

# The Influence of Perenniality and Seed Banks on Polymorphism in Plant-Parasite Interactions

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**ABSTRACT:** Antagonistic interactions, such as diseases, play an important role in natural populations. Understanding the mechanisms that promote long-term polymorphism at loci that are involved in host-parasite recognition is a fundamental problem in evolutionary ecology. Coevolution implies the existence of indirect frequency-dependent selection because the fitnesses of parasite genotypes depend on the frequencies of host genes and vice versa. Polymorphism can be maintained in both organisms if there is also negative, direct, frequency-dependent selection, when natural selection for host resistance or parasite virulence declines with increasing frequency of that trait itself. In this article, using the gene-for-gene relationship as a model, we show that two plant life-history traits, seed banks and perenniality with parasite density-dependent disease transmission, generate frequency-dependent selection on host resistance and are thus capable of stabilizing frequencies of coevolving host and parasite genes. The host population's response to selection by the parasite is modified by the contribution of past selective events stored in long-lived seed banks or in a growing population of perennial plants that have a long life span in the absence of disease. While fitness costs determine whether coevolutionary cycles occur in interacting host and parasite populations, the ecology of the two organisms determines whether stable polymorphism is maintained.

**Keywords:** natural selection, host-parasite interactions, coevolution, boom-and-bust cycle, gene-for-gene, resistance, avirulence.

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## Introduction

Parasites may limit the reproductive fitness of infected host organisms so that genes conferring resistance to disease are favored by natural selection if they increase reproductive success. In both plants and animals, defenses can be induced through recognition of parasite molecules, while parasites may avoid recognition, evading host defenses by the loss or mutation of these molecules (Jones and Dangl 2006;

Schmid-Hempel 2008). In natural populations, there is substantial allelic diversity at host loci, enabling parasite recognition, such as the major histocompatibility complex (MHC) in vertebrates (Apanius et al. 1997) or gene-for-gene (GFG) resistance loci in plants (Thrall et al. 2001) and in corresponding parasite antigen genes.

Two groups of hypotheses have been proposed to explain such polymorphism. In the trench-warfare model, stable polymorphism of two or more alleles at host and parasite loci is maintained by balancing selection (Stahl et al. 1999). The arms-race model, by contrast, predicts transient polymorphism caused by recurrent selective sweeps (Holub 2001). In the latter scenario, new alleles arise constantly by mutation, and the population remains polymorphic, even though at any point in time most alleles are either fixed or extinct (Holub 2001). Surveys of host and parasite variation in natural populations require long time series—dozens of generations at least—to distinguish these hypotheses (Thrall et al. 2001, 2002; Thrall and Burdon 2003). A fruitful, alternative approach is to study molecular diversity to examine selective pressures occurring over hundreds of generations. Signatures of balancing selection have been observed at host (Stahl et al. 1999; Bakker et al. 2006; Rose et al. 2007) and parasite (Allen et al. 2004; Stukenbrock and McDonald 2009) loci, consistent with the trench-warfare hypothesis, but evidence supporting the arms-race model is comparatively scarce (Bakker et al. 2006; Stukenbrock and McDonald 2009).

A significant area for theoretical research, therefore, concerns the conditions that promote long-term, stable polymorphism at these loci (Bergelson et al. 2001). Host-parasite interactions are characterized by indirect frequency-dependent selection (FDS), where selection for host resistance ( $R$ ) depends on the frequency of parasite infectivity ( $I$ ) and vice versa. A necessary but not sufficient condition for stable polymorphism is that the rates of increase of  $R$ ,  $I$ , or both decline as their values increase (see eq. [2]). Polymorphism in an interacting pair of host and parasite genes may be stable, resulting in trench-warfare polymorphism (Stahl et

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