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Review

Barley yellow dwarf virus resistance in cereals: Approaches, strategies and prospects

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ABSTRACT

The *Barley yellow dwarf virus* (BYDV) complex, belonging to the *Luteovirus* genus, is one of the most economically harmful plant viruses. Apart from fighting the aphid vectors by spraying cereal fields with insecticides, the only protection against this virus is to grow resistant cultivars. However, cereal plant resistance to BYDV is rare and complicated, and a considerable amount of work has been performed to date in the development of resistant cultivars and lines, with mixed results. The aim of this article is to describe the current breeding status of plants in terms of BYDV resistance, including transgenic resistance and resistance to aphid vectors. The goal is to discuss the possible advantages and drawbacks of individual approaches and to suggest future developments.

Contents

1. Introduction

The *Barley yellow dwarf virus* (BYDV) complex causes one of the economically most important viral diseases of cereals worldwide, with significant yield losses in major cereal crops such as wheat, barley, rice, maize, oat and rye-grass (D'Arcy and Domier, 2005). Virtually all species in the family Poaceae (Gramineae) can be infected, thus providing more than 150 species as putative hosts of these viruses (D'Arcy, 1995).

The disease is caused by a group of related single-stranded RNA viruses that have been assigned to the genus *Luteovirus* (*Barley yellow dwarf virus*-BYDV spp. PAV, PAS, MAV and Kerll) or *Polerovirus* (*Cereal yellow dwarf virus:* CYDV-RPV; CYDV-RPS; *Maize yellow dwarf virus*- RMV) as well as viruses not assigned to a genus (BYDV-SGV and BYDV-GPV) in the family Luteoviridae (ICTV taxonomy: 2015, for reviews, see Miller and Rasochová, 1997; Miller et al., 2002; Gray and Gildow, 2003). BYDV can vary strongly with regard to symptom manifestation, vector transmission efficiency,

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host preference and serological and molecular properties. The virus is restricted to the phloem and is transmitted in a persistent manner by more than 25 aphid species (Power and Gray, 1995). BYDV induces yield losses ranging from 5 to 80%, with an average of 30% in affected fields (Perry et al., 2000). The incidence of BYDV in cereal crops (e.g., barley, wheat, and oat) has been very high (recently reaching epidemic levels in many regions of the Czech Republic) and has caused significant yield losses in past decades (Plumb, 1990), particularly in winter crops (Kundu et al., 2009). Warm and long autumn seasons favour infestation of wheat crops by aphids, and higher autumn temperatures in the last few years have caused BYDV to become a serious problem for both winter wheat and barley. Moreover, climate change scenarios predict conditions that would make BYDV one of the most dangerous diseases of cereal crops (Saulescu et al., 2011). The most effective and sustainable control method to date is the use of plant material that is resistant/tolerant to the virus complex (Henry et al., 2002).

Plant responses to viral infection can cause different types of host-virus interactions, including compatible interactions, interactions that lead to host infection (infectible) and non-compatible interactions, and interactions that do not result in host infection (non-host, immune). A compatible interaction is defined as either susceptible or resistant: in the former, the virus infects the host, replicates within the host, and severe disease symptoms occur; in the latter, the virus may or may not replicate to some extent in the host, but invasion is restricted relative to a susceptible host, and the obvious disease symptoms are highly localised or do no develop (for a review, see Kang et al., 2005). Host resistance is also classified into two categories: (1) tolerance-when symptoms and yield losses are reduced, though virus multiplication is not altered; (2) resistance-when virus multiplication and spread are significantly reduced (for a review, see Cooper and Jones, 1983). This article provides an overview of our present knowledge of both types of resistance to BYDV in plants and vectors.

2. BYDV resistance in crops

2.1. Resistance in barley

Barley and wheat are the two cereals most economically affected by *Barley yellow dwarf virus* infections. Yield losses in barley can reach up to 80% (Dedryver et al., 2010). Four genes and some QTLs in barley have been described in connection with resistance/tolerance to BYDV. The first gene, the recessive *ryd*1 allele of which is responsible for an intermediate level of tolerance, was identified by Suneson (1955) in the cultivar Rojo. The location of *Ryd1* is unknown (Niks et al., 2004), and because of its low efficiency, this gene is rarely used in barley breeding. The *Ryd*2 (or *Yd*2) gene was discovered through extensive screening of Ethiopian barley landraces (Schaller et al., 1964). This gene has been introduced into many barley cultivars and has remained the primary resistance gene used in barley breeding programmes (Kosová et al., 2008). Although *Ryd*2 has been reported to reduce the virus titre of BYDV-PAV, -MAV and -PAS in young plants (Jarošová et al., 2013; Šíp et al., 2006; Riedel et al., 2011), it confers field tolerance to only certain CYDV-RPV isolates (Banks et al., 1992; Scholz et al., 2009). *Ryd*2 does not prevent the virus from spreading systemically from the point of infection, but it appears to act by reducing the rate of virus replication in the phloem (King et al., 2002). The *Ryd*2 locus is multiallelic and maps close to the centromere on the long arm of chromosome 3H (Collins et al., 1996). The effect of the semi-dominant *Ryd*2 gene varies according to the genetic background, environmental conditions and virus isolate. However, no differences in the BYDV-PAV virus titre of plants carrying *Ryd*2 or susceptible plants were observed in studies in which older plants were tested (Riedel et al., 2011). Collins et al. (1996) constructed a detailed linkage map of the *Ryd*2 region encompassing 27.6 cM of chromosome 3 and containing 19 RFLPs, 2 morphological marker loci, the centromere and *Ryd2*. Scheurer et al. (2001) mapped QTLs in mapping populations segregating quantitatively for tolerance to BYDV-PAV and found a quantitative effect in the cultivar Vixen, which carries *Ryd*2. This finding suggests that in some genetic backgrounds or with some allelic forms or against certain viral isolates, this gene may appear to be a minor gene, requiring QTL-mapping software to establish its position (Niks et al., 2004). All markers used in the mapping of barley and wheat genes are listed in Table 2. A list of barley cultivars possessing the *Ryd2* gene is provided in Table 1.

Table 1
List of wheat and barley cultivars and lines with resistance or tolerance to BYDV (a selection).

Species	Cultivar/Line	Gene
	Atlas68	
	Vixen	
	Coracle	
	Sutter	
	Abate	
	Franklin	
	Nomin	
	Prato	*Ryd*2
	Shannon	
	Shyri	
	Venus	
Barley	Wysor	
	CI 2376; CM 67; CM 72	
	UC 337; UC 476; UC 566; UC 603	
	Granado	*Ryd*3
	Laurel	*Ryd*2 and *Ryd*3
	Perry	
	Sigra	
	Post	
	Malvaz	QTLs for tolerance
	Atribut	
	Madras	
	Penco	
	Anza	
	Condor	*Bdv*1
	Frontana	
	Mackellar (TC14)	*Bdv*2
	Glover (TC6)	
	Linkang 11 (Zhong 4 Awnless)	*Bdv*4
	Saskia	
	Rialto	
	Meritto	
Wheat	Rexia	
	Svitava	
	Leguan	
	Milan	QTLs for tolerance
	Altar 84	
	Ae. Squarrosa	
	Nanjing 8508	
	Ducula	
	Lira	

The data in brackets are the names of amphiploids or translocation lines from which the wheat cultivars are derived.

Niks et al. (2004) identified the novel major gene *Ryd*3 for BYDV-PAV resistance in barley of Ethiopian origin (L94) and mapped it to the short arm of chromosome 6 near the centromere. *Ryd3* explained approximately 75% of the phenotypic variance. Although Niks et al. (2004) reported that the gene conferred resistance rather than tolerance (with ELISA values close to zero), 20% of the plants carrying the *Ryd*3 gene developed symptoms and had virus concentrations similar to those of susceptible accessions (Niks et al., 2004). Double haploid lines combining *Ryd*2 and *Ryd*3 genes were tested against BYDV-PAV, which resulted in quantitative resistance instead of tolerance. Furthermore, the *Ryd*3 tolerance allele has been transferred to winter barley, in which yield losses due to