Can Horizontal Resistance be Recognized in the Presence of Vertical Resistance in Plants Exposed to a Mixture of Pathogen Races?

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Vanderplank (5) distinguished vertical (VR) from horizontal resistance (HR), the former being characterized by the presence, the latter by the absence of differential interactions between genotypes of the host and genotypes of the parasite. He clearly meant two different types of resistance governed by different genes. Nelson (3), however, assumed that VR and HR are conditioned by the same genes depending on the genetic backgrounds of the host and pathogen genotypes. According to Nelson (2), residual effects of VR genes after being overcome by corresponding races of the pathogen would give HR.

Irrespective of the underlying mechanisms, the breeder (who wishes to select for HR) often is confronted with a host population varying for both VR and HR. In such cases, the breeder frequently uses a broad mixture of pathogen races to reduce the variation due to VR and to enhance the recognition of the HR. As Parlevliet (4) indicated, however, using mixtures of pathogen races will not enhance recognition of the HR. The data reported by Ahn and Ou (1) confirm this. Unfortunately, they explained the results differently. They tested the 18 international rice differentials against 242 Philippine races of the rice blast fungus, *Pyricularia oryzae*, and observed that resistance spectra of the rice cultivars against these races varied greatly. Zenith had the widest resistance spectrum with resistance to 218 of the races (90%), and Khao-tah-haeng 17 the narrowest with resistance to only 26 races (11%). When Ahn and Ou (1) determined the number of lesions on these cultivars after exposure to the inoculum occurring naturally in the blast nursery, they observed that the wider the resistance spectrum of a cultivar, the fewer lesions it had. Similar results were obtained when the resistance spectra of the cultivars to the 69 races detected in the nursery were related to the number of lesions on the cultivars. Table 1 shows data from Ahn and Ou (1) for five of the 18 cultivars. Ahn and Ou concluded that these results fit Nelson's (3) hypothesis that accumulation of vertical resistance may contribute to or confer horizontal resistance and that "several genes collectively conditioning HR individually condition VR and single genes controlling VR collectively condition HR."

The results of Ahn and Ou (1) have an important bearing on the selection for HR in the presence of VR, provided that the data are interpreted properly. Nelson's hypothesis (3) is not needed to explain their observations; there is a much simpler explanation. In rice, at least 14 VR genes have been recognized. The 18 international differentials differ in the identity and number of the resistance genes that they carry. If such cultivars are exposed to a pathogen population like that of *P. oryzae*, which consists of a great number of races, the result will be the sort of data reported by Ahn and Ou (1). A simplified example may be used for illustration (Table 2). Four rice cultivars are assumed to vary only for VR to seven races of the pathogen, but not for HR. The variation may be due to differences in the identity and/or in the number of the resistance genes. None of the genes or gene combinations is effective against all races. When the VR is qualitative (ie, no lesions produced in incompatible cultivar-race combinations) the lesions on a cultivar can only originate from compatible cultivar-race combinations. In the example, the four cultivars are inoculated with a mixture of equal amounts of spores of the seven races. On cultivar A, only 1/7 of the inoculum can cause lesions; on cultivars B, C, and D 3/7, 4/7, and 6/7 of the inoculum, respectively, can cause lesions, resulting in large differences in the number of lesions of a susceptible type. These differences suggest variation in HR, which is not the case. The observed variation in disease level is caused solely by the partial effectiveness of the VR genes; partial in the sense that each VR gene or gene combination is effective against only part of the pathogen population. The larger the variation for virulence in the pathogen population, the more it tends to confound the partially effective VR with HR.

If the host population varies for both HR and VR, selection for HR requires that the two types can be distinguished. This is not always easy. Using a mixture of races makes it more difficult if not impossible. Using a single race provides the best conditions for the selection of HR in the presence of VR. This race should have the broadest possible virulence spectrum to suppress the expression of as many VR genes as possible.

TABLE 1 Relationship between the numbers of races of *Pyricularia oryzae* (of the 69 races present in the rice blast nursery) to which five rice cultivars are resistant and the relative numbers of lesions per equal leaf area that developed on leaves of the five cultivars following exposure to natural inoculum in nursery (data from Ahn and Ou [1])

Cultivar	No. of races to which resistant	Lesions (per 100 cm^2)
Zenith	64	2
Kataktara DA-2	55	14
Kanto 51	40	39
Lacrosse	19	66
Khao-tak-haeng 17	4	94

TABLE 2. Relationship of the reactions of four hypothetical rice cultivars to seven races of *Pyricularia oryzae* and the expected relative numbers of lesions on leaves of each cultivar following inoculation with a mixture of equal numbers of spores of the seven races

Cultivar	Lesions (no.)	Races 1	2	3	4	5	6	7
A	14	+[a]	−	−	−	−	−	−
B	43	+	+	+	−	−	−	−
C	57	−	−	+	−	+	+	+
D	86	+	+	−	+	+	+	+

[a] Symbols: + denotes susceptibility; − denotes resistance.

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