

A Reply to L. E. Browder and M. G. Eversmeyer

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A chapter of mine (2) now in the press covers almost all of the points raised by Browder and Eversmeyer. It even covers more about Browder and Eversmeyer's own temperature studies than they themselves now include in their letter to you. I shall not repeat the chapter here; what needs to be covered now is relatively little.

My thesis was (1) and still is: "What specificity there is, is in susceptibility. Resistance is unspecific." Put differently, susceptibility may be, but is not necessarily, specific; resistance is always unspecific. If one goes from disease in general to gene-for-gene disease in particular, the thesis becomes: Susceptibility is specific, resistance unspecific. I deal in this reply with gene-for-gene disease only.

Browder and Eversmeyer clearly do not understand my tables. They strip my 5×5 table (1, Table 2.1) down to a 2×2 table (their Table 1) shedding degrees of freedom in the process. Their 2×2 table is left with only one degree of freedom. That degree of freedom indicates interaction, but more degrees are needed to show the direction of the interaction. Put differently, this 2×2 table indicates specificity, but cannot show where that specificity lies. No 2×2 table can distinguish between specific susceptibility and specific resistance. A distinction between specific susceptibility and specific resistance was the whole point of my original 5×5 table.

My Table 1, given here, extends Browder and Eversmeyer's 2×2 Table 1 into a 3×3 table, and gives the necessary extra degrees of freedom. Specific susceptibility and unspecific resistance begin to glimmer through. A 4×4 table, which readers can construct for themselves, is more emphatic, and my original 5×5 table better still. I hope readers will consult my original tables instead of Browder and Eversmeyer's pointlessly truncated ones. In my chapter (2, Section VII-B) I devise a "multiquadratic" check to supply degrees of freedom in a different way.

Flor, in repeated formulations of his gene-for-gene hypothesis, is entirely consistent and unequivocal. For each resistance gene in the host there is a specific complementary gene conditioning *pathogenicity* (my italics) in the parasite. Flor's hypothesis is about specific pathogenicity. There is unfortunately a large school that surreptitiously contradicts Flor and substitutes a gene conditioning

TABLE 1. Browder and Eversmeyer's 2×2 Table 1 expanded into a 3×3 table.^a The expansion provides the extra degrees of freedom needed to identify specificity in susceptibility

Pathogen genotype	Host genotype		
	<i>R1R1r2r2r3r3</i>	<i>r1r1R2R2r3r3</i>	<i>r1r1r2r2R3R3</i>
<i>v1v1V2V2V3V3</i>	Susceptible	Resistant	Resistant
<i>V1V1v2v2V3V3</i>	Resistant	Susceptible	Resistant
<i>V1V1V2V2v3v3</i>	Resistant	Resistant	Susceptible

^a Genes conditioning susceptibility in the host plant and genes conditioning avirulence in the parasite do not enter Flor's formulation of his gene-for-gene hypothesis, and were rightly omitted from my 5×5 table (1, Table 2.1). They are included here only to conform with Browder and Eversmeyer's Table 1, but are unnecessary.

avirulence for a gene conditioning pathogenicity in the parasite. That is, they substitute a gene-for-gene system in which the gene for resistance in the host is matched by a specific complementary gene conditioning avirulence in the parasite. Thus, Browder and Eversmeyer write "Resistance [in Flor's system] was the result of specific host genotypes and *specific parasite genotypes functioning together*" (italics added by me). In short, Browder and Eversmeyer believe in specific avirulence. I demonstrate (2, Section II-A), I believe conclusively, that no gene-for-gene system can possibly be devised on the basis of avirulence in the parasite. Attempts to launch a concept of specific resistance on the back of specific avirulence must fail.

To digress into terminology, one repeatedly sees references to "specific resistance" to disease when specific resistance does not exist. There is no such thing as specific resistance to disease.

LITERATURE CITED

- Vanderplank, J. E. 1984. Disease Resistance in Plants. Second Ed. Academic Press, Orlando, FL.
- Vanderplank, J. E. 1986. Specific susceptibility and specific feeding in gene-for-gene systems. Adv. Plant Pathol. 5:(In press).