Supplementary Model:

Haploid model for frequency-dependent selection at vegetative incompatibility (*vic*) loci in fungi

Cockerham et al. (1972) developed a model for frequency-dependent selection based on pairwise competitive interactions between genotypes in randomly mating populations. Their model was based on one-locus with two-alleles in diploids, where the fitness of a genotype varies as a function of other genotypes with which it interacts, e.g., in competition. The average fitness of each genotype is weighted by the frequencies of encounters with its own and other genotypes. Equilibrium conditions for this model are complex because of a cubic form of the equation that results when the change in allele frequency in one generation, Δp , is set to 0.

A haploid version of this one-locus, two-allele model is much simpler (without higher order terms in Δp) and a single equilibrium allele frequency can be derived (see equation A5 in Appendix at the end of this document) as

$$\hat{p} = \frac{(W_{21} - W_{11})}{(W_{21} - W_{11}) + (W_{12} - W_{22})},\tag{1}$$

where p is the frequency of allele 2 and W_{ij} is the fitness of an individual carrying allele i interacting with an individual carrying allele j.

This simple model is applicable to the interactions between *vic* genotypes in *C. parasitica* with the rationale explained below, based on a study of virus transmission by Cortesi et al. (2001). Isolates of *C. parasitica* infected with hypoviruses have significantly lower fitness than virus-free individuals (Nuss, 2005; Peever et al., 2000).

1) <u>Inhibition of virus transmission</u>: Heteroallelism at five of the six known *vic* loci (all but *vic4*; see below) inhibits virus transmission in *C. parasitica*. At these five loci, we assume that $W_{21} > W_{22}$ and $W_{12} > W_{11}$ because virus transmission occurs in 100% of interactions between homoallelic individuals and at reduced rates between heteroallelic individuals. We also assume $W_{11} = W_{22}$, that is, all genotypes are equal except in their interactions with other genotypes.

2) <u>Asymmetric transmission</u>: When virus transmission is symmetric, that is, when transmission occurs with equal probability in both directions between strains heteroallelic at a *vic* locus, then $W_{21} \approx W_{12}$, and therefore, based on equation 1, $\hat{p} \approx 0.5$. However, asymmetric virus transmission has been documented for three loci in *C. parasitica*: *vic1*, *vic2* and *vic7* (Cortesi et al., 2001). Intuitively, asymmetry in virus transmission should favor a *vic* allele that confers stronger inhibition of transmission into the recipient. For example, *vic1-2* strongly inhibits transmission into a recipient isolate carrying this allele. Therefore, based on the asymmetry of virus transmission, $W_{21} > W_{12}$, assuming viruses are present in the fungal population. Based on equation 1, therefore, $\hat{p} > 0.5$ because $(W_{21} - W_{11}) > (W_{12} - W_{22})$. (Recall the assumption that $W_{11} = W_{22}$). This same prediction holds for *vic2*, but equation 1 predicts $\hat{p} < 0.5$ for *vic7* because allele 1 confers higher fitness in asymmetric virus transmission.

3) <u>No effect on transmission</u>: By definition, W_{ij} is the fitness of an individual carrying allele *i* when it interacts with an individual carrying allele *j* at the same locus. In *C. parasitica*, heteroallelism at *vic4* has no effect on virus transmission even though it does result in mycelial incompatibility (Smith et al., 2006). Therefore, we assume $W_{ij} = W_{ii}$ and we cannot use equation 1 to predict an equilibrium allele frequency for *vic4*.

Based on the effects of heteroallelism at *vic* loci on virus transmission, we predict equilibrium frequencies of allele 2 (\hat{p}) in *C. parasitica* as follows:

locus	Predicted \hat{p}		
vic1	$0.5 < \hat{p} < 1$		
vic2	$0.5 < \hat{p} < 1$		
vic3	0.5		
vic4			
vic6	0.5		
vic7	$0.0 < \hat{p} < 0.5$		

Appendix: Derivation of equilibrium frequencies for genes under frequency-dependent selection in haploids.

Our model is based on the model of Cockerham et al. (1972) for frequency-dependent selection at a diploid locus, with two alleles. Instead of genotypes *AA*, *Aa* and *aa* at a diploid locus, we model alleles 1 and 2 at a haploid locus. Following the notation of Cockerham et al. (1972), the fitness of an individual with allele *i* interacting with an individual with allele *j*, W_{ij} is represented in the following matrix:

	Allele 2	Allele 1	Mean
Allele 2	W_{22}	W_{21}	$\overline{W_2}$
Allele 1	W_{12}	W_{11}	$\overline{W_1}$

(A1)

(A2)

Let *p* be the frequency of allele 2, and *q* the frequency of allele 1; and p + q = 1. The mean fitness of allele *i*, $\overline{W_i}$, is weighted by the frequencies of interactions with other genotypes,

 $\overline{W_2} = pW_{22} + qW_{21}$ $\overline{W_1} = pW_{12} + qW_{11}.$

The overall mean fitness of the population is

$$\overline{W} = p\overline{W_2} + q\overline{W_1}$$

The frequency of allele 2 in the next generation, p', is given by

(A3)

$$p^{'}=rac{p\overline{W_{2}}}{\overline{W}}$$
 ,

and

$$q' = \frac{q\overline{W_1}}{\overline{W}}.$$

The change in allele frequency in one generation, Δp , is

$$\Delta p = p' - p$$
$$= \frac{p\overline{W_2}}{\overline{W}} - p$$

$$= \frac{p}{\overline{W}} [\overline{W_2} - \overline{W}]$$

$$= \frac{p}{\overline{W}} [\overline{W_2} - p\overline{W_2} - q\overline{W_1}]$$

$$= \frac{p}{\overline{W}} [\overline{W_2} (1 - p) - q\overline{W_1}]$$

$$= \frac{pq}{\overline{W}} [\overline{W_2} - \overline{W_1}]$$

$$= \frac{pq}{\overline{W}} [pW_{22} + qW_{21} - pW_{12} - qW_{11}]$$

$$= \frac{pq}{\overline{W}} [p(W_{22} - W_{12}) + q(W_{21} - W_{11})]$$
(A4)

To find the equilibrium frequency, \hat{p} , set $\Delta p = 0$. For a non-trivial equilibrium ($p \neq 0,1$), $\Delta p = 0$ when

$$\hat{p}(W_{22} - W_{12}) + \hat{q}(W_{21} - W_{11}) = 0$$
$$\hat{p}(W_{22} - W_{12}) + (1 - \hat{p})(W_{21} - W_{11}) = 0$$

$$\hat{p}(W_{22} - W_{12}) + (W_{21} - W_{11}) - \hat{p}(W_{21} - W_{11}) = 0$$

$$\hat{p}(W_{21} - W_{11}) - \hat{p}(W_{22} - W_{12}) = (W_{21} - W_{11})$$

$$\hat{p} = \frac{(W_{21} - W_{11})}{(W_{21} - W_{11}) - (W_{22} - W_{12})}$$

$$\hat{p} = \frac{(W_{21} - W_{11})}{(W_{21} - W_{11}) + (W_{12} - W_{22})}$$
(A5)

References

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