

**The Gene-for-Gene Concept**

The coexistence of host plants and their pathogens side by side in nature indicates that the two have been evolving together. Changes in the virulence of the pathogens appear to be continually balanced by changes in the resistance of the host, and vice versa. In that way, a dynamic equilibrium of resistance and virulence is maintained, and both host and pathogen survive over considerable periods of time. The stepwise evolution of virulence and resistance can be explained by the **gene-for-gene concept**, according to which for each gene that confers virulence to the pathogen there is a corresponding gene in the host that confers resistance to the host, and vice versa. The gene-for-gene concept was first proved in the case of flax and flax rust, but it has since been shown to operate in many other rusts, in the smuts, powdery mildews, apple scab, late blight of potato, and other diseases caused by fungi, as well as in several diseases caused by bacteria, viruses, parasitic higher plants, nematodes, and even insects. Generally, but not always, in the host the genes for resistance are dominant (R), whereas genes for susceptibility, i.e., lack of resistance, are recessive (r). In the pathogen, however, genes for a-virulence, i.e., inability to infect, are usually dominant (A) whereas genes for virulence are recessive (a). Thus, when two plant varieties, one carrying the gene for resistance R to a certain pathogen and the other lacking the gene R for resistance, i.e., carrying the gene for susceptibility (r) to the same pathogen, are inoculated with two races of the pathogen, one of which carries the gene for a-virulence A against the resistance gene R and the other of which carries the gene for virulence (a) against the resistance gene R, the gene combinations and reaction types shown in Table and Figure are possible.

Table: Quadratic check of gene combinations and disease reactions. Type of Host-pathogen interaction in which gene for gene concept for one gene operates.

Virulence or A-Virulence gene in Pathogen	Resistance or susceptible genes in plants	
	R (Resistance) Dominant	r (Susceptible) Recessive
A (a-virulent) dominant	AR (-)	Ar(+)
a (virulent) recessive	aR (+)	ar (+)

Minus sign indicate the incompatible or resistant reaction and therefore no infection; Plus sign indicate the compatible or susceptible reaction therefore infection will develop.

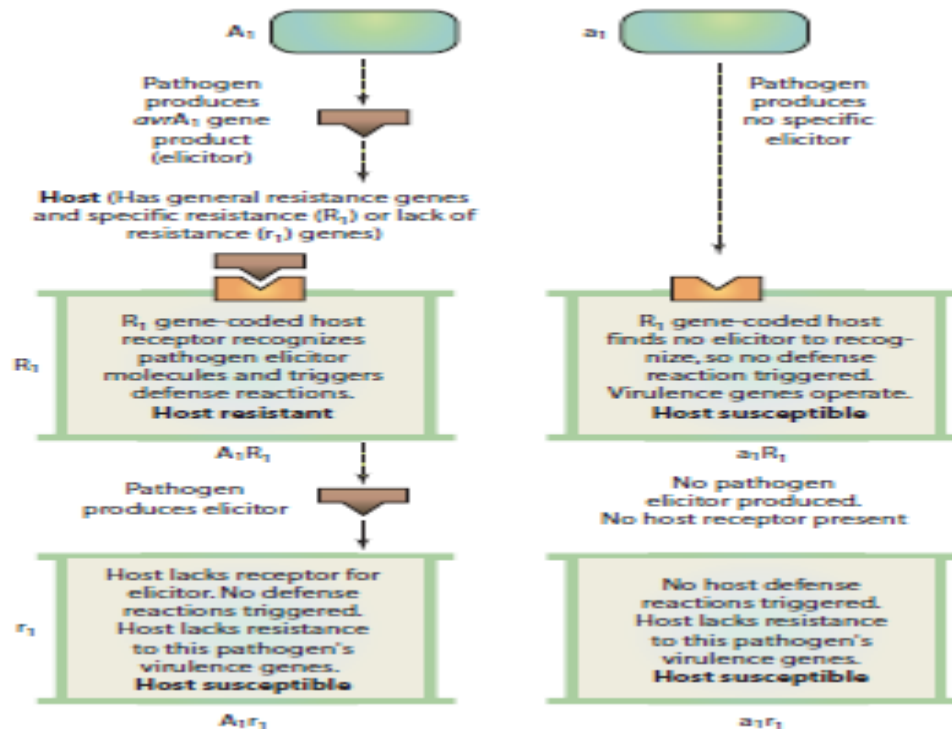


Figure: Basic interactions of pathogens a-virulence (A)/Virulence (a) genes to host resistance (R)/Susceptible (r) genes in a gene for gene concept and final outcome of the interaction.

Each gene in the host can be identified only by its counterpart gene in the pathogen, and vice versa. Of the four possible gene combinations, only the AR interaction is incompatible (resistant), i.e., the host has a certain gene for resistance (R) that recognizes the corresponding specific gene for a-virulence (A) of the pathogen. In the Ar combination, infection results because the host lacks genes for resistance (r) and so the pathogen can attack it with its other genes for virulence (after all, it is a pathogen on this host). In aR, infection results because although the host has a gene for resistance, the pathogen lacks the gene for a-virulence that is recognized specifically by this particular gene for resistance and therefore no defense mechanisms (resistance) are activated. Finally, in the ar interaction, infection results because the plant has no resistance (r) and the pathogen, being a pathogen and therefore virulent (a), attacks it. It is thought that genes for resistance appear and accumulate first in hosts through evolution and that they coexist with nonspecific genes for pathogenicity which evolve in pathogens. Genes for pathogenicity exist in pathogens against all host plants that lack specific resistance. When a specific gene for resistance appears in or is bred into the host, the gene enables the host to recognize the product of a particular gene for virulence in the pathogen. That pathogen gene is then thought

of as the “a-virulence” gene (*avrA*) of the pathogen that corresponds to the plant resistance gene *R*. The change in the function of the pathogen gene is because subsequent recognition of the *avrA* gene product (the elicitor molecule) by the receptor coded by the *R* gene triggers the hypersensitive response reaction in the plant that keeps the plant resistant. A new gene for virulence that attacks the existing gene for resistance appears by mutation of an existing a-virulence gene, which then avoids gene-for-gene recognition, and the resistance of the host breaks down. Plant breeders then introduce another gene for resistance (*R*) in the plant, which recognizes the protein of the new gene for virulence of the pathogen and extends the resistance of the host beyond the range of the new gene for virulence in the pathogen. This produces a variety that is resistant to all races that have an a-virulence gene corresponding to the specific gene for resistance until another gene for virulence appears in the pathogen. When a variety has two or more genes for resistance (*R*<sub>1</sub>, *R*<sub>2</sub>, . . .) against a particular pathogen, it means that each corresponds to one, two, or more genes of former virulence (and now a-virulence) in the pathogen (*a*<sub>1</sub>, *a*<sub>2</sub>, . . .), each of which, once recognized by one of the genes for resistance in the host, subsequently functions as an a-virulence gene. The gene combinations, and disease reaction types, of hosts and pathogens with two genes for resistance or virulence in corresponding loci, respectively, are shown in Table.

Table: Complementary Interaction of Two Host Genes for Resistance and the Corresponding Two Pathogen Genes for Virulence and Their Disease Reaction Types

		Resistance ( <i>R</i> ) or susceptibility ( <i>r</i> ) genes in the plant			
		<i>R</i> <sub>1</sub> <i>R</i> <sub>2</sub>	<i>R</i> <sub>1</sub> <i>r</i> <sub>2</sub>	<i>r</i> <sub>1</sub> <i>R</i> <sub>2</sub>	<i>r</i> <sub>1</sub> <i>r</i> <sub>2</sub>
Virulence and A- virulence genes of the pathogen	<i>A</i> <sub>1</sub> <i>A</i> <sub>2</sub>	-	-	-	+
	<i>A</i> <sub>1</sub> <i>a</i> <sub>2</sub>	-	-	+	+
	<i>a</i> <sub>1</sub> <i>A</i> <sub>2</sub>	-	+	-	+
	<i>a</i> <sub>1</sub> <i>a</i> <sub>2</sub>	+	+	+	+

Table makes clear several points. First, susceptible (*r*<sub>1</sub>*r*<sub>2</sub>) plants lacking genes for resistance are attacked by all races of the pathogen, regardless of the virulence (*aa*) or a-virulence genes (*A*<sub>1</sub>*A*<sub>2</sub>) carried by the pathogen. Second, pathogen races or individuals designated *a*<sub>1</sub>*a*<sub>2</sub>, i.e., which lack genes for a-virulence (*A*<sub>1</sub>*A*<sub>2</sub>) for each

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gene for resistance of the host (R1R2), can infect all plants that have any combination of these genes (R1R2, R1r2, r1R2), as the a1a2 pathogen produces no elicitor molecules capable of triggering the host defense response. When a pathogen has one of the two genes for virulence (a1 or a2), i.e., it lacks one of the two genes for a-virulence (A1 or A2), then it can infect plants that have the corresponding gene for resistance (R1 or R2, respectively) but not plants that have a gene for resistance corresponding to a gene for a-virulence in the pathogen (e.g., pathogen with genes A1a2 infects plant with r1R2 but not those with R1r2 because R1 can recognize the avr gene A1 and triggers defenses against it). The gene-for-gene concept has been demonstrated repeatedly, and both pathogen a-virulence genes and plant resistance genes have been isolated. **Plant breeders apply the gene-for-gene concept every time they incorporate new resistance gene into a desirable variety that becomes susceptible to a new strain of the pathogen.** With the diseases of some crops, new resistance genes must be found and introduced into old varieties at relatively frequent intervals, whereas in others a single gene confers resistance to the varieties for many years.