The Relationship of Host-Mediated Induced Resistance to Polymorphism in Gene-for-Gene Relationships

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ABSTRACT

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Gene-for-gene relationships are a common feature of plant-parasite interactions. Polymorphism at host resistance and parasite avirulence loci is maintained if there is negative, direct frequency-dependent selection on alleles of either gene. More specifically, selection of this kind is generated when the disease is polycyclic with frequent auto-infection. When an incompatible interaction occurs between a resistant host and an avirulent parasite, systemic defenses are triggered, rendering the plant more resistant to a later attack by another parasite. However, induced resistance (IR) incurs a fitness cost to the plant. Here, the effect of IR on polymorphism in gene-for-gene interactions is investigated. First, in an infinite population model in which parasites have two generations per host generation, increasing the fitness cost of IR increases selection for susceptible plants at low disease severity, while increasing the effectiveness of IR against further parasite attacks enhances selection for resistant plants at high disease severity. This reduces the possibility of polymorphism being maintained in host and parasite populations. In finite population models, the number of plants varies over time as a function of the disease burden of the population. Polymorphism in gene-for-gene relationships is then more stable at high disease prevalence and severity if IR reactions are more costly when there is competition for resources between plants.

Additional keywords: coevolution, epidemiological models, natural selection, resistance, virulence.

Gene-for-gene (GFG) relationships govern many plant-parasite interactions (1,8,15,24). In the simplest case, a host resistance (*RES*) locus interacts with a corresponding parasite avirulent (*AVR*) locus. Effective defenses are induced if a plant has a *RES* gene enabling recognition of a specific parasite *AVR* gene (15). The parasite is not detected by the host and defenses are not induced if the host has a susceptibility allele (*res*) or the parasite has a virulence allele (*avr*). Genetically, the *RES* and *AVR* alleles are usually dominant.

The asymmetry of the GFG interaction suggests that in the absence of other factors, there will be an "arms race", as successive pairs of *RES* and *AVR* alleles are driven to fixation in host and parasite populations, respectively (24). In nature, however, there is substantial polymorphism at *RES* and *AVR* loci both within populations and across spatially structured subpopulations (44,49, 50). The fact that some of these polymorphisms are ancient (1,34, 50,52) supports the "trench warfare" group of models in which polymorphism is quasi-stable (44), in contrast to the transient polymorphism in "arms race" models (24).

Several mathematical models have been formulated to understand the coevolutionary process in single-locus (30,33,46) or multilocus GFG systems (41–43). Coevolution implies the existence of indirect frequency-dependent selection (FDS), because the rate of natural selection on a host allele depends on the frequency of a corresponding parasite allele, and vice-versa (20). Most theoretical studies predict the existence of constitutive costs of *RES* and *avr* alleles in order to counteract selection by the parasite or host, respectively (4,20,30,31,33). Some experiments have detected such costs (29,48,51,53), but others have not (5–7,15,53). Costs of *RES* and *avr* alleles are necessary but not sufficient to maintain stable long term polymorphism at host and parasite loci (46). However, increasing constitutive fitness costs of *RES* reinforces indirect FDS because it reduces selection for *RES* when the frequency of *AVR* is high, and enhances selection against *RES* when the frequency of *avr* is high (similarly, increasing the constitutive cost of *avr* reduces net selection for *avr*) (4,20,30,33,46).

Polymorphism can be maintained in both host and parasite populations only if there is also negative, direct FDS, such that the strength of natural selection for either *RES* or *avr* or both, declines with increasing frequency of that allele (46). This general condition encompasses numerous factors previously proposed to account for polymorphism at corresponding GFG loci such as biological characteristics of plants (perenniality or seed banks) and environmental heterogeneity (46).

Most plant diseases are polycyclic, as the parasite passes through more than one generation on the same plant. This also helps to stabilize polymorphism in GFG systems (46). In a polycyclic disease, the stability of GFG systems depends on the outcome of infection in one parasite generation influencing the next parasite generation. As a plant grows, each new leaf may be infected by a spore produced either on the same plant or on another plant (auto-infection and allo-infection, respectively) (3). Increasing the rate of auto-infection tends to enhance the stability of polymorphism in GFG systems (46).

Here, the influence of an important characteristic of polycyclic diseases, host-mediated interactions between parasite genotypes, on GFG coevolution is investigated. An *RES* plant is not only constitutively resistant to *AVR* parasites by a GFG interaction, but may also express induced resistance (IR) against further attack by parasites, whether *AVR* or *avr* (19,26,28,40). Two important types of IR are known, systemic acquired resistance (SAR), mediated by salicylate (19,26,40,45), and induced systemic resistance

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