THE SPECIES CONCEPT FROM THE POINT OF VIEW
OF A PLANT PATHOLOGIST

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To the plant pathologist the problem of the species concept is not only of academic interest but also of intense practical importance. While pathologists as well as other botanists love to seek truth for truth's sake, most of them are under obligation to seek the truth for the good it may do in the complex process of preventing the world from starving. The delimitation of species is prerequisite to the experimentation and research of the pathologist. It is essential that the specific purity both of the host plant and of the pathogene be known. If these fundamental facts are not assured, the pathologist is likely to find not truth but error; or, at best, the truth is in danger of being badly garbled. The accurate description of species, then, is of primary importance, but it is not an end in itself, but only the means to an end. However, being the means to an end, the accurate description of pathogenic fungi is of greater practical importance to pathologists than to any other class of botanists.

It is to be hoped that there will be no unduly severe criticism on account of what may seem to some an ultra-utilitarian viewpoint. The fact is that the pathologist must learn the effect of pathogenes on the host plant. In order to do this, he first must know thoroughly both the pathogene and the host plant. He must depend, therefore, on systematic mycology and other systematic botany for the tools of his trade. If the tools be unsuitable for his work, either he must improve them or he must make his own. Therefore it is pertinent to inquire what quality of tools have been furnished him in the past.

To the taxonomist of higher plants, and particularly to the geneticist, the pathologist is indebted for the proper attitude toward the host plants which he uses. The geneticists have given us the pure-line conception for higher plants. Pathologists now are avoiding many serious mistakes by taking the simple but fundamental precaution of using pure-line host material. For example, wheat generally has been considered to be close-pollinated. But Hayes has shown that natural crossing may occur in the field. Supposing, then, experiments are made on the biologic specialization of pathogenic fungi attacking varieties of wheat; what reliance can be placed upon the results when bulk material of wheat seed is used? Some of the plants very likely will be heterozygous for resistance. This may

1 Read in the symposium on "The Utility of the Species Concept," at the joint meeting of Section G of the American Association for the Advancement of Science, the American Phytopathological Society, and the Botanical Society of America, at Toronto, December 28, 1921.
lead to the deduction of entirely erroneous conclusions regarding the pathogenicity of the parasite, especially when the experiments are being made by investigators who are a little over-zealous in detecting evidence of inconstancy in pathogenes. Serious mistakes of interpretation often are made on account of the use of supposedly pure, but actually impure, host material. It is not sufficient for the careful investigator of wheat diseases, especially when fundamental relations are being sought, to know which variety he is using, but he also must be sure that he is using a single pure line of that variety.

If it is true that the greatest caution is necessary to assure the use of pure lines of host plants, it certainly is true that still greater precautions must be taken to use "pure lines" of the pathogene, because it usually is more difficult to detect genetic differences in the lower organisms. Does the practice under the present species concept give the pathologist the necessary assurance regarding the specific purity of the pathogene?

It will be agreed, at least by most pathologists, and I believe by many mycologists, that pathologists often have derived but little aid and comfort from published descriptions of pathogenic fungi. Possibly this has been due not so much to the lack of a proper species concept as to the failure properly to apply that concept. Until recently species have been delimited primarily on the basis of morphology. But the pathologist cannot be content to know what fungi look like; he must know also what they can do, because that is his primary concern. He is compelled to study fungous behaviorism, and, in so far as morphological descriptions aid him in this study, they are extremely valuable. It probably is superfluous, however, to state that morphology alone no longer can be considered a sufficiently accurate basis for determining the specific purity of many organisms.

It would scarcely be profitable, even if it were possible, to define species. In general, however, as applied to fungi, the concept seems to be based on the general underlying ideas, (1) that all the individuals comprising a species are sufficiently alike morphologically to make it possible to differentiate them from individuals of other species by means of morphological characters, and (2) that the characters are relatively stable through successive generations—"a perennial succession of like individuals," according to Farlow.

The grouping of individuals into species, then, is an attempt to make it possible quickly to recognize closely related plants and to call them by name readily. The morphology of the fungus has been used as a criterion of essential similarity of individuals. And unfortunately it often also has been misused. The careless, premature, and rather reckless naming of new species of fungi has been a tremendous handicap to the pathologist. Everyone is so familiar with the unfortunate consequences of this tendency, now happily disappearing, that it is scarcely necessary to cite specific examples. Too often temporary modifications, which are not inherited at all, have
been used as a basis for the multiplication of one true morphologic species into several imaginary ones. And, on the other hand, several distinct species sometimes have been described as a single species, either on account of faulty technique or on account of the fact that the range of conditions under which the fungi were studied was not sufficiently wide to make possible the detection of differences which become apparent only under certain environmental influences. The range of variability of many species of fungi is very wide. The character of growth, the ability to reproduce, and the morphology of the organism may be influenced profoundly by the amount and kind of food available and by environmental conditions. Klebs, Thom, Coons, Duggar and his associates, and other investigators have demonstrated this conclusively.

The pathologist is vitally interested in knowing the morphology of a pathogenic organism, not only on one host and under one set of physico-chemical conditions, but under all possible conditions. And he is especially concerned with the question as to whether essential morphologic identity means also essential physiologic identity. In fact he knows that in many species it does not.

Every one now knows that there may be physiologic races within a morphologic species, and there has been a growing tendency, therefore, to use physiologic characters for the delimitation of species. The bacteria in general are separated into species on the basis of their physiological reactions, and very little objection is raised. There also is a tendency to use physiologic characters more and more in systematic work on fungi. The taxonomic work of Appel and Wollenweber, and of Sherbakoff on Fusarium, and of Thom on Penicillium was based not only on morphologic, but also on cultural or physiologic characters. More and more the description of species is being based on material grown on standard media or on several hosts, and under known conditions. Unless this is done, descriptions often mean nothing, because the so-called species may contain not only several morphologic, but also several physiologic, races.

There seem to be different degrees of specialization into biologic forms, specialized races, chemical species, Gewohnheitsrassen, physiologic races, or whatever one chooses to call them. These terms were not all used exactly synonymously originally, but, since the differences represented by the terms seem to be in degree rather than in kind, they are all called biologic forms in this paper. These forms supposedly are practically indistinguishable morphologically, although slight differences are known to occur; but they differ decidedly from each other in their physiologic action. There would seem to be several classes of such forms, although the categories into which they can be placed may represent no really fundamental differences.

Dox has shown that there may be such distinct chemical differences between species of Penicillium and Aspergillus that the species can be recognized more easily by chemical than by morphologic characteristics.
Among pathogenic fungi similar chemical differences apparently exist; there appear to be distinct forms of Sclerotinia sp., causing brown rot of stone fruits in the United States, which consistently produce strikingly different types of growth on various synthetic media. The differences between biologic forms of Erysiphe, of Puccinia graminis, of Puccinia coronata, and other pathogenic fungi, no doubt also are chemical, although the exact nature of these differences has not yet been ascertained. It is significant, however, that the reaction of several biologic forms of P. graminis "tritici" to hydrogen-ion concentration differs perceptibly. Whether the physiologic differences between biologic forms can be detected on artificial culture media or only by the action of the forms on host plants, it would seem that the nature of the difference is essentially the same—that is, physico-chemical.

Why were biologic forms not called species when first discovered? Probably because the morphological concept of species had become so firmly fixed that it was considered too heterodox to use physiologic differences as a sole basis for classification. Furthermore, morphologic differences were considered more permanent than physiologic differences. But, even as early as 1898, Farlow read the following to the Botanical Section of the American Association:

When therefore the botanist denies that physiological species are properly species, he is practically admitting that his own definition, the perennial succession of like individuals, is used by him in a special sense, and he does not seem to be aware that species as he limits them are artificial and not natural. The belief that species should be based on morphological rather than physiological characters rests on the assumption that the former are more likely to be inherited and thus show the temporary attempts of the organism to adapt itself to the environment. It is perhaps a question whether the grounds for this belief are as valid as has been supposed. We readily see the morphological characters which have been inherited, but it is usually only by accident or experiment that we recognize the physiologic or pathological qualities.

Biologic forms long were considered to be unstable. Ward, Salmon, Freeman, Freeman and Johnson, Pole-Evans, and Johnson all obtained evidence which led them to conclude that the parasitic capabilities of biologic forms of Puccinia dispersa, Erysiphe graminis, Puccinia graminis, and Puccinia phleipratensis easily could be changed by bridging hosts and by other influences. The results of these investigations indicated that biologic forms readily acquire the ability to parasitize normally immune hosts, provided they are grown first on some closely, or sometimes even distantly related, susceptible species of host plant. Thus P. graminis tritici is incapable of attacking oats, but can grow on barley. On barley, according to Freeman and Johnson, the rust acquires the ability to attack oats slightly, presumably on account of some chemical change in the biologic form. If biologic forms could be changed so easily, the objection to using their physiologic characters in classification certainly would be valid. But do they change easily?

The so-called plasticity of biologic forms of Puccinia graminis has been
investigated thoroughly. For ten years the writer and various colleagues have tried in every conceivable way to change the hereditary parasitic capabilities of *P. graminis tritici* and *P. graminis secalis*. Considerable work also was done with *P. graminis phleipratensis*, *P. graminis avenae*, *P. graminis agrostis*, and *P. graminis tritici-compacti*. It was impossible to induce hereditary changes, or, indeed, any fundamental changes, although the growth of these fungi, like that of other plants, is influenced by environmental conditions. These biologic forms were as constant genetically as were the species of wild and cereal grasses upon which they were cultured. There was no evidence whatever that the inheritance of physiologic characters by these biologic forms depends any less upon real germinal specificity than does the inheritance of structural characters in morphologic species. Reed states that “in studying the races of *Erysiphe graminis* one also gets a strong impression of their constancy and definiteness and they seem as real as though separable by structural features.” Dox concluded that species of *Penicillium* and *Aspergillus* could not acquire new ability to produce enzyms by any special methods of nutrition; and Brierley was unable to “educate” *Botrytis cinerea* unless the initial culture consisted of a mixed population, although a form with colorless sclerotia did suddenly appear from a single-spore strain. This phenomenon, however, can be explained on the basis of known principles of genetics. Brierley points out clearly that it is quite essential to use pure lines of the organism in “fungus-educability” studies. This point can not be emphasized too strongly. Any one is likely to obtain very striking evidence of rapid changes of biologic forms unless his supposed biologic form itself is pure. For example, until a few years ago it was supposed that the *tritici* form of *P. graminis* could change readily. But the so-called *P. graminis tritici* itself consists of at least thirty-seven biologic forms which can be distinguished from each other readily by their action on certain pure-line varieties of various species of *Triticum*. All of these forms develop normally on various pure lines of *Triticum compactum* and apparently also on several wild grasses. It would be strange, in using such mixed cultures, if changes were not observed. Those hosts which were attacked by several of these forms naturally would appear to act as bridges to the normally immune forms. The longer one works with these forms, the deeper becomes the conviction that they represent as real, as constant, and as genetically pure entities as do morphologic species.

But many biologic forms differ from each other not only physiologically but morphologically as well. The forms of *P. graminis* which are separable on the basis of their action on different genera of host plants (in the United States) can be recognized by the size, shape, and color of the urediniospores and also by the size of teliospores and aeciospores, provided these spores are developed on hosts of the same approximate degree of susceptibility and in approximately identical environmental conditions. The differences
between some forms may be only two or three microns, but these differences easily can be recognized by quantitative methods; and they are as constant as are the differences between many recognized species of fungi. There is a consistent average difference of ten microns between the length of the urediniospores of the tritici form and that of urediniospores of the agrostis form. But even if there were no morphologic differences, these biologic forms are distinct and constant pathogenically, and we must recognize their existence.

In a recent paper Brierley expresses views similar to those expressed in this paper and makes the concrete suggestion that Lotsy’s terminology, proposed for the phanerogams, be modified to meet mycological needs as follows. He suggested that the term linneon replace the species in the Linnaean sense—the description being based on morphological grounds only; jordanon would be based on morphological characters which were demonstrated to be transmissible; and species would be established only on the basis of morphologic and physiologic reaction under standardized conditions. The term modification would be used to designate non-transmissible effects of external conditions. Whether or not this terminology is adopted, the principles involved are worthy of serious consideration.

The physiological concept already has been added to a certain extent to the morphologic concept of species. We raise no particular objection to basing the determination of a species of the Uredinales partly on life history, and all pathologists use physiologic characters in establishing species of phytopathogenic bacteria. If everything which the pathologist must know is classified, it will be necessary to add more and more of the physiologic concept. The simple fact is that as scientists we ought to want to classify plants on the basis of those characters which are really characteristic, whether they be morphologic or pathologic, and as practical pathologists we must do so. We shall no doubt encounter difficulties, but, as technic becomes more standardized and refined, it will become possible to recognize still less obvious differences in species of pathogenic fungi than we now do.

If the criticism be made that the proposed recognition of physiologic characters in classification would be drawing too fine distinctions, all that can be said is that the real distinctions were drawn by Nature; and, if we are dealing with pathogenic fungi in a practical way, we must recognize these distinctions; and, if we are seeking the ultimate truth regarding fungi, surely we ought to accept it in plant behavior as well as in plant structure.

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