Letter to the Editor

Virulence Structure in *Puccinia graminis* f. sp. *tritici*: A Reply

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In letters to you, Roelfs and Martens (5) and Knott (3) discussed my suggestion, elaborating an earlier analysis (6), that wheat stem rust resistance genes fall into three groups: an ABC group, an XYZ group, and an N group (7,8). Virulence for genes in the ABC group dissociates more than randomly from virulence for genes in the XYZ group. Virulence for gene pairs within the ABC group associates more than randomly, as does virulence for gene pairs within the XYZ group. The N group includes genes that are either neutral or provisionally unclassified simply because of inadequate evidence.

The core of the criticism that needs to be rebutted is found in Knott's sentences: "A single race, 15-TNM, has made up 38–72% of the isolates collected in a given year . . . Even though a few other races are detected each year, their frequencies are sufficiently low that no race other than 15-TNM has a major effect . . . Vanderplank's association and dissociation are artifacts that result from the fact that North American wheat stem rust is an asexual population dominated by one race in the years he analyzed." Roelfs and Martens (5) join Knott (3) in finding an explanation in asexual reproduction. They write: "Association of patterns of virulence, avirulence, or virulence and virulence may exist due to the predominantly asexual reproduction of *P. graminis* in North America. Asexual reproduction results in a complete linkage (association) of the entire pathogen genome." I disagree for various reasons.

First, the associations and dissociations hold quite independently of race 15-TNM or other single race. Take virulence for wheat rust resistance genes *Sr*6 and *Sr*9e for example. Race 15-TNM is virulent for *Sr*9e but avirulent for *Sr*6, i.e., in this race virulence for *Sr*9e and *Sr*6 is dissociated. It is also dissociated in the rust population as a whole, including races other than 15-TNM. But even if we excise data for race 15-TNM from the analysis, the dissociation remains. With the exception of the very rare Canadian race C50, found only in 1975, all races in North America, from Mexico to Canada, that are virulent for *Sr*9e are avirulent for *Sr*6, and, conversely, all races that are virulent for *Sr*6 are avirulent for *Sr*9e. Virulence dissociation in most years is complete, even in races which with respect to virulence for *Sr*6 and avirulence for *Sr*9e are the very opposite of 15-TNM. Evidence for dissociations and associations of virulence for other gene pairs, although generally less complete, also survives the excision of data for race 15-TNM from the analysis.

Second, Knott's criticism shows a North American fixation. On the evidence (7, Table 2.12) virulence for *Sr*6 and *Sr*9e is also dissociated in Australia, where the race pattern differs greatly from that in North America, and race 15-TNM is unknown. Other evidence (8) from Australia suggests that the ABC-XYZ system holds generally there, too.

Third, the criticism shows not only a North American fixation but also a northern North American fixation. The race pattern in the south (Mexico, Texas, etc.) differs greatly from that in the north, and race 15-TNM is unimportant. Yet, if one allows for the relative paucity of data, the ABC-XYZ system does not seem to differ greatly from south to north. My (7) Table 2.18 traces the dissociation of virulence for *Sr*9e and *Sr*15 and the association of virulence for *Sr*9e and *Sr*Tmp through 10 areas from Mexico to Canada, and from east to west of the Rocky Mountains. The dissociation and association are maintained despite large changes of race in the areas.

Fourth, if observed dissociations and associations were simply reflections of the predominant race, one would expect to find the reflection in all gene pairs. This is not so.

Fifth, sexuality would be an issue only if the ABC-XYZ groupings in sexual populations disagreed with those in asexual populations because of sexuality. No disagreement has yet been demonstrated. Alexander et al (1) analyzed a sexual population. The gene pairs they classified overlap with seven which I classified in the ABC-XYZ system (7,8). In all seven their results confirm mine. Virulence for the gene pairs 9a/9e, 9a/10, 9a/11, 9a/Tmp, and 15/7b dissociates more than randomly, and virulence for the pairs 9a/15 and 15/17 associates more than randomly. Table 4 of Alexander et al and my (8) larger Tables 4.1 and 4.2, where they overlap, agree fully. Readers should consult the tables for themselves.

The environment contributes toward differences between sexual and asexual populations, especially if sexual populations are sampled at an early date, soon after rusted wheat is found near barberry bushes. Katsuya and Green (2) and Roane et al (4) found an effect of environment on races, and I (8) found an effect on the dissociation of virulence for some gene pairs. This warns us that, for reasons other than sexuality, full agreement between sexual and asexual populations is not always to be expected.

Sixth, in discussing sexuality Roelfs and Martens (5) and Knott (3) miss the point that, in the examples I analyzed, the necessary phenotypic variation was already there. In simplified terms, there were isolates virulent for gene 1 but avirulent for gene 2, isolates avirulent for gene 1 but virulent for gene 2, isolates virulent for both genes, and isolates avirulent for both genes. It seems to be irrelevant to our particular analysis of existing variation whether this variation originated sexually or asexually.

Seventh, Knott's artifact shaft is wrongly aimed. It is races that are artifacts. Physiologic races are identified by differential host plants selected by man. Change the selection and you change the races, but the virulence dissociations and associations stay the same.

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