores places the species in the genus Puccinia. A very similar rust, *Uromyces hordei* Tracy, is found in southwestern United States upon a wild barley, *Hordeum pusillum* Nutt. This, however, produces only one-celled teliospores, but is otherwise very similar. Arthur (*2*) has shown that this rust has its aecial stage on *Northoscordium bivalve* (L.) Britton, a species very similar and fairly closely related to *Ornithogalum umbellatum*. Although Arthur was not able to infect Ornithogalum with *Uromyces hordei*, the evident relationship of the two rusts invited further study. In March and April, 1920, a telial collection of *Uromyces hordei*, sent by R. S. Kirby from Norman, Oklahoma, was used four times in an effort to infect plants of *Northoscordium bivalve* and *Ornithogalum umbellatum*.

Abundant infection was obtained upon Northoscordium (Pl. 1, D) while no signs of infection were detected on Ornithogalum. Aeciospores from the infection on Northoscordium were sown two different times on seedlings of *Hordeum pusillum* and of common barley, *Hordeum vulgare*, which is susceptible to *Puccinia anomala*. Infection resulted only on *Hordeum pusillum*. Telia obtained from these cultures were overwintered and again sown upon *Northoscordium bivalve* and *Ornithogalum umbellatum* in March, 1921. Infection developed only on the Northoscordium. In addition, five different uredinial cultures of *Puccinia anomala* from different localities, while infecting barley varieties heavily, produced no infection when sown on *Hordeum pusillum*. It seems evident, therefore, that although *Uromyces hordei* and *Puccinia anomala* are somewhat closely related, they are distinctly different as to host specialization, in both the aecial and telial stages.

These results show that *Ornithogalum umbellatum* is an aecial host for the leaf rust of barley in this country as well as in Russia. The four widely separated localities from which the telial collections were made also would indicate that this is likely to be the case for this rust generally over the entire country. The writers have no evidence at the present time to show that the aecial stage is naturally produced, as aecia on this host have never been collected or reported in this country. However, it is entirely possible that they may be produced but have been overlooked, attention not having been directed to this plant, as the rôle of Star-of-Bethlehem as an aecial host was discovered quite recently and apparently is not generally known.

Star-of-Bethlehem may become, if it already is not, of considerable importance in barley-growing areas because of its tendency to escape from cultivation and become a weed. In some places, notably in the Southern States, this plant has become a pest almost equal in importance to wild onion (garlic), as far as occupying cultivated land is concerned. It is a bulbous plant, coming up in the early spring and dying down in midsummer. It multiplies rapidly by division of the bulb and may be scattered widely over the field in plowing and cultivating. It is obvious, therefore, that its presence in barley-growing areas is very undesirable.

Unlike the leaf rust of rye, the leaf rust of barley has not been shown to overwinter in the uredinial stage in this country. In consequence, the aecial host may be an important factor in the survival and spread of this rust. It must be acknowledged, however, that in the two places where the rust has been observed by us to be most severe, Arlington Experiment Farm, Rosslyn, Va., and Blacksburg, Va., Star-of-Bethlehem is not known as a weed.

SUMMARY

1. The leaf rust of rye, *Puccinia dispersa*, is able to produce aecia on species of Anchusa in the United States.

2. *Anchusa officinalis*, and *A. capensis* are susceptible. *Nonnea rosea* may be infected occasionally with production of pycnia only. The other boraginaceous species tested remained uninfected.

3. *Anchusa capensis* has been found naturally infected by the leaf rust of rye and may become of some importance in the spread of the disease.

4. Apparently unlike the usual situation in Europe, the teliospores of the leaf rust of rye are capable of overwintering, and may germinate the following spring.

5. The leaf rust of barley, *Puccinia anomala*, from four widely separated localities in the United States has been used in inoculation experiments which have resulted in the development of aecia on *Ornithogalum umbellatum*, agreeing with results obtained by Tranzschel in Russia.

6. Although the aecial stage of *Puccinia anomala* has not been found occurring naturally, Star-of-Bethlehem possesses weed-like characteristics in this country which make it a dangerous plant near barley fields.

7. *Puccinia anomala* in its host specialization is distinct from the closely related *Uromyces hordei*. So far as known, neither is able to infect the hosts of the other.

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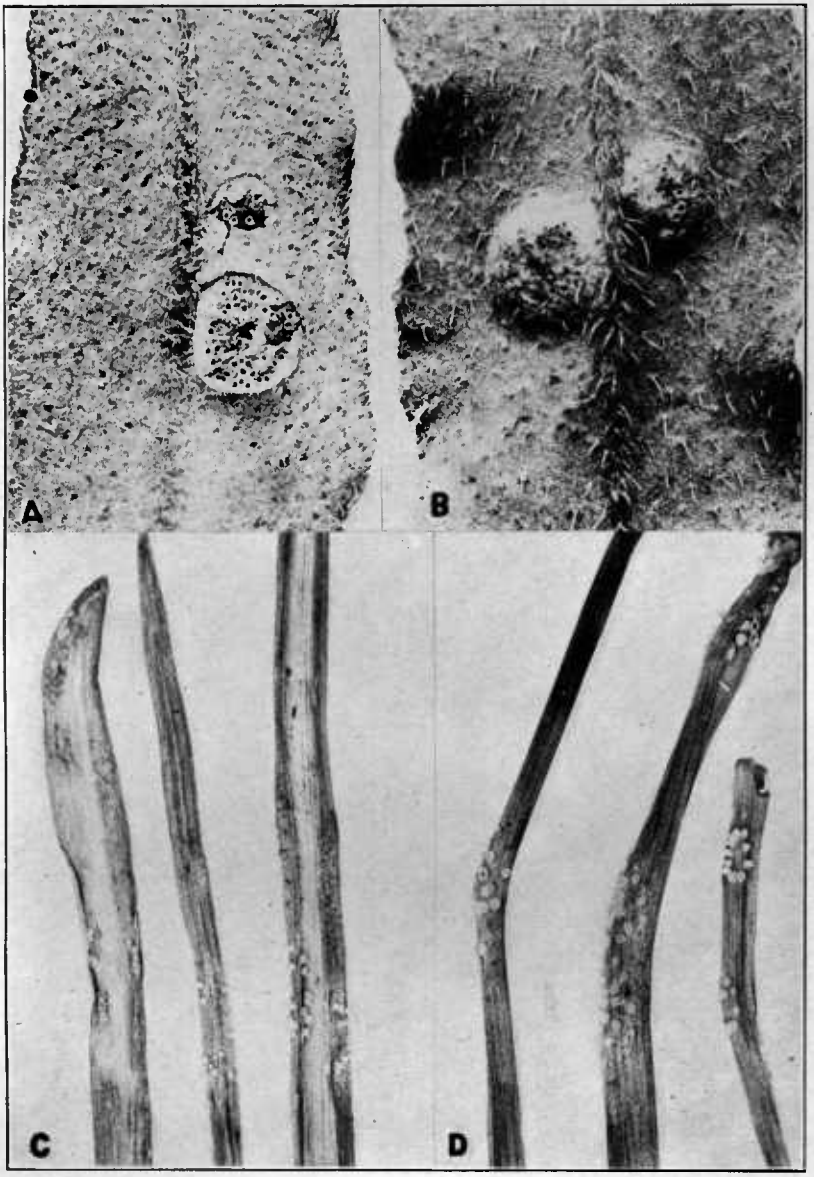
PLATE 1

A.—Aecial stage of *Puccinia dispersa* upon leaf of *Anchusa officinalis.*

B.—Aecial stage of *Puccinia dispersa* upon leaf of *Anchusa capensis.*

C.—Aecial stage of *Puccinia anomala* upon leaves of *Ornithogalum umbellatum,* obtained from infection with teliospores from barley.

D.—Aecial stage of *Uromyces hordei* upon leaves of *Northoscordium bivalve,* obtained from infection with teliospores from *Hordeum pusillum.*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