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## Infection, Genetics and Evolution

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## Review

## Durable resistance: A key to sustainable management of pathogens and pests

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## ARTICLE INFO

Article history:  
Available online xxx

Keywords:  
Durable resistance  
Host mixtures  
Landscape ecology  
Pathogen evolution  
Quantitative resistance  
Resistance gene pyramids

## ABSTRACT

This review briefly addresses what has been learned about resistance durability in recent years, as well as the questions that still remain. Molecular analyses of major gene interactions have potential to contribute to both breeding for resistance and improved understanding of virulence impacts on pathogen fitness. Though the molecular basis of quantitative resistance is less clear, substantial evidence has accumulated for the relative simplicity of inheritance. There is increasing evidence for specific interactions with quantitative resistance, though implications of this for durability are still unknown. Mechanisms by which resistance gene pyramids contribute to durability remain elusive, though ideas have been generated for identifying gene combinations that may be more durable. Though cultivar mixtures and related approaches have been used successfully, identifying the diseases and conditions that are most conducive to the use of diversity has been surprisingly difficult, and the selective influence of diversity on pathogen populations is complex. The importance of considering resistance durability in a landscape context has received increasing emphasis and is an important future area of research. Experimental systems are being developed to test resistance gene deployment strategies that previously could be addressed only with logic and observation. The value of molecular markers for identifying and pyramiding major genes is quite clear, but the successful use of quantitative trait loci (QTL) for marker-assisted selection of quantitative resistance will depend greatly on the degree to which the identified QTL are expressed in different genetic backgrounds. Transgenic approaches will likely provide opportunities for control of some recalcitrant pathogens, though issues of durability for transgenes are likely to be no different than other genes for resistance. The need for high quality phenotypic analysis and screening methodologies is a priority, and field-based studies are likely to remain of signal importance in the foreseeable future.

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## 1. Introduction

A discussion of durable resistance must be considered in context of major global challenges. It has been predicted that a combination of changing diets and human population growth will result in an increased demand for agricultural production of 60–110% between the years 2005 and 2050 (Alexandratos and Bruinsma, 2012; Tilman et al., 2011); increased demand for forest products could be even greater (WWF, 2012). Given the substantial losses caused by disease and pests globally (Oerke, 2006; Strange and Scott, 2005) and the increasing number of epidemic invasions resulting from globalization (Anderson et al., 2004; Crowl et al., 2008), meeting this demand will require an intense focus on disease and pest control. Further, these demands must be met while avoiding negative environmental impacts caused by current practices (Tilman et al., 2001) and in the face of significant global climate change (IPCC, 2007). Mean changes of temperature and precipitation can have positive, negative, or neutral impacts on specific diseases (Chakraborty, 2011; Garrett et al., 2006). Of greater concern may be the expected increase in climatic variability (IPCC, 2012), which could increase the number of diseases and pests of importance in a given locality, as well as the yearly fluctuations of their prevalence. Host plant resistance is generally the most favorable control method for environmental, economic, and social reasons. Thus, genes for resistance to diseases and pests can rightfully be considered one of the most important natural resources determining the survival of the human species (Mundt, 1994), while the evolutionary potential of plant pathogens to adapt to host resistance (McDonald and Linde, 2002) makes good stewardship essential to attain sustainable use of this precious resource.

The evolution of both organisms (Gould and Eldredge, 1977) and scientific thought (Kuhn, 1996) commonly experience periods of relative stasis punctuated by periods of rapid change. I suggest that the field of durable resistance had been in a period of relative stasis for some years, but recent information presented in this conference clearly suggests that the field is entering another period of significant advancement. This article will attempt to summarize what has been accomplished in this field of study and what remains to be done, with an emphasis on changes that have occurred since the last international conference on this topic held in 2000 (proceedings published in Vol. 124, Issue 2 of *Euphytica*). Throughout this short review, significant questions that remain to be answered will be listed as italicized “bullet points” in an attempt to frame future directions for the field, while recognizing that a summary by any individual is bound to contain gaps and shortcomings. I will focus primarily on genetic aspects of durability, though it is important to recall that other disease control practices can influence both the epidemiological impact and the durability of host plant resistance (Mundt et al., 2002).

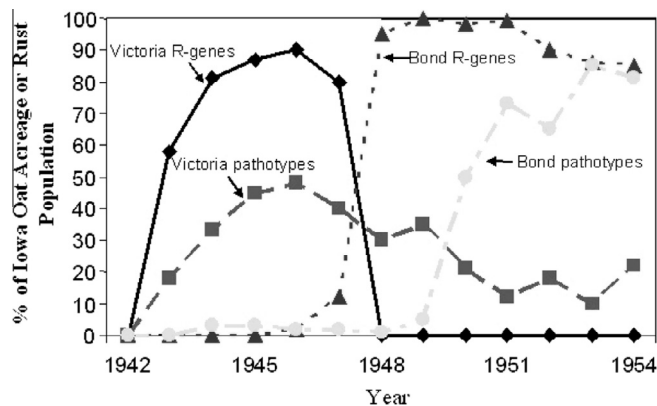
## 2. Changes in outlook and approach

The field of durable resistance was once dominated by rigid dogma and competing views of both mechanism of resistance (e.g., horizontal versus vertical resistance) and resistance deployment strategies (e.g., pyramids versus mixtures). The field has

largely moved beyond this outlook to a more mature one recognizing that all approaches of attaining durability have a potential value in different circumstances and, in fact, may complement each other when used in concert. The field of durable resistance also has broadened substantially in terms of host/pathogen systems under study. For many years, the field of durable resistance was largely dominated by studies of rusts and powdery mildews of small grain crops and of potato late blight. Over time, the field has expanded to a diversity of annual and perennial crops, to natural ecosystems, and to a wide range of fungi, oomycetes, bacteria, viruses, and nematodes (Zadoks, 2002), a healthy process that continued in the 2012 conference. This review will be dominated by plant pathogens, my area of familiarity, but it is very positive that the conference itself also included contributions regarding durability of host plant resistance to insect pests. Finally, the field of durable resistance has broadened in scope by more widely incorporating the information from the fields of molecular genetics/genomics, ecology, and population genetics.

## 3. Molecular mechanisms of host/pathogen interactions

A clear advance since 2000 has been exciting progress in understanding the elusive nature of gene-for-gene interactions in plant host/pathogen systems. Despite elucidation of the basic genetic system several decades ago (Ellingboe, 1976; Flor, 1971) and cloning of the first avirulence in the 1980s (Staskawicz et al., 1984), it had remained unclear why dominant genes conditioning avirulence would exist in pathogen populations. More recently, computational genomics has demonstrated that avirulence genes also serve as effectors of pathogen virulence, with substantial redundancy among effector genes (Cunnac et al., 2001; Jones and Dangl, 2006). These advances could have substantial relevance to understanding the dynamics of pathogens populations in response to resistance deployment (Michelmore et al., 2013). As one of many examples, it has often been observed that virulent races rarely



**Fig. 1.** Example of a classic boom-and-bust cycle of major gene resistance to plant pathogens. Lines indicate the percentage of the Iowa oat area planted to cultivars possessing either the Victoria or the Bond major resistance and the percentage of the surveyed oat crown rust population virulent on cultivars carrying those resistance genes. Modified from McDonald (2004); used with permission. Original data from Browning and Frey (1969).

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