Ecological Aspects of Host Specialization in Fungi

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The role of fungi as parasites of higher plants has been recognized now for just about 100 years. And the significance of fungi as destructive agents, recognized centuries before their exact nature was understood, has led within the last fifty years to such advances in knowledge concerning them as can be duplicated in few, if any, of the other branches of natural science.

Because they are minute, obscure, and often secretive in their activities until they have done so much damage that human efforts against them are futile, the greatly merited investigations and researches aimed at finding means for combating them naturally have fallen into three chief categories: first, development of poisons which can be applied as preventives; second, life history studies, chiefly of a laboratory nature, aimed at an explanation of the obscurities of their existence; and third, discovery or breeding of races of plants resistant to their attack.

Control measures now in wide use are based largely, though it is true not entirely, upon knowledge gained in these three fields. Poisons, in the form of sprays, dusts, and washes, are used extensively as applications often intended for one parasite but as often acting more or less efficiently as blanket preventives of anything and everything that may happen along. Interruption of the normal progressions of life histories is the basis for barberry eradication in controlling stem rust on small grains, for *Ribes* eradication in controlling white pine blister rust, and for local eradication of red cedars in controlling cedar rust of apples. In recent years, agriculturalists have favored greatly the development of resistant varieties; and if the varieties secured have not always been as satisfactorily resistant as might be desired, certainly much has been learned about plant breeding, *per se*, and many varieties of crops have been obtained that are valuable in other ways.

More direct in approach, if less favored in research and in use, is physiological control, exemplified at one extreme by the hot water method of seed treatment, which differentiates so closely between the temperature resisting abilities of parasite and host, and at the other by the planting of crops in relation to soil temperature, which stresses differences between host and parasite in ability to grow.

Nearly ignored in research, and entirely so in practice as a means of control, though by no means omitted from extensive speculation as an influence in the development of wide-spread and destructive epiphytotics, have been the ecological relationships of parasite fungi. And plant disease specialists are by no means alone in neglecting this broad field. Plant ecologists have, to the present, dismissed fungi with few words and correspondingly little thought. Unfortunate it is, perhaps, that in science, as in society, size and conspicuous domination attract interest and command thought and effort to the exclusion of obscure, behind-the-scenes and, perhaps therefore, more influential relationships.

The sole point in all the foregoing is to bring out, with the emphasis incident to enumeration, that there is extant now in the science of plant pathology an accepted set of beliefs, on which present day practice is largely based, that is adhered to with much the same literality that the St. James version is accepted by many religious believers. And it is the purpose of the remainder of this paper to suggest, on the basis of a number of circumstances falling directly within my knowledge in the State of Illinois, that it is high time to examine with considerable care our original text, with a view toward modernization of our tenets in plant disease control as well as with the intention of stimulating new research and, what may be much more important, new and original thought.

One can have no objection to the present use of poisons. This is entirely a commercial matter, in which the collaborating interests of poison manufacturer and crop producer can be depended upon to increase effectiveness and reduce cost to the highest and lowest degrees possible. Neither is there much cause to discourage those who believe in the efficacy of plant breeding. It is, undoubtedly, a field without limit, exceedingly complex in its aspects, interrelationships, and consequences and worthy of most extended attention.

It is life histories, and particularly the thinking that is based on what we know about them, that I want to bring into question, today.

The first suspicion that dependence on current knowledge of life histories might be not entirely safe as a foundation for control measures came with the publication in 1927 of Craigie's[1] simple and conclusive experiments, which demonstrated the function of the pycnospores of the rusts.

For nearly a quarter of a century, in fact following the cytological researches of Sappin-Trouffy[2] in 1896 and of Blackman[3] in 1904, it had been supposed that the phenomenon of combination and resegregation of characters attendant on cross-fertilization had been reduced among rust fungi to a vestigial and only partially completed process accomplished entirely within the thallus unit. Craigie's effective experiments proved that cross-fertilization was by no means the vestigial process it had been supposed to be but was, instead, an absolutely necessary function accomplished upon the aecial or "cluster-cup" hosts, without which the life histories of many types of rust fungi could not be completed, and that instead of being accomplished in a vague sort of way within a single thallus it was accomplished in the regular manner by the crossing over of fertilizing cells from one thallus to another. The inescapable conclusion had therefore to be that the rust fungus organism, as to species, was not an agglomeration of specialized and stabilized races, but, instead, that the species were composed of constantly changing races and that the origin of new races with new characteristics, especially of parasitism, might take place whenever the fungus was inhabiting its so-called alternate host.

The bearing of this discovery of Craigie's upon control measures in practice and under development was naturally two-fold. In the first place certain control measures, such as Barberry eradication, were based on the assumption that if the alternate host could be eradicated or nearly eradicated, it would be impossible for the parasites to develop in quantities injurious to the economically valuable host. In the second place, with parasite races genetically stabilized in parasitic ability and invariable, as required by the life history of the parasite, it would be possible to develop races among the economic hosts which would be resistant to all of the parasitically differentiated races of parasites. The effects of Craigie's experiments were, first, to suggest the possibility that, with reduction in number of alternate hosts, some few of the continually changing forms brought about by recombination and segregation of characteristics among the parasites might possibly be adapted to survive without dependence on the alternate host and, second, that with continually changing characteristics in parasitism it would be impossible for geneticists to develop a sufficiently large number of resistant crop races or varieties, or any one race with resistance complete enough to assure escape under all circumstances from the ravages of the parasites to which they were supposed to be resistant.

The latter consequence is, of course, a matter for the consideration of a specialist in plant breeding. It presents questions that can be answered only after many years of experiment and it may in the end make the plant breeder's problem both the more difficult and the more interesting because of its increased complications. The real problem from the point of view purely of plant disease control lies in the first consequence. And of course we should ask, first of all, whether there is at hand any experience or knowledge which bears directly or indirectly upon it.

Within the State of Illinois we have every year experience with, among many, two diseases which it seems to me bear definitely on the problem. One of these is the well-known leaf rust, *Puccinia triticina*, of wheat. The other is the prevalent but not so destructive rust of corn, *Puccinia Sorghi*. Both of these rust fungi are known to have alternate hosts. That of the common and destructive leaf rust of wheat is a species of Meadow Rue (Thalictrum). The alternate host of corn rust is a species of the genus Oxalis, which includes the common sheep sorrel of gardens, *Oxalis stricta*. In spite, however, of the fact that the alternate hosts of both of these parasitic fungi are known, as a matter strictly of scientific information, to function in the life history of the parasites under at least experimental conditions, it remains an uncontrovertable fact that both organisms persist from year to year in some manner, so as to reattack each growing season, sometimes with disastrous results, the crops upon which they have become specialized, and do so independently of their alternate hosts.

These two examples have the disadvantage in the first place of being exceedingly well known, and in the second of being selected with respect to attacked hosts which are grown abundantly over exceedingly wide geographic ranges, so that variations in climate may readily account, if the proper type of reasoning is used, for the persistence of the parasites in milder-climated portions of the host range during those seasons when survival in the severer climates would seem impossible.

It is, therefore, desirable to search out other examples with a stricter and less critical bearing upon the question of alternate host and life history control. In the State of Illinois two of these are now available.

The first, it seems to me, is outstanding in particular respects. There is a rust, known technically as *Pucciniastrum americanum*, which has for its two hosts a spruce, *Picea canadensis*, and a bramble, *Rubus strigosus*. The natural range of both hosts lies much to the north of Illinois, and the range of the fungus on the first host is only known to include the Canadian province of Ontario, while the range on the second host has been reported to include territory as far south as Connecticut, Ohio, and Iowa. The striking circumstance in Illinois is this. The Latham raspberry, which is a very popular, cultivated red raspberry derived from the native host, *Rubus strigosus*, has been planted commercially in the extreme southern tip of the State, from Carbondale southward, and particularly on that east and west highland known as Villa Ridge. There is not any native alternate host, the spruce species, within many miles of these raspberry plantings. Yet unfailingly the rust makes its appearance upon the raspberries late in the season in the Villa Ridge region and as far north as the hills to the south of Carbondale. Here apparently is a case of a rust requiring two hosts for the completion of its life history, which has followed, in one phase only of its life history, the particular host upon which that life history is passed a very considerable distance, perhaps as much as 500 miles, south of its normal range, where it appears to propagate itself year after year in connection with its particular host and utterly without regard for the absence of the other host.

The second instance has to do with white pine blister rust. This destructive pine disease, caused by a fungus known as *Cronartium ribicolum*, has been known for a considerable number of years in New England and northeastward. More recently it has occurred in northwestern states. Within the last two years the white pine blister rust fungus has been found in Illinois on one of its hosts, *Ribes nigrum*. Infections have been definitely reported in Lake, Boone, Kane, and Winnebago counties. The natural range of the other host, white pine, in Illinois does not include any of these counties, and if white pine does occur in these counties it is only as an occasional decorative planting. It is important to note that up to the present time no case of infection of white pine blister rust has been observed in the State on white pine, either in the counties where infection has been found on the alternate host or in regions where white pine is native.

A point that seems full of significance in all of these cases, including the important rusts of cereals, is that the disease-producing fungus is able, by some means we do not now understand, to propagate itself through as wide a range as that occupied by its host and does so quite independently of the presence or absence of its alternate host. It is significant, also, that this propagation occurs in connection with a very definite phase of the fungus life cycle. This phase is usually, though not always, the one that attacks the economically important host. The significant thing about it, however, is not that it attacks the economic host but that it is the phase of the fungus which has a very definite means of abundant propagation by means of vegetative spores. In the case of the stem and leaf rusts of wheat and the rust of corn, there is a period known as the "red rust" stage, where propagation from one host individual to another takes place rapidly and freely. This likewise is true of the rust on the Latham raspberry and of the white pine blister rust on Ribes.

This fact may be considered to account for widespread infection of the host on which the fungus is found, but it does not account for the manner in which original infections of the host occur. We are unwilling to admit, what has often been maintained, that early spring infections must take place by means of spores produced on the alternate host.

It seems to me that there is room at this point for very serious thoughtfulness with regard to permanent interrelations between host and fungus. The suggestion that may be drawn from our examples is this, that any fungus parasitic upon plants, which has in any given part of its life history a definite vegetative reproductive phase, possesses a degree of adaptability that makes it possible for the fungus to exist and multiply in any region favorable to its host.

And if such an assumption as this can be tenable, a logical step is to admit that parasite and host constitute together a definite interrelationship, whereby in any environment, whether under cultivation or in nature, the multiplication of the host is restricted by the activities of the parasite and the multiplication of the parasite is conditioned by both the presence and the abundance of the host.

In the development of epidemics of plant disease, especially as they affect hosts or crops of economic value, a great deal of importance has been attributed to weather. This perhaps is the natural outlook from the standpoint of economics, since crop acreages, although varying in total from year to year, always remain so large that an abundance of hosts is always present and furnishes opportunity for large increase in parasite numbers through the growing season. But from the standpoint of the ecologist, who deals with the world's natural inhabitants, undisturbed by man's economic needs, it is perhaps more important to consider the relative effects of alternate increase in host abundance and increase in parasite abundance, followed by decrease in host abundance and more than proportional decrease in parasite abundance.

This in a sense may be looked upon as paralleling certain well-known zoological examples, where the rise and fall of large populations of rodents in the northern part of our continent is attributed to a similar but delayed rise and fall of predators, and possibly in some cases also of internal parasites.

From the ecologists point of view, it is also worthwhile to examine certain relationships of fungi which cannot definitely be said to be parasitic, and in this connection I should like to bring forward certain experiences that have occurred in our own laboratory.

During the past several years, we have been examining as a routine matter considerable numbers of chinch bugs, particularly for the purpose of determining the relative prevalence of the so-called chinch bug fungus, *Sporotrichum globuliferum*. These tests were begun in the late winter and early spring of 1935, following the exceptionally destructive outbreak of chinch bugs in the summer of 1934. That spring the chinch bug fungus was isolated without fail in our laboratory cultures from practically every sample of chinch bugs brought in from their dormant winter quarters. In the succeeding years, which have been characterized by diminishing numbers of chinch bugs during the crop season, the number of isolations of the chinch bug fungus has steadily decreased. And it has been remarkable that, during the winter just past, chinch bugs taken in dormancy in certain localities have yielded not so much as a single instance of the chinch bug fungus.

In the same connection, this also is of interest. In the late winter and early spring of 1936, the list of fungi isolated from chinch bugs was dominated by a type known as *Chaetomium*. Isolations are likewise made in our laboratory from diseased plants, particularly diseased trees, and it was a striking and noteworthy fact that during the same period the same fungus was commonly and abundantly isolated from diseased bark of trees, thus indicating some circumstance favorable to the development of this particular kind of fungus.

In succeeding years, *Chaetomium* has rarely been obtained in culture, but so far as the chinch bug work is concerned there has been a complete change of complexion in the lists of fungi obtained. It is significant that during the present late winter and spring we have not once obtained the Chaetomium fungus in culture. However, the greatest abundance of fungi tend to be those most definitely considered saprophytic and includes especially members of the two genera, Penicillium and Aspergillus. Whether this change in fungus flora accompanying chinch bugs in their winter quarters portends a renewed outbreak of chinch bugs dangerous to economic crops remains of course to be proved, yet the suggestion is very apparent that such may be the case.

While the points that have been brought out in the foregoing are not in the nature of exact and measurable data such as can be obtained and tabulated from laboratory experiments, it seems to me that they have an exceedingly important bearing upon the manner in which fungi should be regarded from the point of view of the ecologist. There is definite indication that certain types of fungi, particularly those which display the phenomenon known as heteroecism, may propagate themselves quite independently of alternate hosts and, in doing so, become controlling factors in determining the population of the plants upon which they are parasitic. This relationship applies not merely to plants economically important but particularly and especially to plants of interest and value from the purely scientific point of view. The inference is that fungi deserve a place in the thought of the ecologist, whether plant or animal, considerably larger than has hitherfore been accorded them.

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[1] Craigie, J. H. Discovery of the function of the pycnidia of the rust fungi. Nature 120:765-767. 1927.

[2] Sappin-Trouffy, T. Recherches histologiques sur la famille des Urédinées. Le Botaniste 5:59-244. 1896.

[3] Blackman, V. H. On the fertilization alternation of generation and general cytology of the Uredineae. Ann. Bot. 18:323-375. 1904.