

Yield penalties of disease resistance in crops

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Recently, there have been rapid developments in understanding the costs of disease and pest resistance in model plants and their ecological relevance in wild plants. In crop plants, however, much (although not all) of our current understanding of costs of resistance must be inferred from research on model species. To determine the true costs of resistance in crops and the likely benefit of resistance genes in new cultivars, however, other aspects of the plant's phenotype must be studied alongside resistance.

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Abbreviations

Avr	avirulence
GFG	gene-for-gene
IR	induced resistance
PR	partial resistance
PT	pathogenicity target
QTL	quantitative trait locus
R	resistance
TGW	thousand-grain weight

Introduction

Disease resistance is often assumed to be costly. Indeed, many traits that are associated with resistance to pathogens and herbivores reduce plant fitness, although others do not [1]. Research on costs of resistance is currently enjoying a surge of interest. This is particularly true of studies of the mechanisms underlying costs in model organisms, such as *Arabidopsis*, and their ecological significance in wild plants. Although crops have not been completely neglected, it is fair to describe research in this area as sporadic. There has long been evidence that disease resistance may affect crop performance [2], but several of the most informative experiments were done a decade or two ago and have not been properly followed up. In this review, therefore, although I cover research progress in the past year, I also attempt to identify critical areas where our knowledge or understanding is most seriously lacking.

I focus particularly on yield, the single most important indicator of crop performance. In a breeding programme, many factors must be weighed against one another, and disease resistance is rarely the most important. In the UK, for example, the key targets for wheat breeding are yield, quality and standing power, in that order. Disease resistance as a whole is no higher than fourth in a breeder's list of priorities, whereas resistance to any one disease is simply one of several factors that must be considered when

deciding whether or not to market a cultivar. If resistance has a substantial cost, therefore, it has commercial significance because it may hinder the more important objective of increasing yield.

Two useful, general reviews on costs of resistance have been written by Purrington [3], who focuses on the mechanisms of costs, and Bergelsen and Purrington [1], who comprehensively review research published before 1995 on costs of resistance to pathogens, herbivores and herbicides. Bergelsen and Purrington [1] emphasise studies in which the genetic background was controlled so that the effects of resistance (*R*) genes could be distinguished from those of other genes. They include meta-analyses of the influence of several factors on the ability of experiments to detect costs of resistance. Some caution should be exercised in this respect, because the unit of analysis was the research paper. Hence, four papers that reported a cost associated with the *mlo* gene in barley for resistance to powdery mildew (*Blumeria graminis* [syn. *Erysiphe graminis*] f. sp. *hordei*) [4–7] were treated as four separate data supporting the hypothesis that resistance is costly. In contrast, three papers in which no cost was associated with any of ten or more gene-for-gene (GFG) resistances to barley powdery mildew [5,8,9] were treated as just three data against that hypothesis.

Linkage or pleiotropy?

A direct effect of an *R* gene on yield implies an underlying mechanistic relationship. However, genes that are linked to an *R* gene may also affect yield and hence hamper the selection of commercially successful resistant cultivars. Such linkage is especially likely to create problems when the *R* gene has been introgressed from a wild relative of the crop. Under these circumstances, there is little recombination between the introgressed segment and the homoeologous segment in the crop species. It is generally only worthwhile for a breeder to analyse such a linkage and to try to break it when the yield penalty in the absence of the target pathogen or pest is commercially significant.

Wild-relative species are especially important in the breeding of wheat. In wheat, recombinants have been found in which the *Pch1* gene for resistance to eyespot (*Tapesia* spp., a stem-base disease) from the wild grass *Aegilops ventricosa* is no longer linked to a gene for reduced yield [10]. On the other hand, linkage between yield depression and the *Lr9 R* gene from *Aegilops umbellulata*, which confers resistance to wheat brown rust (also known as leaf rust [*Puccinia triticina*, syn. *Puccinia recondita* f. sp. *tritici*]), has not been broken [11]. Other *R* genes on introgressed segments that are associated with reduced yield are *Wsm1* for resistance to wheat streak mosaic virus from *Thinopyrum intermedium*, which is associated with a mean yield reduction of