

Letter to the Editor

The Concept of Durable Resistance

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In a recent review, Nelson (10) suggested that the term 'horizontal resistance' was unacceptable as currently defined. The definition referred to was that given by van der Plank (12) as follows: "When the resistance is spread against all races of the pathogen we shall call it horizontal or lateral" and "By definition, horizontal resistance is spread evenly against all races". In other words, horizontal resistance was defined as not race-specific. To Nelson these definitions were unacceptable because van der Plank then described the potato cultivars Kennebec and Maritta as each having intermediate horizontal resistance to some races of *Phytophthora infestans* and complete 'vertical' (race-specific) resistance to others. The resistance of these two cultivars therefore was greater towards some races than others and Nelson suggested that this conflicted with the definition of horizontal resistance but satisfied van der Plank's definition of vertical resistance. Nelson implied that it was this confusion of ideas that led Johnson and Law (5) to describe the resistance of certain wheat cultivars to yellow rust as 'durable' rather than horizontal. He then proposed to redefine horizontal resistance as resistance "that reduces the apparent infection rate" and supposed that Johnson and Law might have been happy to use the term horizontal resistance thus defined.

Unfortunately he is mistaken in this supposition. I believe that one of the most misleading ideas connected with the concept of horizontal resistance is the belief that it can be recognized as any resistance that reduces the apparent infection rate, in contrast to vertical or race-specific resistance which, it has been suggested (12), only delays the onset of an epidemic. Horizontal resistance was equated by van der Plank with resistance that reduces the infection rate, as illustrated by his statement "the infection rate and therefore horizontal resistance are the main theme of this chapter" (12, p. 164).

Browder (1) showed that the slow-rusting characteristic of Bulgaria 88 wheat to leaf rust (caused by *Puccinia recondita*) was race-specific and could be overcome by certain strains of the pathogen. He concluded that slow-rusting of the type seen in Bulgaria 88 could slow down the rate of development of epidemics in a way similar to that attributed to horizontal resistance by van der Plank, although, in showing race-specificity, it clearly was not horizontal resistance. There are many examples of wheat cultivars with intermediate levels of resistance to some races of *P. striiformis*, able to slow down the development of epidemics of those races, but with greater susceptibility to other races (8,9,11,14). Johnson and Taylor (7) agreed with Browder that slowing down an epidemic is not solely a characteristic of horizontal resistance. The wheat cultivar Joss Cambier was considered to have incomplete but adequate resistance to yellow rust when first released commercially in Britain in 1967. In 1971 high levels of yellow rust were observed on it and an isolate of *P. striiformis* from these infections was compared with an earlier isolate that caused moderate infections on Joss Cambier (6). A differential interaction between these isolates and the wheat cultivars Hybrid 46 and Joss Cambier showed that the resistance of Joss Cambier, although incomplete, was race-specific and therefore not horizontal. Johnson and Bowyer (4) confirmed these results, yet so strong is the idea of the association

of horizontal resistance with quantitatively expressed resistance that their results were interpreted by Dinooor (2) as indicating that there could be differential interactions, or race-specificity, in horizontal resistance. The most important feature of the resistance of Joss Cambier for the breeder was that, even though intermediate, it was quickly overcome (3).

These results show that incomplete or intermediate resistance is not necessarily horizontal and that it is false to conclude that resistance is horizontal because it is intermediate. It is only possible, therefore, to demonstrate that resistance is horizontal by testing it against many different cultures of a pathogen. Even if many cultures are used without revealing race-specificity, the use of one more culture might demonstrate that resistance is not horizontal. My colleagues at the Plant Breeding Institute and I agreed that absolute proof of horizontal resistance is impossible. There was no doubt, however, that resistance of some cultivars had lasted a long time in commercial use while that of others had not and that it was the durability of resistance that was of primary concern to the breeder. Therefore, in 1972 I suggested to my colleagues that resistance that lasts a long time should be called durable. These arguments were not explicitly presented by Johnson and Law (5) who indicated that resistance of certain wheat cultivars to yellow rust could not be called horizontal because they had greater resistance to some races of *P. striiformis* than to others. This statement was criticized on one count by van der Plank (13). In addition, I accept that, in theory, a cultivar could possess both vertical and horizontal resistance. Nelson (10) appears to have overlooked the distinction between the definition of types of resistance and their manifestation in a single cultivar. Our statement (5) would have been more accurate if we had indicated that we were unable to prove that the durable resistance we were studying was horizontal, especially towards races of *P. striiformis* not used in our experiments.

The term durable was proposed because it embodied fewer assumptions than did the concept of horizontal resistance and it easily conveyed an important practical aspect of resistance to both specialists and laymen. Durable resistance can only be recognized in cultivars that have been widely grown for a reasonably long period (3); such cultivars are therefore especially valuable in studies of the factors leading to durability of resistance and in breeding for more durable resistance. I am aware that the recognition of durable resistance is a retrospective judgment. It is preferable to accept this as a fact rather than to presume that resistance will be durable from the observation that it is intermediate, or to make the unprovable claim that resistance is horizontal. The fact that it can only be recognized retrospectively is no barrier to its use, once recognized, in breeding programs (3). Whether it is transferred successfully by breeding will, again, only become clear after sufficient testing. It is worth remembering, however, that this limitation applies to all systems of controlling plant diseases over the long term, including the widespread use of fungicides, cultivar mixtures, or multilines.

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