BRIDGING HOSTS

by

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For success in breeding disease-resistant varieties of plants it is of fundamental importance to know whether pathogenes and their biologic races can acquire the ability to parasitize newly developed immune and resistant hosts. If it is a rule that a highly resistant plant may occasionally become mildly infected by some pathogene, and if it is possible that this parasite, as a result of its sojourn in the host, can acquire increased virulence, then the outlook for successfully growing resistant varieties is not very hopeful.

Some examples, gathered from experience and from the literature on plant-parasitic nematodes seem to prove that adaptation to new hosts, as well as weaning nematodes away from hosts to which they are accustomed, are very common phenomena.

In the North of Holland, in the province of Groningen, *Heterodera Schachtii* Schmidt was a very common pest of oats in the last decades of the nineteenth and the first decade of the twentieth century. Since that time the percentage of arable land planted with oats has decreased from 25-27, during 1870—1910, to 18 in 1924, and H. Schachtii has now become rare in Groningen. In the south of Holland H. Schachtii has become a pest of sugar beet since the time that it lost its importance for oats in the North. The area of arable land planted with sugar beet in the South, in the province of Zeeland, has increased from 4—18 per cent., during 1870—1910, to 29 in 1924. (Kalisvaart 1927).

Baunacke (1923) mentions, amongst others the following case; on a field where sugar beets were badly infested with Heterodera Schachtii Schmidt, barley was grown for three successive years. During the first two years no injury became apparent, but in the third year it suffered heavily under the attacks of the nematode.

Liebscher (1892) describes what happened on an experimental plot, where peas had been planted continually for about thirteen years; they became badly infested with H. Schachtii. In the immediate neighbourhood oats had been planted for seventeen successive years; this plot also at last became highly infested with the nematode. But when both plots, separated only by a path of one metre in width, were planted subsequently with a number of crop-plants in order to find out how the nematode would behave towards them, it turned out, that the nematode that had lived for years on peas had acquired parasitic abilities quite different from those of the nematodes that had lived on oats; the former attacked peas and related Leguminosae only, the latter attacked oats, sugar beets and Cruciferae.

A large number of similar observations concerning H. Schachtii could be added. As we understand the situation well this nematode can adapt itself to new hosts little by little, and only after some considerable time can it become truly specialized on them. The number of plants on which it has been found parasitic has gradually increased; in recent manuals on plant diseases about 60 species of host plants are enumerated.

It is probable that similar conditions apply to *H. radicicola* Greef, for which pest 500 hosts belonging to the most different families have already been found, and to *Tylenchus dipsaci* Kühn, which is known to attack about 100 different species of host plants.

Quanjer (1927) found the stem eelworm, *T. dipsaci,* on permanent meadows in a number of wild hosts such as Ranunculus repens, Cardamine pratensis and Trifolium repens. The nematodes in these plants were entirely unspecialized. Whereas about 70 species of host plants for the stem eelworm had been enumerated by Ritzema Bos (1922) the present author succeeded in infecting about 30 species of plants not yet known as hosts, with the polyphagous T. dipsaci from the meadows.

On the other hand, in the bulb growing district of Holland, Van Slogteren (1923) has found strains of *Tylenchus dipsaci* which possess a high degree of specialization. The strain which he finds in hyacinths is not able to attack daffodils, nor will the daffodil strain attack hyacinths. According to Ritzema Bos the specialization of such strains of eelworms is not constant. If the ancestors of a population have lived for a number of generations on a single species of host plant, their descendants will not attack any other plant known to be their host, only a host plant of near relationship will be attacked, and that only with difficulty and in small numbers. It requires generations before this new host is again attacked to the same degree as the old one. From this host the nematode can adapt itself to another new host, and so on. Steiner (1925) agrees with this conception and bases it upon the morphology of the parasitic forms involved.

Although the term „bridging species" has not yet been used by Ritzema Bos or Steiner it is clear that, provided they are right, it must be possible to attract the offspring of a specialized nematode to all the known host plants by changing the host for the succeeding generations in such a way that each following host would be of the closest relationship to the foregoing one. It will even be possible by using the known hosts as „bridges" to infect plants not yet known as hosts. The experience of the present author with the stem eelworm of the meadow is in favour of this conception, though a lot of experimental work is still required to prove its correctness beyond doubt.

Similar „educability" has also been met with in the relation between plants and bacteria, although the situation in plant pathology has not been investigated on such a wide scale as in medical science. Honing (1913) found that *Bacillus solanacearum* E. F. S., cultivated *in vitro*, often loses its virulence quickly. This loss does not make its appearence at once, but gradually, first towards Capsicum annuum, later towards Nicotiana tabacum, and finally towards Solanum melongena and S. lycopersicum. Strains from tobacco which failed on Capsicum became infectious to this plant after having passed through Mucuna sp. Honing concludes from his experiments that the differentiation of the slime bacterium of tobacco in Japan as *Bacillus nicotianae* Uyeda from *B. solanacearum* E. F. S. is invalid since it is based not on genetic differences but only on partial and restorable loss of virulence.

There is a great deal of analogy between these results of Honing who included *B. nicotianae* as an invalid species in *B. solanacearum*, and Ritzema Bos who relegated *Tylenchus allii* Beyerinck, *T. hyacinthi* Prillieux, *T. Havensteinii* Kühn and *T. Askenasy* Bütschli, as invalid species, to *T. dipsaci* Kühn.

Another analogy is the ever increasing number of host species of B. solanacearum. Honing found it as a parasite not only of Solanaceae, but also of Urticaceae, Leguminosae Verbenaceae and Compositae. Palm and Jochems (1924) extended the number of families in which it has been found as a parasite to 15.

The parasitism of the Uredinales, Erysiphaceae and Peronosporaceae' is of quite another type to that of the eelworms and bacteria described above. The rusts, powdery mildews and downy mildews are obligate parasites; their contact with the protoplasts of their hosts is a very intimate one, and their faculty of distinguishing generic and specific peculiarities is not only highly developed but also hereditarily fixed. Whereas the number of known hosts of parasitic eelworms and of the brown-rot bacterium is steadily increasing, the rusts, powdery mildews and downy mildews are split up into physiologically and morphologically distinct entities, narrowly and constantly limited to one or a few nearly allied species or varieties of hosts.

Eriksson (1894) was the first who recognized „formae speciales" of *Puccinia graminis* in Sweden; one of them, *P. graminis tritici* Eriks. & Henn., can only affect wheat, barley and some wild grasses; another, *P. graminis avenae* Erikss. & Henn., affects oats and a number of wild grasses; a third, *P. graminis secalis* Erikss. & Henn., affects rye, barley and many wild grasses, and so forth. E. Marchal in Belgium, amongst others, detected a similar specialization in *Erysiphe graminis*. One strain can infect oats and Arrhenatherum elatius, but not other grasses; another, certain species of Bromus only; another, wheat and related species of Triticum; while still others affect barley and rye and various groups of wild grasses. Gäumann (1918) and others recognized similar specialized forms in *Peronospora parasitica* (Pers.) Fries.

A more systematic testing of wheat varieties for resistance to different biologic forms is in progress in the United States. In the fifteen years during which Stakman and his co-workers have been analysing the old „formae speciales" of Eriksson, by means of their reaction towards 12 „differential hosts", they have succeeded in isolating 37 biologic forms of P. graminis tritici (1922), 5 biologic forms of P. graminis avenae (1923) and several of P. graminis secalis. They subjected the ability of these biologic forms to change their feeding habits to a very thorough test (1918). It proved to be impossible to induce heriditary changes when they used pure-line host material and mono-spore cultures of the pathogenes. They came to the conclusion that these biologic forms are as constant genetically as are the species of wild and cultivated grasses upon which they were cultured, and they believe that earlier investigators were led to erroneous conclusions by the use of impure host material and of mixtures of biologic forms of the rusts. Hosts which are attacked by several of these forms may, of course, give the impression of acting as „bridges" to normally immune plants; and the same holds true for hosts not belonging to pure lines.

Reed, in his experiments with biologic form of the grain mildew, comes to the conclusion that they are as constant as if they were separable by structural features.

Indeed, Stakman and others found that many biologic forms of rusts differ from each other not only physiologically but morphologically as well. Many forms of P. graminis can be recognized by the size, shape and colour of the uredospores, and also by the size of teleutospores and aecidiospores. These differences are as constant as are the differences between many species of fungi. Thung was the first who described morphologically different forms of *Peronospora parasitica* of cabbage (1926). Morphologic differences between biologic strains of this fungus were also described subsequently by Gäumann (1926).

It may be concluded from the foregoing that the biologic forms of rusts and powdery mildews must be recognized as species, and that they are resistant to the modifying action of „bridging hosts", in contrast to the above mentioned specialised eelworms and bacteria, the parasitism of which is liable to modification by „bridging hosts" and other influences.

As regards the question whether bridging hosts exist for groups of fungi with rather specialized, but not obligate, parasitism, consideration may be given to the genera, Colletotrichum and Gloeosporium. The occurrence of biologic forms has been detected in the last decade in nearly every group of fungi, but the genera named above have a peculiar ability to produce aberrant forms. One of the most remarkable is a form of *G. fructigenum* Berk., found in Holland on *Phaseolus multiflorus,* which host acted as a „bridge" between apple and tomato on the one hand and runner bean, *P. vulgaris,* on the other. The discovery of this fact is due to H. R. A. Muller (1927). From his publication some details may be of interest:

An investigation was first made of four biologic forms of *Colletotrichum Lindemuthianum* (Sacc. et Magn.) Bri. et Cav., isolated in Holland. It was proved by the method of differential hosts, that they were not identical with the strains of the fungus found in America. Constant differences were found not only in their power of infection for bean varieties but also in the mode of infection and in physiological and morphological characters. Then a Gloeosporium was found on a diseased pod of Phaseolus multiflorus growing under an apple tree; isolated on agar plates it showed great differences in mode of growth as compared with strains of C. Lindemuthianum. In order to compare the Gloeosporium with the Colletotrichum strains inoculation experiments were made on the bean varieties which had served as differential hosts; only one plant of one of the varieties became heavily attacked, and this plant, which differed in genotype from the others, exerted a peculiar influence on the fungus. After re-isolation in single spore cultures, two morphologically new forms of Gloeosporium developed, one of them with markedly increased virulence for beans. Inoculation experiments with the Gloeosporium isolated from P. multiflorus on apples and tomatoes and, re-isolation from these fruits, resulted in the development of a Gloeosporium with increased virulence for these fruits, differing however in some details from the available German and American strains of G. fructigenum. It was named *G. fructigenum* forma *hollandica.*

In these experiments Phaseolus multiflorus has played the role of „bridging host". The fungus isolated from the pods of this bean species had a decreased virulence for apples and tomatoes. After passage through a plant of Phaseolus vulgaris, which also acted as „bridging host", a form was isolated with increased virulence for P. vulgaris, with larger conidia, resembling a little more the conidia of C. Lindemuthianum, and having further decreased virulence for apples and tomatoes. The question arises whether this adaptation cannot go still further, so that forms may arise which produce setae in the acervuli, and thus will belong to the genus Colletotrichum.

In conclusion we may state that by the investigations of Stakman and his American colleagues „bridging hosts" have been banished from the Uredineae, but that the studies of Muller in Holland have introduced them in a genus of non-obligate, but specialised parasitic fungi i.e. the genus Gloeosporium. The „bridges" he found not only led at once to a definite new host plant but also to very notable new morphological characters.

In the groups of eelworms and bacteria „bridging" is a much slower process, leading step by step to nearly every family of plants.

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