Letter to the Editor

Durable Resistance: Definition of, Genetic Control, and Attainment in Plant Breeding

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Durable disease resistance in plants has been defined as resistance that remains effective while a cultivar possessing it is widely cultivated (4–11,17). This definition includes no statement or implication about the genetic control of the resistance, its mechanism, its degree of expression, or its race-specificity. Furthermore, the recognition of resistance as durable does not imply that it will remain permanently effective (17). In several of the publications cited above, distinctions were drawn between the concept of durable resistance and those of horizontal resistance, partial resistance, incomplete resistance, and other terms. Mortensen and Green (15) suggested that some authors considered that there were two kinds of resistance, one race-specific and the other variously known as horizontal, partial, generalized, or durable. It was implied in their paper that these terms were synonymous and that the terminology was confused. Green and Campbell (2) confirmed this opinion, but then used the adjective "enduring" to describe the resistance of some wheat cultivars to stem rust in Canada. In view of their previous suggestion that "durable" was part of a confused nomenclature, it would be of interest to know the meaning they attribute to "enduring" if it is other than resistance that remains effective for a long period while cultivars containing it are widely used and, if so, how they think its use will lead to clarification of the terminology.

Green and Campbell (2) suggested that wheat cultivars with durable resistance to stem rust (caused by *Puccinia graminis*) in Canada "have more genes for resistance and different gene combinations than the cultivars that became susceptible." They also proposed that "the resistance of western Canadian cultivars released since 1950 can be explained, in most cases, by the genes they are known to possess." In addition they implied that all resistance is controlled by genetic factors that are individually race-specific and that durable resistance was the result of complex combinations of these factors.

Some of these opinions may be questioned on the grounds of logic, on the basis of published data, and in the light of our experience of breeding for resistance to yellow rust of wheat (caused by *Puccinia striiformis*) at the Plant Breeding Institute (PBI).

In my view, it is no more logical to assume that all resistance is race-specific than that some resistance is race-nonspecific since neither point can be proved. The recognition of durable resistance does not require the acceptance of either of these extreme views (7). The genetic basis for durable resistance may vary and there is no reason to assume that it is always complex. Indeed, in most cases, the exact genetic causes of durable resistance remain to be identified unequivocally and those of Canadian wheat cultivars durably resistant to stem rust are apparently no exception.

Green and Campbell (2) described two Canadian wheat cultivars as each possessing five stem rust resistance (*Sr*) genes. One of these, Canthatch, never occupied more than 2% of the Manitoba wheat area and was grown commercially for very few years. Nevertheless, its resistance was much less at the end of the period than initially and it cannot be classified as having durable resistance. In contrast, the cultivar Selkirk was widely grown for many years. It remained adequately resistant to stem rust and its resistance was durable. Green and Campbell (2) indicated that the resistance of Selkirk was controlled by the five genes *Sr6*, *Sr7b*, *Sr9d*, *Sr17*, and *Sr23*. They suggested that the effectiveness of this resistance may have been due to the rarity of combined specific pathogenicity for the genes *Sr6* and *Sr9d* and that this combination of pathogenicity genes may have been harmful to the pathogen. However, races with pathogenicity for these genes separately were not rare and, in view of the lack of data to support the hypothesis, other interpretations may be suggested. One is that the resistance of Selkirk was partly due to additional genes, so the cultivar was not highly susceptible even to pathogen races carrying specific pathogenicity for all five named genes. Data from the permanent stem rust nursery at Winnipeg (2) indicate this possibility and it is supported by the data of Hare and McIntosh (3) who showed that Selkirk carries the gene *Sr 2*, which they described as a gene for durable resistance because of the durability of its effectiveness in several cultivars. Knott (13) described *Sr2* as a gene for adult plant resistance to stem rust in wheat cultivars Hope and H44, of which the latter was an ancestor of Selkirk. It is also possible that Selkirk contains other genetic factors, not yet described, for resistance to stem rust.

These features of the genetic control of stem rust resistance in Canadian wheat cultivars have several implications. First, resistance controlled by as many as five race-specific *Sr* genes does not automatically result in durable resistance, as in the case of Canthatch. In addition, it is difficult to be sure that the entire resistance genotype of a cultivar has been described, and therefore to identify the genetic causes of durability with certainty in a single cultivar. It is probable that the gene *Sr2* and perhaps other unidentified factors contributed to the durable stem rust resistance of Selkirk, and their presence may have helped to prevent multiplication of races with combined pathogenicity for *Sr6* and *Sr9d*.

Despite these uncertainties Green and Campbell (2) reached the conclusion that wheat lines "with appropriate combinations of classical, hypersensitive 'seedling' genes can be readily selected and many combinations of these genes are highly effective." They did not, however, suggest trying to reconstruct the particular combinations of genes they believe to have led to durable resistance. In fact, the breeding program they described does not involve a test of stem rust resistance in seedlings until the F_9 generation. This would not preclude the occurrence of complex groups of *Sr* genes but it is difficult to see how particular gene combinations could be developed systematically at this stage of a breeding program. Indeed, the actual combinations of *Sr* genes in Canadian wheat cultivars have usually been identified retrospectively, and no identified genes for resistance were named in the most recent Canadian cultivars (2).

At the PBI, attempts to produce yellow rust resistance by combining recognizably race-specific genes that were effective in seedlings but were already known to have shown low durability individually, resulted in at least four high yielding cultivars with initially effective resistance that was overcome either before or shortly after their commercial release. These cultivars all derived race-specific resistance factors from Cappelle-Desprez or Hybrid 46 combined with *Yr6* in Maris Ranger, *Yr1* in Maris Envoy and Maris Templar, and *Yr2* in Maris Beacon. When these combined resistance factors were overcome, all were more susceptible in the field than the durably resistant parent Cappelle-Desprez (12). This indicated that certain factors, not detectable in seedlings of

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Cappelle-Desprez and perhaps including those carried by chromosome 5BS-7BS (14), were not successfully transferred. In view of the very high susceptibility of some of the cultivars, such as Maris Envoy and Maris Beacon, their known combination of race-specific genes did not appear to make any residual contribution to resistance. Although the combinations of *Yr* genes in these susceptible cultivars were less complex than those described for stem rust resistance (2), the most important feature of our results was that lack of durability was associated with the loss of certain unidentified factors for resistance that were present in Cappelle-Desprez. If these had been retained, all these cultivars could probably have had a useful commercial life.

Cappelle-Desprez was susceptible as a seedling to several races of *P. striiformis* but adequately resistant as an adult plant in widespread commercial use for many years (5). The pattern of seedling susceptibility and adult plant resistance was not, however, a criterion for the identification of durable resistance. Cultivars such as Joss Cambier, Maris Bilbo, and Hobbit had this pattern initially but rapidly became highly susceptible to new races of *P. striiforms* (4,11). I concluded that durable resistance could only be identified in cultivars that remained adequately resistant during widespread and prolonged commercial use, and that cultivars possessing such resistance were the most obvious parents to use in breeding for durable resistance. In using these it appeared advantageous to avoid the creation of new combinations of race-specific genetic factors conferring resistance to all available races of the pathogen, but whose resistance individually was of low durability (5). This would help to ensure selection of resistance from the durably resistant parent.

This system is applied in some crosses at the PBI in the normal pedigree system of wheat breeding; a donor of durable resistance is used as a parent and there is selection in the F_5 and later generations against combinations of known race-specific genes that give resistance in seedlings to all available races of the pathogen. In addition, screening in the field is carried out by using races with specific pathogenicity for the known adult plant race-specific factors. No other attempt is made to reduce the number of known race-specific genes present, although there is no detailed testing to select for them. Many such genes remain in various combinations in the newer cultivars. They may have been selected by chance or perhaps less randomly if they have residual effects on resistance or interact with other genes. Alternatively, the disease nursery contains many different combinations of such genes in the presence of a mixture of pathogen races so that those lines carrying certain combinations are susceptible to only a proportion of the pathogen population and may therefore become less diseased, as in a cultivar mixture or multiline. The race-specific genes are useful as the basis of schemes for cultivar diversification that are recommended to British farmers (16) to reduce disease hazards. It may also be true that by rendering cultivars resistant to some components of the pathogen population they contribute to the durability of resistance. This might apply particularly where the pathogen spends seasonal periods on other cultivars with different combinations of such genes, as in the case of *P. graminis* in North America. However, such effects would tend to diminish as a cultivar was more widely grown. So far, no combinations of race-specific genes for seedling resistance to yellow rust have remained effective during the widespread use of cultivars in Britain, and their durable resistance has always been detected after those genes have been overcome.

A promising example of the breeding method I have proposed is provided by the new PBI winter wheat cultivar Bounty (1). From the parents of Bounty it would have been possible to combine race-specific resistance genes from Hybrid 46 with the gene *Yr1*, giving complete resistance to all races of *P. striiformis* available at that time. However, this was avoided by selection against the race-specific factors from Hybrid 46 and the progeny were screened by using an appropriate race to ensure that the resistance in Bounty was derived from the adult plant resistance of the durably resistant ancestral cultivar Maris Widgeon. In addition to this adult plant resistance, the seedling resistance genes *Yr1*, *Yr3a*, and *Yr4a* from cultivar Durin were incorporated without elaborate tests of seedlings with selected races.

This method may not be the only way to achieve durable resistance, but it does not require elaborate methods of selection or special breeding procedures that would result in overemphasis on only one of the many characters for which the breeder must select. It stands a good chance of being tested in some of the successful products of the wheat breeding program at the PBI.

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