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## Review

# Vegetative incompatibility in fungi: From recognition to cell death, whatever does the trick

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### ABSTRACT

Allorecognition in fungi takes the form of vegetative incompatibility (VI), a process leading to the programmed cell death of heterokaryotic cells formed after anastomosis between hyphae of genetically incompatible isolates, thereby keeping different genotypes separated. VI is ubiquitous amongst ascomycetes and basidiomycetes, determined by loci named *het* or *vic*, and responds to both promoting and limiting selective constraints. While VI has been widely used to analyze fungal populations, genes controlling VI systems have only been characterized at the molecular level in three ascomycete species. VI systems can be considered as having a modular organization, comprised of a polymorphic component for recognition associated with a cell death inducing component often (but not exclusively) including a HET domain protein. However, the actual genes involved differ in sequence and properties. Some VI genes display a patchy phylogenetic distribution, whereas others appear widely conserved in fungal genomes, but their function in controlling VI is restricted to a single or a few related species. It also appears that evolutionary trajectories generating and maintaining polymorphism at these loci differ. Some *het* genes show low allelic diversity and signs of long term balancing selection and may be specifically selected for allorecognition. Others show high allelic diversity, evidence of positive selection and fast evolution and their products are believed to correspond to immune receptors whose functions have been coopted for allorecognition. Finally, where known, mechanisms for initiating cell death and the cell death reaction itself display similarities and differences between different model species. All these data support the hypothesis that VI is a ubiquitous phenomenon acquired time and time again independently in different fungal lineages.

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## 1. Introduction

Allorecognition mechanisms, the ability to discriminate self from non self within a species, exist in all kingdoms of life, and include kin recognition in amoebas (Buss, 1982), self-

incompatibility during reproduction in plants (Iwano and Takayama, 2012), sexual (Dyer et al., 2016) and vegetative incompatibility in fungi (Glass and Dementhon, 2006; Sauepe, 2000), tissue fusion in marine colonial invertebrates (Rosengarten and Nicotra, 2011), and the highly refined Major

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Histocompatibility Complex governing graft rejection in metazoans (Muraille, 2014). These organisms span the whole eukaryotic kingdom and although their allorecognition mechanisms are quite diverse, they all rely on one common feature to ensure recognition, a set of loci polymorphic between individuals (Nydham and De Tomaso, 2011). In consequence, independent of the actual mechanisms specific to each recognition systems, an understanding of how polymorphism emerges and is maintained at these loci is fundamental to explaining non self recognition. Indeed, it appears that depending on the organisms and systems investigated, allorecognition might be the driving force for the evolution of these recognition systems, while in other circumstances allorecognition might be an undesirable consequence of other recognition mechanisms (Chae et al., 2014; Nydam and De Tomaso, 2011; Ostrowski and Shaulsky, 2009; Rosengarten and Nicotra, 2011).

In ascomycete and basidiomycete fungi allorecognition occurs during the sexual cycle or after anastomosis between vegetative hyphae that results in the formation of a heterokaryon. Sexual reproduction is governed by alternative mating-type loci and has been largely reviewed recently (Dyer et al., 2016; Heitman, 2015). Vegetative incompatibility (VI; also known as heterokaryon incompatibility) manifests itself when incompatible alleles of specific loci called *het* (heterokaryon) or *vic* (vegetative) are co-expressed in a common cytoplasm, usually after anastomosis between genetically different hyphae, and induces a programmed cell death (PCD) reaction. VI thus contributes to define individuals by maintaining the separation of genetically different entities.

In some model species VI is easy to visualize on culture plates as it results in an altered contact zone between incompatible isolates that is not detected upon fusion between compatible isolates (Fig. 1A). VI can also be visualized by forcing the formation of heterokaryons by growing compatible complementary auxotrophic mutants on minimal media, or by genetic transformation of an allele into a recipient strain, the resulting phenotype depends on the *het* alleles expressed by the recipient heterokaryon or strain. One can define Vegetative Compatibility Groups (VCG) as being constituted of compatible isolates that are genetically related. The ease of testing sexual and vegetative compatibility was used to great length and is still a tool of choice to study fungal populations (Chang et al., 2014; Hoekstra, 1994). These approaches have been instrumental in analyzing population structure (Cortesi and Milgroom, 1998), in demonstrating the fast evolution of invasive pathogens such as *Ophiostoma novo-ulmi* (Brasier, 1988), and in analyzing selective constraints acting on VI (see below). These approaches are also central to the development of biocontrol strategies of plant pathogens such as *Cryphonectria parasitica* (Milgroom and Cortesi, 2004) or to control toxin producers such as *Aspergillus flavus* (Atehnkeng et al., 2016; Grubisha and Cotty, 2015; Moore et al., 2013). VI testing has been used for analyzing populations of numerous fungal species and revealed that ascomycete usually contain about 10 *het* loci and basidiomycetes less than five generally multi-allelic *het* loci (Van der Nest et al., 2014). Basidiomycetes are not the most amenable models for studying vegetative incompatibility because of the essentially heterokaryotic life cycle. The molecular-genetic basis of VI has been studied in great details in only three ascomycete species, *Neurospora*

*crassa*, *Podospora anserina* and *C. parasitica* (Table 1). Consequently the present review will focus on data gained from these three models with input from other species where possible.

## 2. Selective forces acting on vegetative incompatibility

VI is selectively advantageous as it restricts the horizontal propagation of deleterious cytoplasmic elements. For example, there are numerous demonstrations that virus transmission is restricted to various degrees by the different VI systems in *C. parasitica* (Brusini et al., 2011; Cortesi et al., 2001; Nuss, 2005). Consequently a *C. parasitica* strain lacking all incompatibility systems has been engineered as an universal donor to help propagate hypovirulent viruses in populations as a tool for biocontrol (Zhang and Nuss, 2016). In *O. novo-ulmi* populations decrease in virus prevalence was associated with a parallel increase in *vic* genotype diversity (Brasier, 1988). In *Podospora anserina*, distribution of the deleterious plasmid pAL2.1 depends on *het* genotypes (Bastiaans et al., 2014a; Debets et al., 2012; van Diepeningen et al., 2008). VI can also restrict resource plundering by aggressive genotypes (Debets and Griffiths, 1998), or the propagation of cheater genotypes thereby facilitating emergence of multicellularity (Bastiaans et al., 2016).

However, selection also limits VI. For instance, it was recently demonstrated by *in vitro* evolutionary studies that unrestricted fusion between isolates was favorable for the development of *N. crassa* (Aanen et al., 2008; Bastiaans et al., 2015) and VI decreased cooperation between isolates. In a *P. anserina* population, *Pahet-c* alleles producing stronger incompatibility reactions with a set of tester strains were less frequent in a population (Bastiaans et al., 2014b). VI also potentially restricts parasexuality, a mechanism allowing mitotic recombination after vegetative fusion (Pontecorvo, 1956). Parasexuality might be important for generating genetic variation in asexually reproducing fungi, and has even been reported to occur between incompatible isolates (McGuire et al., 2005) suggesting that certain conditions might suppress VI to allow parasexuality. It is also noted that VI can be suppressed in certain conditions such as during sexual reproduction or during Conidial Anastomosis Tube (CAT) fusion occurring between incompatible germings (Ishikawa et al., 2012). Thus, the acquisition and maintenance of non-self recognition loci will involve a balance of opposing evolutionary constraints.

## 3. Genetic control of VI

VI is genetically controlled by about ten different loci in ascomycete fungi and less than five in basidiomycetes. Two forms of VI have been reported. First 'allelic interactions' where co-expression of incompatible alleles from a single gene results in VI; second, 'non-allelic' interactions where co-expression of incompatible alleles from different genes results in VI. Efforts to clone *het* genes started in the late 80's in *N. crassa* and *P. anserina* using combinations of positional cloning, phenotypic expression and functional analysis (Espagne et al., 2002; Glass et al., 1988; Saupe et al., 1994, 1995, 1996;

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