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Host Plant Resistance or Tolerance for Control of Yellow Dwarf Viruses in Cereals

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ABSTRACT

Yellow dwarf viruses are the most economically important and devastating viruses affecting cereal crops, resulting in yield and quality losses. Because of recent global climate change, there has been an increase in vector-borne viruses, particularly yellow dwarf viruses transmitted by aphids. YDVs comprise a complex group that includes barley yellow dwarf viruses (BYDVs)/cereal yellow dwarf viruses (CYDVs), as well as newly renamed species. One of the most effective control methods for YDVs is to grow resistant or tolerant cultivars, in addition to late sowing, spraying and covering seeds with insecticides to control aphid vectors, as well as other cultural practices. Resistance to BYDV is complex, and numerous studies have been conducted to date in many efforts to develop resistant cultivars and lines to manage YDVs. Those studies included BYDV resistance derived from wheat-related and wild relatives, as well as resistance attained against aphids. This review will examine breeding studies addressing BYDV resistance in cereals, including wheat, barley, oats, and maize, to date.

Keywords: Cereal, BYDV, resistance, tolerance

Introduction

Yellow dwarf viruses (YDVs) are the most economically important and devastating viruses, causing yield losses in cereal crops worldwide. YDVs infect cereal species, such as wheat, barley, and oats, as well as many annual and perennial monocotyledonous grasses in the Poaceae family (D'Arcy, 1995). YDVs have also been found to infect dicotyledonous grasses, *Geranium dissectum* and *Juncus compressus*, in recent years (İlbağı et al., 2019). They are characterized by yellowing or reddening, depending on the hosts, dwarfing, delayed heading, and reduced cereal grain numbers. Characteristic symptoms include stunted growth of the host, resulting from diminished internode elongation. The discoloration is pervasive on older infected leaves (Oswald and Houston, 1953). Wheat, triticale, and rye leaves are commonly yellow, and sometimes they are red. It has been reported that serration along the leaf margins in wheat and oats, apart from inhibiting root growth, was observed in plants infected with YDV (Kolb et al., 1991; Hoffman and Kolb, 1997). YDV infection may be confused with symptoms of abiotic stress in plants. Thus, the diagnostic methods should confirm the visual diagnosis of YDV infections. YDVs affect yield by causing sterility, suppressing heading, and reducing the number of tillers and kernels per spike (D'Arcy, 1995). It can cause severe losses, especially in wheat, depending on the YDV species, wheat varieties, weather conditions, and aphid populations. YDVs are phloem-limited and are transmitted in a persistent circulative manner by over 25 aphid vectors. The most common vectors of BYDV are *Rhopalosiphum padi, Rhopalosiphum maidis, Sitobion avenae, Metopolophium dirhodum, Schizaphis graminum*, and *Sitobion fragariae* (Parry et al., 2012). Among them, *Rhopalosiphum padi* L. and *Rhopalosiphum maidis* Fitch are the most common and efficient species (Smith and Plumb, 1981). The bird cherry-oat aphid, *Rhopalosiphum padi* L., is a frequent vector of BYDV species (Halbert and Voegtlin, 1995).

The mechanisms associated with YDV infections in the field conditions are complex and influenced by many factors. Given the direct interactions among viruses, aphid vectors, and cereal host plants, it is also crucial to investigate the presence of grass hosts in these agroecosystems (Power and Gray, 1995). After BYDV was named by Oswald and Houston (1953) in California/USA, Rochow (1969) identified five serotypes, classified by their preferred aphid vector species. YDVs comprise a complex virus group, including barley yellow dwarf viruses (BYDVs)/ cereal yellow dwarf viruses (CYDVs), as well as newly identified species such as MYDV-RMV and WYDV-GPV (Krueger et al., 2013; Zhang et al., 2009). YDVs cause yield losses of 15-25% in wheat, barley, and oats (Lister and Ranieri, 1995; McKirdy and Jones, 1997). It has been reported that YDVs caused 30% losses in wheat in the UK (Perry et al., 2000) and 80% losses in early-planted winter wheat in Türkiye (İlbağı, 2020). Nancarrow et al. (2021) pointed out that BYDV-PAV caused yield reductions of up to 84% (1358 kg/ha) in wheat and 64% (1456 kg/ha) in barley. Disease control strategies could also be partially achieved by applying insecticides, crop rotation, removing virus reservoirs, avoiding frequent sowing, and using germplasm with tolerance/ resistance to the virus or its vectors (Royer et al., 2005; Kennedy and Connery, 2012). Chemical application for controlling aphid populations is an effective and easy method; however, it is not economic. Due to the negative environmental and other organism impacts, the use of pesticides is restricted in certain regions of the world (McNamara et al., 2020). Moreover, specifically, once symptoms become obvious, it would already be too late to control the vector. On the other hand, the sowing of resistance/tolerant varieties adapted to each location (i), late sowing; as of second week of November for the Trakya region, Türkiye (ii), combating of weeds as inoculum sources (iii), rotation; avoiding planting wheat after other cereal or maize crops (iv), avoiding of planting with stubble in the cereal fields (v), and avoiding of frequent sowing were suggested to combat YDVs by İlbağı (2020). In this respect, late sowing is a crucial cultural practice for combating YDVs. Thanks to the late sowing of wheat, YDVs have been successfully managed in the Trakya region of Türkiye (İlbağı, 2020). As shown in Figure 1, the importance of late sowing for controlling YDVs is evident based on late- and early-sowing wheat fields in Trakya/Türkiye. Similarly, the studies worldwide have shown that late sowing is important for controlling YDVs. McKirdy and Jones (1997) noted that delaying sowing reduced BYDV incidence in wheat. Aghnoum et al. (2017) indicated that late planting plays a crucial role in escaping BYDV infections in the BYDV hot spot region. Foster et al. (2004) noted that virus and aphid incidence may be associated with crop and field characteristics, particularly sowing date. Sowing winter cereals and correctly timing insecticide applications are critical components of BYDV management, as reported by Walsh et al. (2022). On the other hand, breeding resistant or tolerant varieties is the most effective method for controlling YDVs and is a cost-effective approach for controlling BYDV, as reported by Ordon et al. (2004). Arodittir and Crespo-Herrera (2021) noted that challenges and opportunities in resistance to BYDV and its vectors in wheat breeding programs and indicated the importance of identifying resistance sources for Host Plant Resistance (HPR).

BYDV resistance in wheat

Four primary genetic sources of resistance in wheat, three of which are derived from the secondary gene pool (species which are progenitors of the three hexaploid wheat genomes: e.g., *T. dicoccoides*, *T. dicoccum*, *Aegilops tauschii*), though no resistance is known in the primary wheat gene pool. *Bdv1*, *Bdv2*, *Bdv3*, and *Bdv4* resistance genes, which have been reported in wheat; however, their introduction into commercial cultivars has not been effective (Ayala et al., 2001; Kosova et al., 2008). Previous studies have reported that true resistance to BYDV has not been naturally found in wheat; however, BYDV resistance genes have been identified in more than 10 wild relative species belonging to the genera *Thinopyrum*, *Agropyron*, *Elymus*, *Leymus*, *Roegneria*, and *Psathyrostachy* (Zhang et al., 2009). Some *Thinopyrum* species are widely used as sources of combined resistance to BYDV and various rusts in wheat breeding programs (Larkin et al., 1995). Evaluation of resistant sources carrying the *Bdv1* and *Bdv2* genes suggests a polygenic nature for BYDV resistance (Veˇskrna et al., 2009). The only exception among other genes is the *Bdv1* gene, a semidominant gene, which was detected in the North American bread wheat cultivar Anza. Although *Bdv1* confers tolerance to BYDV-MAV based on field observations, it does not confer resistance to all BYDV serotypes or across all environments. *Bdv1* for a "tolerance" known as "partially effective" and conferring "slow yellowing of infected leaves". *Bdv1* was reportedly associated with the *Lr34/Yr18* rust resistance gene complex on 7DS, which is also associated with a leaf tip necrosis trait (Singh et al., 1993). Tolerance to BYDV in wheat, which reduces crop losses at high virus concentrations, has been reported to be polygenically controlled (Cisar et al., 1982). A QTL located in the same position as

Bdv1 accounted for approximately 7% of the total variability, like the polygenic nature of BYDV tolerance in wheat (Ayala et al., 2002). Additionally, *Bdv1* was reported to be associated with the *Lr34/Yr18* rust resistance gene complex on 7DS, which is also associated with a leaf tip necrosis trait and powdery mildew resistance (Singh et al., 1993; Spielmeyer et al., 2005). Ayala et al. (2002) indicated that, despite Anza having reduced visual symptoms, especially yellowing, no statistically significant differences were found between genotypes in any of the measures of disease effects. The presence or absence of the *Lr34/Yr18* complex was determined by Lagudah et al. (2006; 2009). Previous studies have shown that *Bdv1*, linked with the *Lr34/Yr18* gene complex, may reduce visible symptoms of BYDV infection; however, there is limited evidence that it is effective in preventing grain or biomass yield losses. The first BYDV resistance gene in *Thinopyrum intermedium* was identified in a disomic chromosome addition line, L1, derived from the wheat-*Th. intermedium* partial amphiploid TAF46 (Cauderon et al., 1973). This gene was located on the long arm of homoeologous group 7 chromosome 7XL (7Ai#lL) of *Th. intermedium* (Brettell et al., 1988; Xin et al., 1991), and was designated as *Bdv2* (Zhang et al., 1999; Stoutjesdijk et al., 2001). Some wheat-*Th. intermedium* translocation lines, such as the Yw series, that show good BYDV resistance, were developed using the CS ph mutant (Xin et al., 2001). Banks and Larkin (1995) transferred the alien chromatin carrying *Bdv2* from L1 to the common wheat background and developed several wheat-*Th. intermedium* translocation lines, including 7D-7Ai#1 recombinants (e.g., TC5-TC6, TC8-TC10, and TC14), and one 7B-7Ai#1 translocation (TC7) (Banks and Larkin 1995; Hohmann et al., 1996; Larkin et al., 2002). These lines were used to produce resistant wheat cultivars with *Bdv2*, such as a winter wheat, Mackellar (with TC14), and a spring wheat, Glover (with TC6) in Australia (Larkin et al., 2002). Some *Th. intermedium* - *Th. ponticum* translocations were recovered, which carry the resistance genes *Lr19* and *Bdv2* through homoeologous pairing in the presence of gene ph1b (Ayala-Navarrete et al., 2007). Ayala Navarrete et al. (2007, 2009) developed several EST-based PCR markers for the 7Ai#1L segment, containing *Bdv2*. EST-based PCR markers associated with the *Bdv2*-harbouring segment (Gao et al., 2009). A dominant SCAR marker was also developed for the *Bdv2* resistance gene, which originates on the long arm of chromosome 7Ai1 of *Thinopyrum intermedium*, by Stoutjesdijk et al. (2001). The BYDV resistance locus in P29 and P107 was named as *Bdv3* (Ohm and Anderson, 2007). Anderson et al. (1998) reported that P29 is completely resistant to CYDV-RPV and MYDV-RMV, and moderately resistant to BYDV-PAV and BYDV-MAV. Kong et al. (2009) suggested the SSR-*Bdv3* diagnostic marker and investigated the transmission of the *Th. intermedium* 7E segment carrying *Bdv3* in different genetic backgrounds. Another BYDV resistance gene, *Bdv4*, is located on chromosome 2 (2D-2Ai-2) (Larkin et al., 1995; Lin et al., 2006). The BYDV resistance observed in Zhong 5 was determined to be the same as that of L1 to BYDV-GAV and more effective against BYDV-GPV and PAGV (a Chinese wheat yellow dwarf virus strain related to PAV) (Lin et al., 2007). Identifying genome regions associated with BYDV resistance and applying this knowledge to marker-assisted selection (MAS) would enable faster progress in cereal crop breeding (Choudhury et al., 2017). As noted by Shang et al. (2025), comprehensive studies over the past few decades have focused on identifying and characterizing candidate genes associated with resistance to BYDV and its aphid vectors in barley and wheat. Jiang (2013) indicated that very limited information exists on commercial cultivars concerning BYDV resistance genes in wheat. However, current studies have demonstrated promising improvements in BYDV resistance genes in wheat, which can be utilized in breeding programs. A winter wheat variety (G1) was identified as exhibiting significant aphid resistance through antixenosis and antibiosis, and restricted phloem access and salivation by viruliferous *R. padi* in the G1 wheat variety were associated with lower BYDV transmission efficiency (Ilma et al., 2025). Recently, the wheat variety RGT Wolverine, carrying the *Bdv2* gene, was commercially introduced in the United Kingdom. Pichon et al. (2022) indicated that a newly developed wheat variety named RGT Wolverine, carrying the *Bdv2* gene, will allow for observation under natural conditions in terms of the impacts of the *Bdv2* gene on the evolution and adaptation of YDVs, the durability of the resistant phenotype, and the impact of the deployment of a BYDV-resistant material on the epidemiology of YDV diseases. The ensuing study flow for developing resistant cereal cultivars through breeding programs is shown in Figure 2.

BYDV resistance in barley

Four genes and several QTLs in barley have been reported to be associated with resistance/tolerance to BYDV. The first gene, called *Ryd1*, which carries recessive intermediate tolerance, was identified by Suneson (1955) in the cultivar ‘Rojo.’ It has been rarely used in breeding programs. However, the second resistance gene, *Yd2*, was identified by Schaller et al. (1964) and subsequently introduced into many barley cultivars, where it was utilized in barley breeding programs. Later, this gene was defined as *Ryd2* by Søgaard and von Wettstein-Knowles (1987). The barley cultivars carrying the *Ryd2* gene exhibit tolerance to BYDV-PAV and BYDV-MAV; however, this gene may be ineffective in inducing resistance to CYDV-RPV (Niks et al., 2004). *Ryd2* has been located on chromosome 3HL (Collins et al., 1996; Paltridge et al., 1998), and markers have been used in breeding programs to incorporate *Ryd2* (Ovesna et al., 2000; Jefferies et al., 2003). The *Ryd2* gene was then transferred to chromosome 3H of the American spring barley cultivar Atlas 68 by crossing Schaller and Chim, (1969). *Ryd2* has been successfully used in breeding tolerant spring and winter barley cultivars (Delogu et al., 1995; Šip et al., 2006). Some QTL for tolerance against BYDV-MAV and BYDV-PAV have been mapped on chromosomes 7H, 4H, and 1H (Toojinda et al., 2000). Additionally, a new locus, *Ryd3*, derived from an Ethiopian landrace, was identified and located on chromosome 6H (Niks et al., 2004). In barley, no complete resistance to BYDV is known to exist. Through extensive screening, three tolerance genes, including *Ryd1*, *Ryd2*, and *Ryd3*, have been identified. Among these, *Ryd2*, located on chromosome 3HL, has been successfully incorporated into different commercial spring and winter barley cultivars (Ordon et al., 2009). Habekuss et al. (2009) determined that reducing symptom expression and virus extinction in lines combining *Ryd2* and *Ryd3*. Riedel et al. (2011) reported that DH lines carrying the combination of *Ryd2* and *Ryd3* exhibited a significant reduction in virus titre, and a significantly higher relative grain yield was obtained in spring barley DH lines in comparison to lines carrying only *Ryd2* or *Ryd3*. They stated that a combination of *Ryd2* and *Ryd3* confers quantitative resistance to BYDV-PAV rather than tolerance. Additionally, significant levels of resistance to BYDV were obtained by combining the resistance gene *Yd2* with genes detected in moderately resistant cultivars by Ovesna et al. (2000). An additional two QTLs for the relative yield after BYDV infection were detected on chromosomes 2HL and 3HL, accounting for approximately 50% of the phenotypic variance in the relative yield after BYDV infection (Ordon et al., 2009). Collins et al. (1996) determined that the protein product of the gene at the *xylP* locus could provide a convenient assay for the selection of *Yd2* during the breeding of BYDV-resistant barley varieties. Recently, a study reported that *Ryd* genes limit the success of infection (low infection rates) and increase the latency period in infected hosts. These characteristics allow the *Ryd2*- and *Ryd3*-genotypes to be described as partially resistant to YDVs (Souquet et al., 2025). Jarosova et al. (2020) investigated miRNA profiles in new barley lines and in cultivar Wysor (carrying one resistance gene, *Ryd2*), with and without BYDV infection. They determined that the profile of miRNAs expressed in Vir8:3 and Vir13:8 in response to BYDV was similar and differed from that of Wysor. To identify a novel resistance gene, a study was conducted in 2019. This study demonstrated that the consistently detected new gene on chromosome 5H has the potential to serve as a novel source of tolerance, thereby achieving more sustainable resistance to BYDV in barley. *Ryd4* was identified and localized on chromosome 3HL in barley by Scholz et al. (2009). This resistance was introgressed from *Hordeum bulbosum*, the secondary gene pool of barley. However, it cannot be efficiently used in barley breeding programs, as indicated by Scholz et al. (2009). *Ryd2* and *Ryd3*, when combined, are the most promising approach for barley cultivars expressing quantitative resistance to barley yellow dwarf virus (Riedel et al., 2011). Pidon et al. (2024) reported that high-throughput molecular markers will permit more targeted selection of resistance in breeding for the use of *Ryd4* in barley varieties.

BYDV resistance in oat and maize

Tolerance to BYDV in oat is heritable Mckenzie et al. (1985). Comeau and Burnett (1984) noted that breeding for tolerance to BYDV was greatly accelerated following the severe North American epidemic in 1959. Then, a source of BYDV tolerance was identified in oats, leading to the development of several prominent BYDV-tolerant lines (Brown and Jedlinski, 1973). Endo and Brown (1964) found tolerance in oats to BYDV, which is heritable and easily identified in segregating populations. Jenkins (1966) stated that early BYDV infections caused a decrease in yield in susceptible oat varieties by 93% and 97% in the more tolerant oat varieties. Mckenzie et al. (1985) reported that two to four quantitatively inherited genes could contribute to the tolerance of the four tolerant oats. The highest levels of resistance were found in certain *Avena* species, including *Avena sterilis, A. occidentalis, A. barbata, A. fatua, A. hybrida, A. macrostachya, A. nuda,* and *A. strigosa* (Comeau and Burnett 1984). Landry et al. (1984) developed a model with two to four genes for the segregation of tolerance in hybrids between *A. sativum* and *A. sterilis*. Virus-derived transgenic resistance in oat was investigated, and Koev et al. (1998) proposed a strategy for genetically stable transgenic resistance to BYDVs applicable to all virus hosts. In oat (*Avena sativa*), several QTLs contributing to BYDV tolerance have been detected (Ordon et al., 2009), of which three loci were shown to be of major importance (Jin et al., 1998). Gray et al. (1993) reported that resistance to BYDV in a spring oat was released as a reduction in the accumulation of viral antigen in the whole plant. In studies on maize, Körber et al. (2013) reported a high potential for breeding BVDY-resistant/tolerant maize. Horn et al. (2014) suggested using SNPs (associated with BYDV resistance) in marker-assisted selection, indicating that this approach can accelerate the breeding process for developing BYDV-resistant maize genotypes. Horn et al. (2015) found that a QTL on chromosome 10 explained 45% of the phenotypic variance, affecting virus extinction traits and infection rates, and suggested that maize resistance is oligogenically inherited; this QTL should be utilized in breeding programs. Recently, Schmidt et al. (2025) reported BYDV-PAV resistance mechanisms in maize that act directly on the virus, rather than on its vector, *R. padi.*

Conclusions

Managing YDVs successfully depends on several factors, including the biology of the aphid vectors, the plant host, and the virus species. The use of insecticides to control aphid vectors is neither environmentally friendly nor economically efficient, making it an unsustainable strategy. However, the use of resistant/tolerant cultivars is an environmentally safe method to control viruses. To this end, breeding programmes have been conducted to find sources of resistance to BYDV/CYDV and its aphid vectors. So far, resistance sources have been found in a primary gene pool and a few species in the secondary gene pool. However, exploring BYDV and aphid-resistant genes in other related species may offer future research. Even so, recent advances in BYDV resistance genes are promising, but further studies are needed to detect resistance genes against YDVs. On the other hand, in controlling YDVs, it is essential to consider cultural practices, as optimizing planting dates is fairly effective for managing vector aphids of YDVs. Because late sowing reduces virus infections by delaying winter cereal emergence after aphid migrations, early-sowing cereal can significantly increase virus prevalence during the seedling stage. Thus, optimizing sowing dates and combating virus sources, such as grasses, should always be considered strategies for managing YDVs.

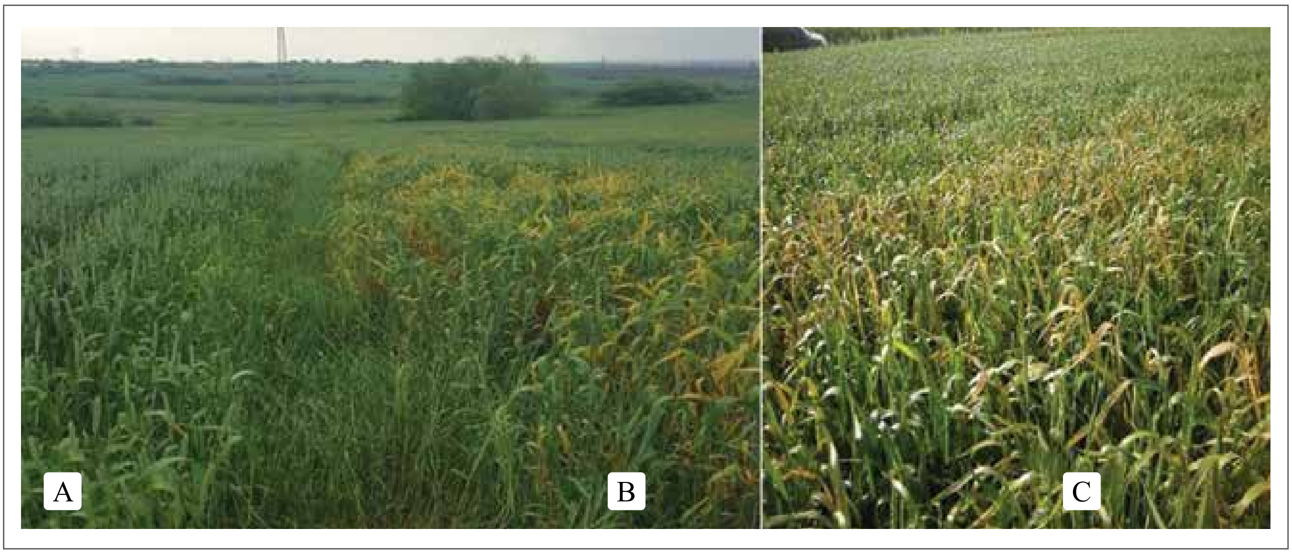

Figure 1. Late sown wheat field (A, on the left), early sown wheat field (B, on the right), resistant/tolerant and susceptible wheat cultivars to YDVs in the field (C) (İlbağı, 2017; İlbağı, 2020)

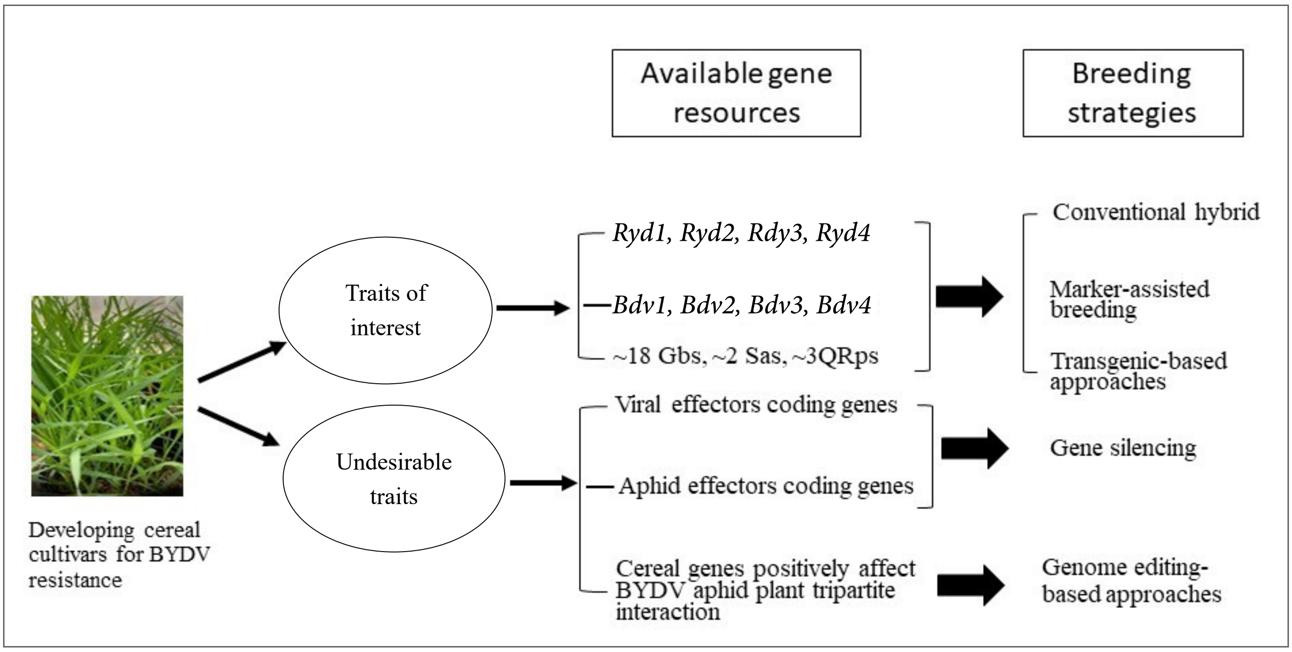

Figure 2. Strategies in breeding programs to develop cereal cultivars against BYDV. Bdvs, BYDV-resistant genes derived from wheat cultivars; Ryds, BYDV-resistant genes derived from barley cultivars; Gbs, greenbug (*Schizaphis graminum*) resistance genes; Sas, English grain aphid (*Sitobion avenae*) resistance genes; QRps, bird cherry-oat aphid (*Rhopalosiphum padi*) resistance QTLs (Shang et al., 2025).

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