THE WATER-RELATION OF PUCCINIA ASPARAGI.

A CONTRIBUTION TO THE BIOLOGY OF A PARASITIC FUNGUS.

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(WITH TWENTY-ONE FIGURES)

WHETHER the use of the term "ecology" would be consistent and proper throughout the present article, the writer must confess his inability to decide. With plants of independent existence ecology has become a well-defined branch of botanical science, but when complicated with the phenomena of parasitism there must be distinguished two fairly distinct classes of life-relations; those which act upon the parasitic organism directly, and those which affect it, even more decidedly perhaps, in a secondary or indirect manner through their effects upon the host-plant. "Biology," in the European sense, seems on the whole a more fitting term for the present purpose; since at many points it is difficult to say whether we are considering the relation of the parasite to its environment, or to its host's environment, or whether its host is its environment. The subject is one of ecology in the broadest sense, yet a distinction must be made between the relations of an organism to natural influences, and its relations to the effects of perhaps the same influences upon another organism upon which it lives as a parasite. The fungus has no soil-relation, of course, but its connection with the host-plant is much more than this, though corresponding to a certain extent. Without extended discussion on this point, it will suffice to say that it has seemed to the writer very desirable to establish upon a systematic basis the relations existing between parasitic fungi in general and the various influences exerted upon them in nature, either directly or acting through the medium of the host-plant. While many scattered observations of this kind exist, very little definite work has been done in establishing general principles or in drawing definite conclusions. The observations contained herein are offered as a modest contribution in this direction.

It is well established in a general way that the development of

those fungi that live upon higher plants is favored by wet weather. This is so universally the case that we may almost conclude without further consideration that under normal conditions the water-relation of such parasites is of more importance in their development than any

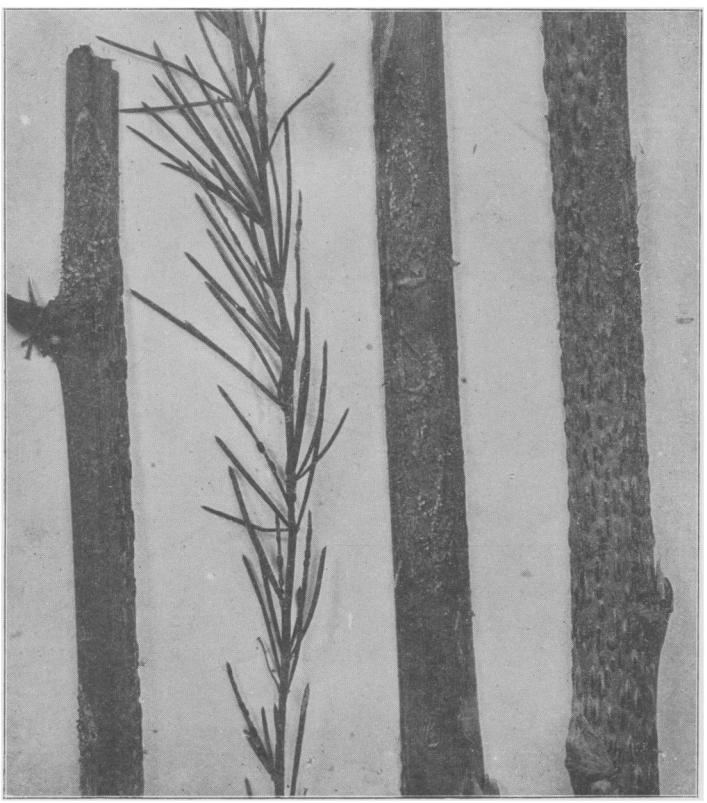

FIG. 1.—Asparagus rust, *Puccinia Asparagi* DC., in all stages. Milpitas, Calif., July 4, 1903.

other condition. Considering this as established, there still remains a broad field for research in determining just why this is true, and in general in analyzing the conditions and their results. This has been the writer's object in the case of the destructive parasite *Puccinia Asparagi* DC., which has proved especially favorable for such study.

The asparagus rust is caused by one of the Uredineae of the subdivision *Auteupuccinia* of Schroeter's classification; that is, the spermogonia, aecidia, uredospores, and teleutospores all develop upon the same plant. This is shown in *fig. 1*, where the various spore forms may be readily recognized. Upon the stalks represented at the extreme right and left all four forms are present at once. This disease has long been known in Europe, but attained no prominence in this country until the fall of 1896, since which time it has spread entirely across the continent from Massachusetts to California, with extremely disastrous results to the asparagus industry.

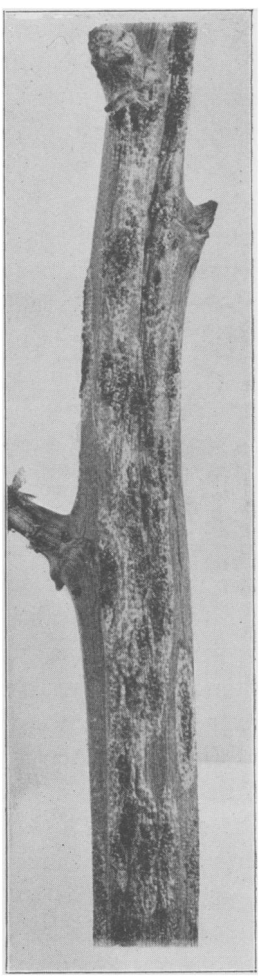

FIG. 2.—Aecidial development of the rust as seen in California. Bouldin Island, April 29. 1903.

The development of this rust is practically the same as that of others of the same class, the spermogonia and aecidia appearing in spring, followed by the uredo stage in summer, after which the teleuto or black rust appears. The development of the aecidial stage has varied, according to the writer's observation, with the nature of the spring climate in various sections of the country. In Massachusetts, where the spring is comparatively late and short, the aecidium of *Puccinia Asparagi* is not unknown, but is by no means common, and the development of this stage of the rust is decidedly limited. Going south to Long Island and New Jersey, the spring form is common, but by no means noticeable; while in California the "spring rust" is almost as well known to asparagus-growers as the later stages, and upon old beds, volunteer growth, or beds too young for cutting, it reaches a development quite unknown in the east, sometimes covering the main stalk and branches of the plant completely and causing considerable damage. *Fig. 2* illustrates a case of

this sort. The uredo and teleuto stages follow in order as the season progresses, and while the simultaneous occurrence of these forms is by no means unknown, it is usual, as with most similar rusts, for the uredo stage to develop almost exclusively during the summer, when the plants are most active, followed by a pure teleuto growth upon the dead stalks in fall. The latter stage in all the Eupuccinia group is regarded, therefore, as typically the fall rust, and as a form which develops to any extent only in the latter part of the season as a result of the approach of winter and the death of the host-plant.

The relation of the development of the asparagus rust to soil and atmospheric moisture has received some attention in previous publications. Stone and Smith[1] found a decided difference in the prevalence of the disease according to the moisture-retaining properties of the soil, the trouble being worse upon the drier soils. So marked was this difference in Massachusetts that in regions equally exposed to infection, and in fact equally affected with the teleuto stage in the fall, the beds upon heavier, moist soils did not show, and have never shown, any rust previous to September (when the plants mature in that climate); while those upon light dry soils became badly affected with the uredo stage early in the season. The difference not only appeared in different sections of the state in the same season, but also in the whole state in different seasons, the amount of rust in the most affected localities varying as the season was wet or dry, being least in the wet seasons. Although not universally accepted at first, this idea has received much support from subsequent experience over practically the whole country.

In most of the large asparagus regions of the eastern states but little difference exists between the soils of the various plantations, the characteristic soil being of a light, sandy, dry nature. In the first violent epidemic of the rust everything was affected in such sections, and differences in soil, as well as in varieties of asparagus and other factors now recognized by all, were overlooked or imperceptible. A tour of these districts at present, however, will convince the most skeptical that of the original beds those few which now remain are almost entirely upon the heavier soils, and of the new beds the most

[1] Bulletin 61, and Ann. Reports 12, 14, 15, Hatch Exper. Station of Mass. Agric. College.

thrifty are likewise on the heavier soils, other things being even approximately equal. Most of the growers in the large eastern asparagus districts recognize this, and likewise attribute the marked freedom from rust of the past two seasons to the very unusual rainfall, which fact is in itself strong evidence of the unfavorable effect of abundant soil moisture upon the fungus.

This is, of course, contrary to the established principle above mentioned that such parasites are greatly favored by wet seasons. One of the most prominent features in the observations of Stone and Smith was the occurrence in the asparagus beds least affected of the teleuto stage alone coming on at the usual time, but not preceded by any trace of the other stages, so far as could be found by thorough search. These beds were, as just mentioned, upon soils of high water-retaining capacity. Furthermore, as brought out by two extreme seasons, in a very dry summer (1897) the uredo stage appeared upon some beds which never showed it before or since, while in a season of excessive rainfall (1898) some of the places most affected with red rust in other years had only the teleutospores late in the season.

These facts were regarded as showing the indirect relation of the rust fungus to water. In the dry seasons and upon the drier soils lack of moisture unquestionably reduced the vitality of the asparagus plants. Consequently, they became more susceptible to disease and suffered in inverse proportion to the amount of soil moisture available. As to the direct relation of the parasite to water, the conclusion must be drawn from the observations of these investigators that the host-plant, depending upon the soil, felt the effects of unusual dryness to a more serious extent than did the parasite, thus turning the balance more strongly in favor of the latter; while, on the other hand, in a wet season or heavy soil the asparagus derived more benefit from such conditions than did the fungus, and thus the activity of the latter was checked. In other words, the fungus appeared to obtain sufficient moisture for its requirements even in the dry season, and received no proportionate invigoration from an excess of moisture in seasons of abundant rainfall. It is also indicated by these observations that the uredo stage is characteristic of conditions favorable to the fungus, while in the unfavorable seasons or localities no develop-

ment of the parasite took place until the plants began their natural loss of vitality at maturity, and under these conditions, when little nourishment was left for an active parasite, only teleutospores appeared.

Another side of the relation of *Puccinia Asparagi* to water was brought out particularly by Sirrine,[2] who, from his observations in New York, was led to conclude that the relation of the rust to atmospheric moisture in the form of dew or fog was the most important factor of this nature in the development of the disease. In the cases described by this writer the progress of the fungus seemed to be accelerated by excessive dew-fall, while with the absence of the latter the rust was less prevalent. In an asparagus bed upon a sloping hillside, for instance, the most rusty portion was at the base, decreasing with the rising grade. It has also been frequently observed that asparagus growing in the shade, as where a tree stands in the midst of a bed, remains free from rust when all about it is dead with the disease. This fact shows certainly that the protection thus afforded prevents infection by the fungus, and can be explained only on the ground of the prevention of dew being deposited. Stone and Smith maintained, however, that under ordinary conditions no such differences existed in their section as were observed by Sirrine, since some of the least rusted beds were in regions most subject to heavy dews, and in the case of asparagus growing on a slope, that at the bottom was likely to be least affected, on account of the usually heavier soil there. They held in regard to the influence of dew that, "when plants are not resistant enough to stand uredospore infection, it is not difficult to understand how this might take place, but the presence of any amount of dew fails to infect some beds in this state;" the beds referred to being those in heavier soil.

In the writer's opinion both of these theories as to soil and atmospheric moisture were correct, but modified by local conditions. In Massachusetts asparagus is grown upon a great variety of soils and showed from the first more decided differences in susceptibility to the rust than in any other section. These conditions were studied with great thoroughness by field observation and mechanical analysis of soils all over the state, and the conclusions arrived at have been

[2] Bulletin 188, N. Y. (Geneva) Exper. Station.

repeatedly verified from year to year. In New York and New Jersey large asparagus districts exist of practically uniform soil and of the nature characterized by the Massachusetts investigators as most favorable to rust. In these districts the disease became exceedingly virulent at first and completely exterminated the original beds, without regard to slight differences in soil or other features which are well marked in the new plantations of the same districts, now that the severity of the attack has somewhat subsided. Since dew is necessary for infection, it is but natural that where other conditions were equal, the progress of the disease should be temporarily marked by varying amounts of atmospheric moisture, but it must be said that throughout the eastern states dew is so generally abundant, even in the driest seasons, that nothing of permanent value can be credited to this relation. That dew is absolutely necessary to the development of the fungus seems proved from the effects of tree shade in asparagus fields, and this is the direct water-relation of this parasite.

Conditions in California with respect to soil and atmospheric moisture are totally different from those of any eastern state. On account of the long, rainless summers, marked differences in the natural conditions of various parts of the state, and the prevalence of irrigation, any question having to do with moisture problems can be followed with a degree of precision quite impossible under the natural conditions of the east. This refers particularly to the degree of dryness obtainable, both of soil and atmosphere, a degree approximated nowhere else in the country save in the adjoining semi-arid states. The principal asparagus-growing section of California has proved to be especially well-adapted to a study such as that herein described, and a description of this portion of the state must be given at this point.

If in the accompanying map (*fig. 3*) a triangle be imagined between the cities of Sacramento, Stockton, and Antioch, it will include, at a safe estimate, 5000 acres of asparagus. This country is at the confluence of the two great rivers of California, the Sacramento and the San Joaquin, together with a smaller stream, the Mokelumne, which enters the angle formed by the other two where they join. These rivers do not run directly into one another, but form, in the triangle just mentioned, a delta, composed of an intricate network of

channels, sloughs, and low islands. By extensive dredging and levee work much of this extremely fertile country has been reclaimed and brought into cultivation. The soil is a mixture of peat and

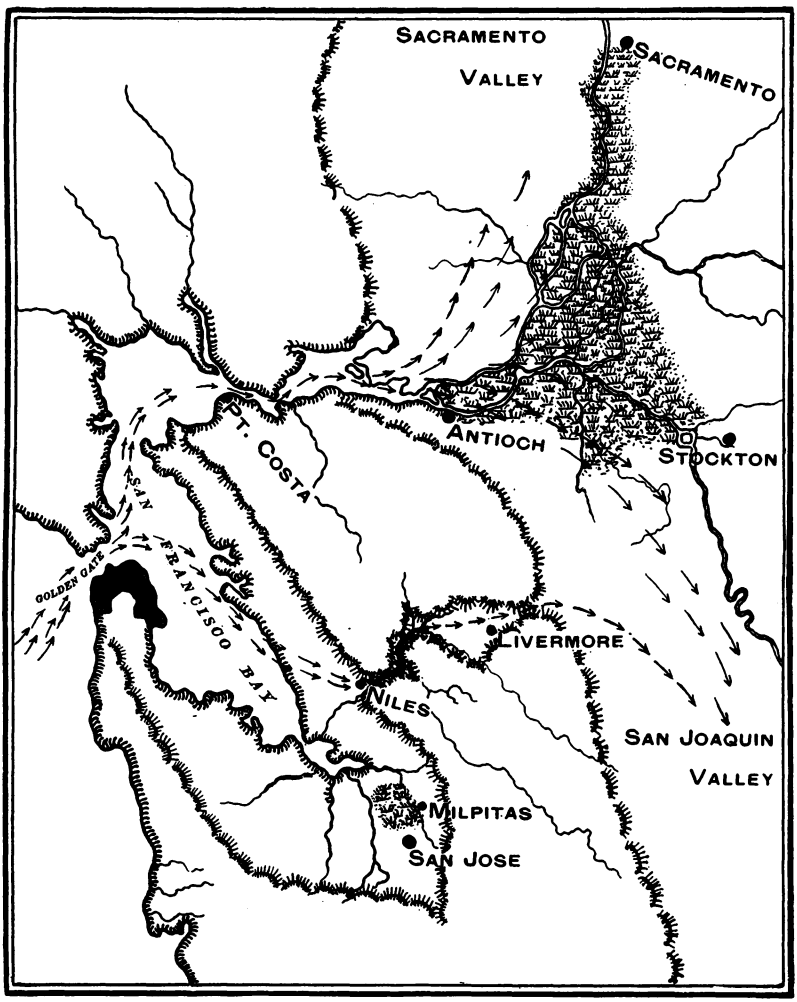

FIG. 3.—Map of central California, showing asparagus districts.

river sediment in various proportions, from almost pure formations of each to an equal mixture of the two. After reclamation and continued cultivation the level of these islands gradually sinks, and they become saucer-shaped, several feet below the river level outside

the levee (*fig. 5*). The soil is naturally full of moisture, but with levees, drainage, and rainless summers it may become extremely dry unless irrigated. Fires frequently occur in the peaty formation and cause serious damage. Irrigation is a simple matter in most cases, requiring only the placing of gates in the levee to admit and shut off the water.

While this country would at first seem to be one of excessive atmospheric moisture, the reverse is true in summer. Much of the reclaimed land becomes extremely dry, but most important is the position of this region directly at the opening of the great interior valley of California into San Francisco Bay and the Pacific Ocean (see *fig. 4*). Through this opening, formed by the Golden Gate at San Francisco and the Carquinez Straits at Port Costa, there blows in summer the strong, steady, so-called trade wind, coming in from the west, passing up through the straits, and then dividing north and south in response to the currents caused by the extreme summer heat of the great interior valley. In this asparagus country there occurs almost every day in summer a strong, dry, west wind which rises early in the morning and quickly dries what little dew may have been formed, except in sheltered spots. This wind, therefore, is an important and perhaps the chief factor in the amount of dew formation. Across the lower left corner of the triangle, where the wind is most constant, there is practically no dew in summer. Approaching the other two angles there is more, though much less than any eastern section.

At various points on the margin of San Francisco Bay are other asparagus districts, most important of which is that near Milpitas, comprising some 600 acres. This is situated, as may be seen, in a sort of pocket at the lower end of the bay, surrounded by high hills on both sides (*fig. 6*). The wind current coming in at the Golden Gate blows across the bay quite constantly and has a tendency to turn south toward Milpitas and the Santa Clara Valley below, but at Niles it is diverted into the interior valley through the Niles Cañon and Livermore Pass, which open through the hills at this point. Without lengthening this already extended description, it need only be said that this produces a condition at Milpitas much similar to that in the East as regards dew. Atmospheric moisture from the

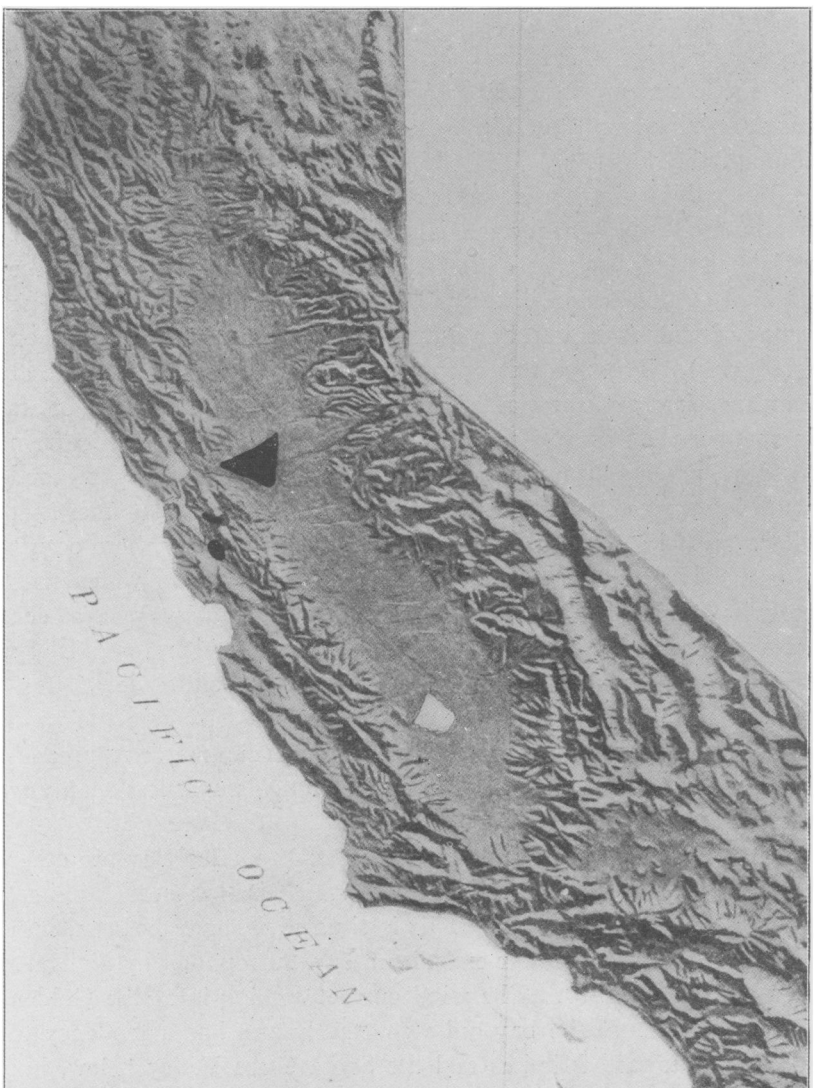

FIG. 4.—Relief map of California, showing the great interior valley and position of asparagus districts; Niles-Livermore Pass also indicated. Adapted from U. S. Department of Agriculture Yearbook, 1902.

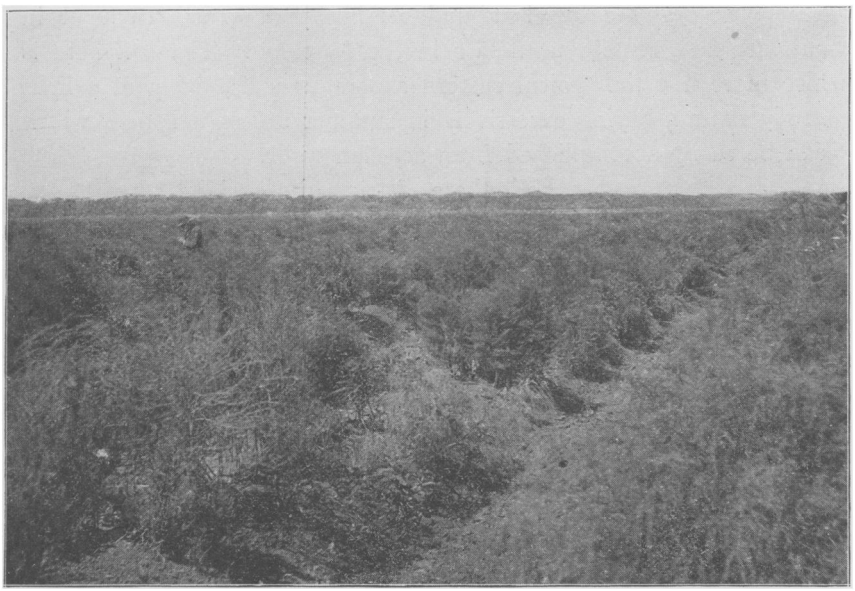

FIG. 5.—Typical island country, showing low level ground surrounded by levee.

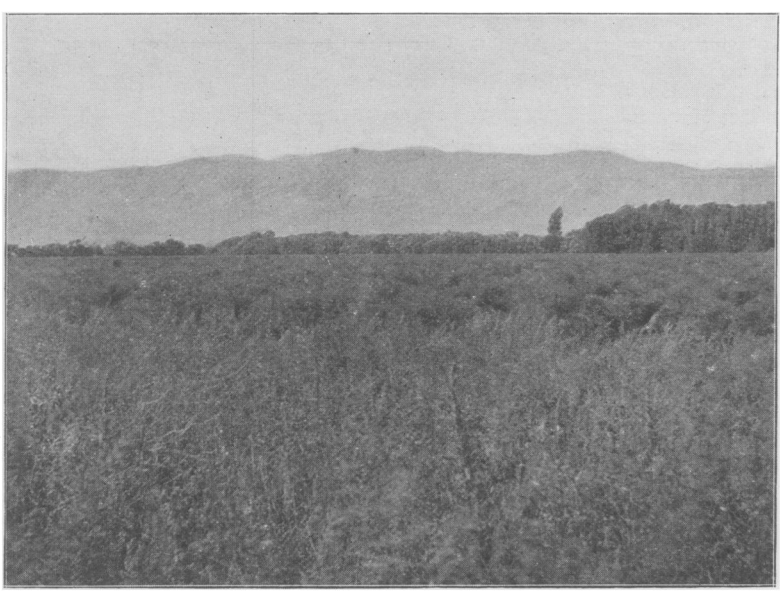

FIG. 6.—Typical asparagus field at Milpitas; high hills in distance.

nearby bay and ocean is abundant; heavy dews are frequent in summer and remain until late in the forenoon. The soil here is also more like the typical eastern asparagus soils, being of a light sandy nature, drying excessively in summer unless irrigated, which can be easily accomplished from artesian wells.

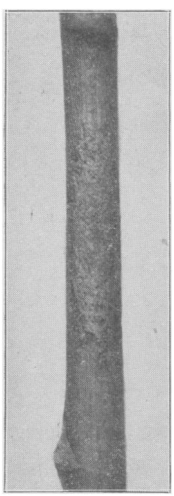

FIG. 7.—Aecidial patch checked by lack of atmospheric moisture. Grand Island, Calif., July 13, 1903.

In both these districts the aecidial stage of the asparagus rust is extremely abundant in spring, following the winter rains, the condition shown in *fig. 2* being of ordinary occurrence in large areas. As the season progresses, this is followed at Milpitas with the usual development of the rust about as seen in the east; the aecidia are followed by an epidemic of uredo on the main cutting beds, which kills the tops quite generally and turns finally into black rust as a final stage. In the river country the progress of the disease is not so regular. As the season changes from moist spring to dry summer, the effect shown in *fig. 7* becomes evident. This is an aecidial patch upon a young stalk which started in the usual manner, but as the air became drier and dews less abundant its development was checked. Soil moisture was abundant, but it is seen from this not only that the fungus requires atmospheric moisture for its spore-germination, but that a certain degree is also needed for the development of spores from the aecidial patches. At this stage the mycelium is

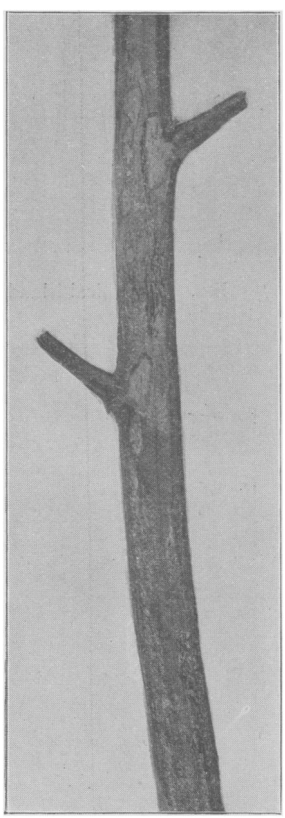

FIG. 8.—Aecidial patches drying out without developing spores; plant green and vigorous. Bouldin Island, July 28, 1903.

vigorous and ready for development, as may be proved by placing such a stalk in a moist chamber, when the "cluster-cups" break out in great luxuriance. This is another direct water-relation of the rust, therefore, being apparently a provision for developing aecidiospores only when conditions are favorable for germination. In the dry, windy districts such aecidial spots remain in this condition far into the

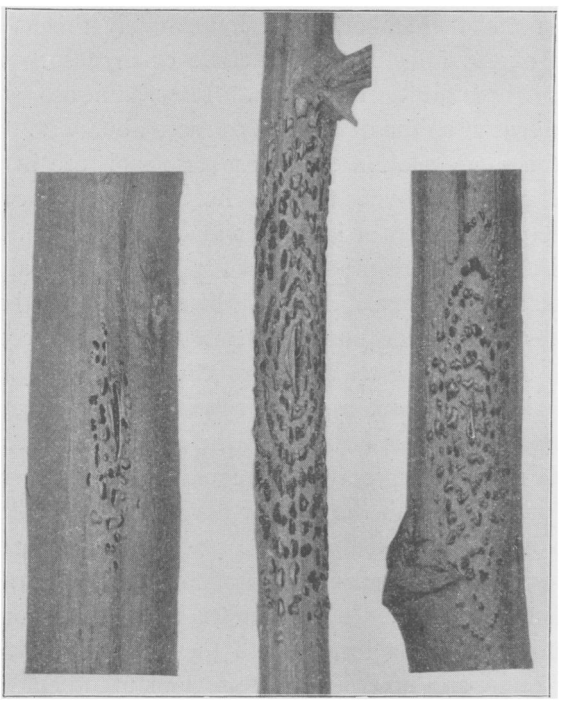

FIG. 9.—Uredo infection on green, vigorous stalks, checked and changed to teleuto by lack of atmospheric moisture. Bouldin Island, July 28, 1903.

summer. Finally, they pass into the state shown in *fig. 8*, the original aecidial areas drying out, leaving a feeble development of mixed uredospores and teleutospores about the edges.

Through the period of midsummer, from June to September, but little trace of rust can be found in most of this country. Careful search, however, reveals here and there on volunteer growth in sheltered nooks the condition shown in *fig. 9*. These are green

vigorous stalks, each with a single infection contracted earlier in the season, which now appears as an almost pure teleutospore formation directly on the green stalks. The value of these spores as reproductive bodies is doubtful, as they will not germinate at any time during the summer. Apparently this is rather the form assumed by the fungus under unfavorable conditions, when infection could not take place, producing only the resting, teleuto stage. If such a stalk be placed in a moist chamber, there immediately breaks out at the outer edge of the infected area a circle of uredosori, with spores capable of immediate germination. The same occurs in nature later in the season as the dew becomes more abundant. Here again is shown the same relation to atmospheric moisture in the case of uredo development, proving that the fungus not only requires moisture for the germination of its spores and for infection, but has the same requirement for the production of spore forms capable of immediate germination. Experiments by the writer show that both the aecidiospores and uredospores of this fungus are comparatively short-lived, but that the teleutospores are capable of lying dormant for long periods and have a strong relation to the effect of frost in their germination. This also shows the teleuto stage as not necessarily a fall rust, but as occurring regularly under other conditions extremely unfavorable to the further development of the fungus.

It is to be understood that these stages described are not individual cases, but the regular development of the asparagus rust in such a district as this. In September moisture becomes a little more abundant, varying locally with the amount of irrigation and other conditions, and now begins the regular uredo epidemic. This starts invariably in the island country in corners and low places sheltered on the west, such as are shown from actual experience in *figs. 10, 11, 12, 13*. These are all of the same nature and represent spots where uredo infection started two or three weeks before the main beds in the open were affected. It is scarcely necessary to say that such places will be avoided by growers in the future.

In the latter part of September the rust gradually works out into the open fields. The trade wind is now subsiding, but blows fitfully for days at a time. The disease still seeks shelter from this drying influence and appears first on the east side of north and south rows,

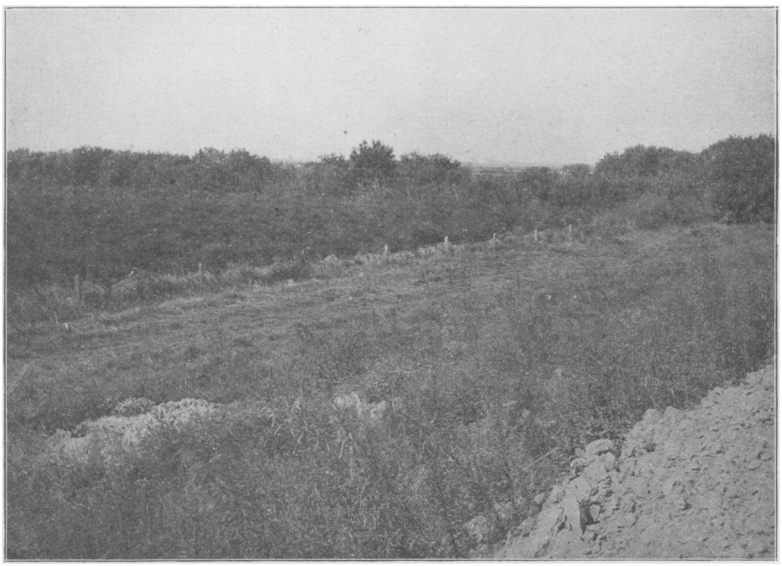

FIG. 10.—Corner of asparagus field sheltered from wind by willows and levee. Bouldin Island.

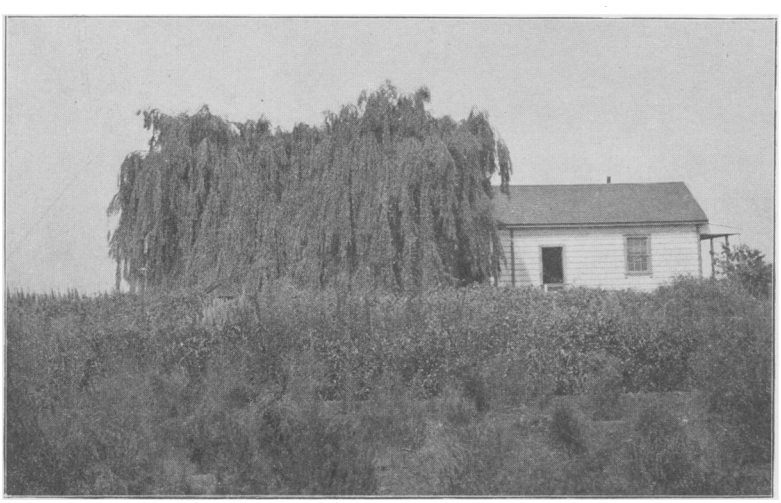

FIG. 11.—Bouldin Island schoolhouse, surrounded by asparagus fields and harboring rust on east side.

or in the sheltered places among the thick tops. Here it starts in scattered spots, each very distinct, and if uninterrupted continues spreading until late November, passing into the teleuto stage in the ordinary manner. The feature shown in *figs. 14* and *15* is, however, one of the most remarkable. In this particular instance the rust started in the uredo form in the scattering manner just described. *Fig. 14* is in a mass of tops sheltered by taller growth toward the west,

FIG. 12.—Old slough bed at Sacramento, with asparagus to left; starting point of rust. August 14, 1903.

and *fig. 15* is the east end of an east-and-west row. Just as this was well started (the condition all over the district was mostly the same), the wind revived in a very dry form and blew steadily for a number of days, with quite cold nights. Immediately the uredo rust on the green stalks turned to teleuto, the rust stopped spreading, and the fields looked exactly as though a fire-brand had been thrust into the green tops here and there, producing a black, dead spot in the green, healthy growth. The tops being still growing, new growth came up through, and the fields were spotted with these perfectly black, dead, teleuto-covered patches, surrounded by and in contact with

green healthy growth. *Fig. 16* shows a branch from the edge of the dead spot with pure teleuto development on the green thrifty branches. This condition lasted so long as the wind continued, then gradually reverted to uredo infection, and the tops all became affected. This shows more strikingly than anything else the effect of real atmos-

FIG. 13.—Asparagus at Sacramento, sheltered on west by trees; same effect as in *figs. 11, 12, 13.*

pheric dryness upon *Puccinia Asparagi* at this stage of its development, and the function of the teleuto form.

At Milpitas, where dew was quite abundant, though probably scarcely as much so as in the east, and no summer rains occurred, no such effects could be seen. Early in September everything was badly rusted. Even here, however, one feature in connection with the dew-relation is marked. This is the progress of the rust from top to bottom of the stalks, seen in all cases of the disease in this state. *Fig. 17* shows the condition well along in the season, the

FIG. 14.—Dead, rusty spot in green asparagus tops where fungus was checked by wind and changed to teleuto form. Bouldin Island, October 20, 1903.

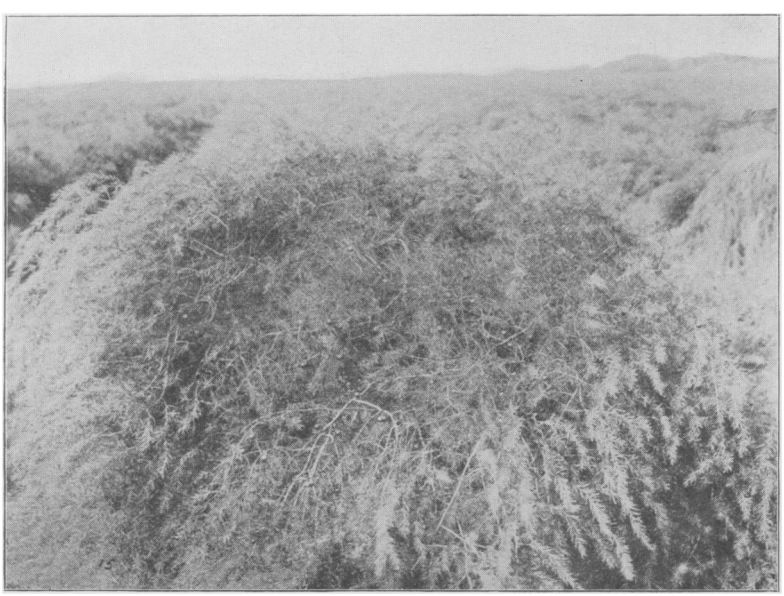

FIG. 15.—Same as *fig. 14*.

top shading and protecting the lower portion. *Fig. 18* shows the bed still later, a condition which in beds well cultivated often lasts until November. The writer has considered that this feature may be due to the absence of rains to drive the spores more rapidly down

FIG. 16.—Teleutosori on green branches at margin of spots as in *figs. 14* and *15*.

through the tops, as he has never observed it in the east. By the means shown in *fig. 19* the rust can be absolutely prevented in California, although in Milpitas the covering must be thicker than on the islands, where one thickness of light cheese-cloth is sufficient.

It may also be said here that from the writer's observations he has concluded that heavy rainfall has little to do in any section of the country with producing infection by the rust, since there is evidence to show that by this means the spores are actually washed from the smooth surface of the plant to a great degree, rather than being afforded opportunity for germination and infection. A copious, misty dew, remaining until late in the forenoon on the thick asparagus

FIG. 17.—Effect of rust at Milpitas, working from above downwards. September 23, 1903.

tops, appears to be the most important factor in producing infection. Experiments with uredospores, placed out of doors on dry glass slides night after night in various situations, support this view, as well as extended field observations. During rain the spores are washed from the slides and carried away. This would not occur so entirely upon the plant, but is true to a very large extent. During nights of very light dew no germination occurred. With slight dew, drying away early in the day, germination started, but the germ-tubes dried up before they would have had time for infection. Most

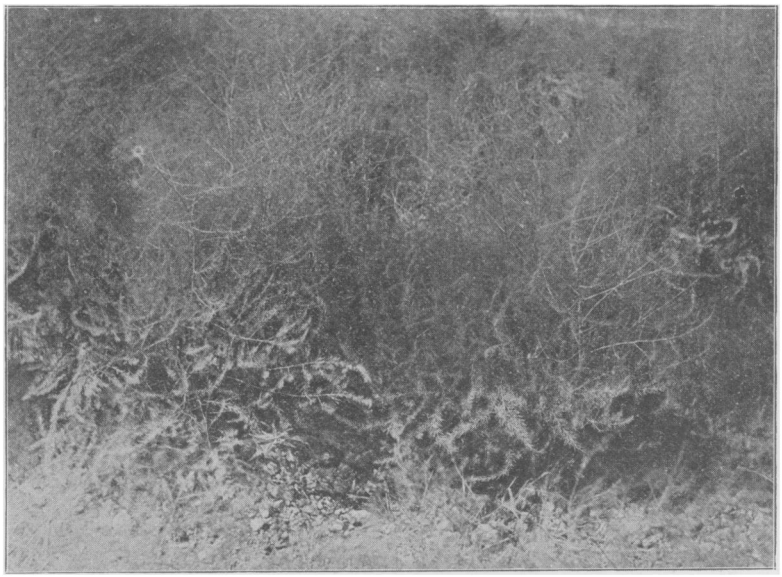

FIG. 18.—Condition late in the season of many California fields; green strip at bottom. November 1, 1903.

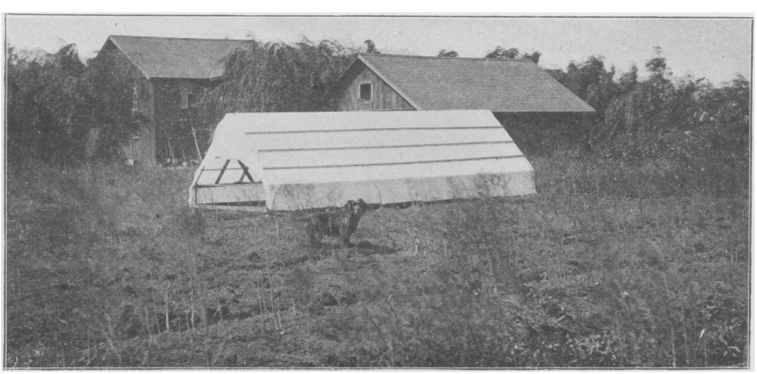

FIG. 19.—Tent over asparagus; tops just growing up. Bouldin Island, July 14, 1903.

of these dews seem to form just before sunrise in California, so that they exist only a short time. On misty nights, with heavy dew, a most vigorous germination takes place, easily sufficient to produce infection. It has even seemed to the writer that germination in this way is more vigorous than in drops of distilled or tap water placed on the slide, though no exact comparisons have been made.

Something remains to be said as to the influence of soil moisture upon the rust in California. In the island district the wind effects are so absolute that all other features are of secondary importance. Soil moisture increases the amount of dew, and since almost all this country has abundant natural subirrigation, it is desirable to keep the surface as dry as possible. In the case of one plantation, particularly, situated in the strongest wind belt and where the nights were particularly dry, no rust whatever has developed, though in a center of infection, although the soil became so dry through neglect that cracks opened six inches wide and four feet in depth, and the asparagus roots were almost killed. It should be fully understood, however, that in this case there was absolutely no moisture in the air to germinate spores. A sheet of tissue paper lying on the ground would be as dry and crisp at sunrise as at noon. Such conditions are never approximated in the east.

At Milpitas, with considerable dew on all the beds, differences in soil moisture are more apparent. Some of the beds here are left unirrigated and uncultivated in summer and become extremely dry. In these the rust makes much more rapid headway than in the irrigated beds, and the tops are killed to the ground, while the others still have the green bottom (*figs. 17, 18*) late in the season. It is a general principle, in fact, that in this district, where conditions resemble those of the east, except for the absence of summer rain, the driest beds rust first and most completely, while those kept wet throughout the summer are the latest and least affected. This could not be shown more plainly than by the field in which *fig. 20* was taken. In this case a stream of water was being run past the end of a very dry asparagus field for irrigating lower down. When the whole field back to the right was dead with rust, the end plants in each row, next the water, were green and vigorous, as shown in the illustration. It is difficult to imagine how more absolute proof

could be found than this. *Fig. 21* is along the same line, showing a low corner of a hundred-acre asparagus field, which portion remained green much after the tops in the drier portion of the field were dead. The water from irrigation accumulated here in the rusty season, with the effect described and illustrated.

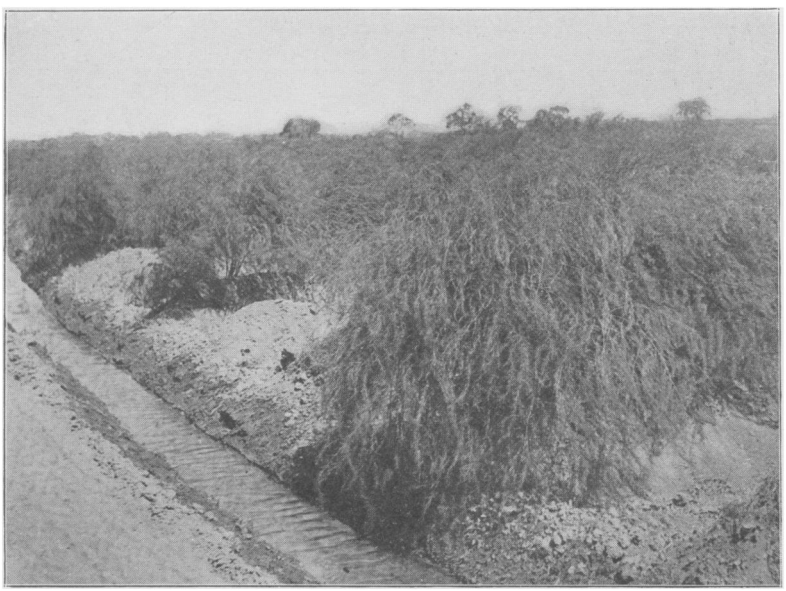

FIG. 20.—Effect of irrigation in region of dry soil and abundant dew. Near San José, Calif., August 20, 1903.

The water-relation of *Puccinia Asparagi* may be thus summarized:

DIRECT RELATION.

By direct relation is meant the effect of moisture (necessarily atmospheric, except possibly in connection with the germination of the teleutospores, which has not been touched upon) acting directly upon the spores or mycelium of the rust. This relation has proved to be of foremost importance when absolute conditions prevail. It has been attempted to show:

That dew is of absolute necessity in infection by the rust and of more importance than rain.

That without moisture of this sort no infection can take place, regardless of all other conditions.

That the effects of atmospheric dryness are not limited to the spore-germination, but produce the following effects upon spore production in cases of previous infection: Aecidial development is checked, no "cluster cups" appear, and the mycelium remains dormant for some time; if moisture conditions occur, spores are at once

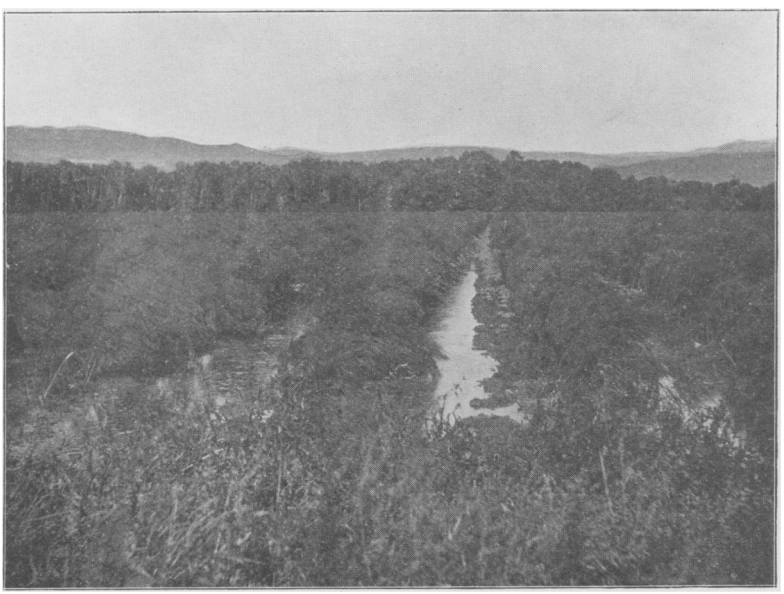

FIG. 21.—Showing same as *fig. 20*. Milpitas, August 20, 1903.

produced, otherwise the mycelium finally dies out. Uredo development is similarly checked and changes to a production of teleutospores in the sori already formed, without regard to season or condition of the host; with moisture uredospore formation begins again at once.

That the teleuto stage is a provision for surviving any condition unfavorable to the fungus, whether of food supply, moisture, temperature, or resistance by the host, without regard to season.

That extremes of atmospheric moisture conditions are insufficient in most sections of the country to bring out or make effective this direct relation.

INDIRECT RELATION.

By this is meant the effect of moisture acting upon the parasite through its effect upon the host, and limited therefore to soil moisture. It has been attempted to show in this respect:

That under any but very unusual conditions of atmospheric moisture the indirect relation is of greatest importance.

That an abundance of soil moisture during the summer has a marked effect in retarding the development of this fungus by giving the host greater vitality and resistance.

That this is shown by the effects of the varying summer rainfall in different seasons, by the differences in the water-retaining capacity of different soils, and by the effects of irrigation.

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