Received: 4 December 2023 | Accepted: 20 January 2024

DOI: 10.1111/ppa.13871

Plant Pathology WILEY

REVIEW ARTICLE

How does vector diversity influence the transmission efficiency of yellow dwarf virus? Perspectives from a review

Daniel J. Leybourne

Department of Evolution, Ecology, and Behaviour, Institute of Infection, Veterinary and Ecological Sciences, University of Liverpool, Liverpool, UK

Correspondence
Daniel J. Leybourne, Department of Evolution, Ecology, and Behaviour, Institute of Infection, Veterinary and Ecological Sciences, University of Liverpool, Liverpool L69 7ZB, UK.
Email: daniel.leybourne@liverpool.ac.uk

Funding information
Royal Commission for the Exhibition of 1851, Grant/Award Number: RF-2022-100004

Abstract

Cereals are some of the most important global crops that contribute directly and indirectly to the production of food for human consumption. Cereal aphids can cause significant damage to wheat, barley and oats, particularly via the transmission of plant viruses that cause devastating plant diseases, such as yellow dwarf disease. High levels of yellow dwarf disease can result in yield losses of around 20%, rising to 80% if infection is severe. Yellow dwarf disease is caused by multiple viruses, including viruses within the families *Tombusviridae* and *Solemoviridae*. These include yellow dwarf virus species within the genus *Luteovirus* (*Barley yellow dwarf virus*) and *Polerovirus* (*Cereal yellow dwarf virus*, *Wheat yellow dwarf virus*, *Maize yellow dwarf virus*). Some yellow dwarf virus species are primarily vectored by one aphid species whereas others can be transmitted by multiple vectors. Biological diversity within a given vector species (e.g., genotype, biotype) can influence virus transmission efficiency. However, it is unclear what biological factors drive this variation within a given vector species. Understanding how biological variation in vector populations influences virus transmission efficiency can help to identify biological traits that underpin successful transmission in competent vector populations. Here, the available literature on yellow dwarf virus transmission efficiency is synthesized and significant variation in yellow dwarf virus transmission efficiency is detected between different populations for several vector species. Three biological mechanisms that potentially underpin this variation are proposed.

KEYWORDS
cereal aphid, endosymbiont, *Solemoviridae*, *Tombusviridae*, transmission efficiency, yellow dwarf virus

1 | YELLOW DWARF VIRUS AND YELLOW DWARF DISEASE: A BRIEF INTRODUCTION

Cereals are some of the most important global crops that contribute directly and indirectly (e.g., as feed for livestock) to the production of food for human consumption (Marshall et al., 2013; Newton et al., 2011; Shiferaw et al., 2013); wheat (*Triticum aestivum*) alone provides 25% of daily calorific intake for the United Kingdom, with calorific provisions comparable in similar countries (e.g., 19% in Germany; Mottaleb et al., 2022). Reliance on wheat as a source of

calories is higher (up to 61%) in countries with greater food insecurity (Mottaleb et al., 2022). Cereal crops are exposed to myriad biotic threats, including multiple herbivorous pests and diseases. Cereal aphids, including the bird cherry-oat aphid (*Rhopalosiphum padi*), the grain aphid (*Sitobion avenae*), and the rose-grain aphid (*Metapolophium dirhodum*), are some of the most important herbivorous pests of cereals (van Emden & Harrington, 2007). Cereal aphids are widely distributed and can cause significant damage to cereal crops. Aphid damage can be caused through direct feeding (Dedryver et al., 2010) and via the transmission of plant viruses that cause devastating plant diseases, such as yellow dwarf disease (Fabre, Dedryver, et al., 2003; Perry et al., 2000). Yellow dwarf disease can result in yield losses of around 20% (Kennedy & Connery, 2005; Liu et al., 2014; Perry et al., 2000), increasing to 80% if infection is high (Nancarrow et al., 2021). Plants are at greater risk of yellow dwarf disease infection at the early stages of plant growth; if plants become infected when mature (beyond growth stage 31), they can tolerate yellow dwarf disease infection and the disease impact is limited.

Yellow dwarf disease is caused by several distinctive viruses that are often collectively referred to as the yellow dwarf viruses (YDVs). These include barley yellow dwarf virus (BYDV, *Tombusviridae*, *Luteovirus*), cereal yellow dwarf virus (CYDV, *Solemoviridae*, *Polerovirus*), maize yellow dwarf virus (MYDV, *Solemoviridae*, *Polerovirus*), and wheat yellow dwarf virus (WYDV, *Solemoviridae*, *Polerovirus*). Yellow dwarf disease can also be caused by other viruses in these genera, including barley virus G (BVG, *Solemoviridae*, *Polerovirus*; Erickson et al., 2023; Zhao et al., 2016) and wheat leaf yellowing-associated virus (WLYaV, *Solemoviridae*, *Polerovirus*; Zhang et al., 2017). For an overview of YDV taxonomy, please see the recent comprehensive reviews by Kidanemariam and Abraham (2023) and Miller and Lozier (2022).

Yellow dwarf disease symptoms vary between cereal species, with stark symptomatic differences between oats (*Avena sativa*) and barley (*Hordeum vulgare*). Disease symptoms are also influenced by the age of the plant when initially infected (Armand et al., 2023). Table 1 summarizes the known yellow dwarf disease symptoms for the main cereal crops (wheat, barley and oats). However, it is important to note that there may be differences in symptoms between crop cultivars, the virus transmitted, and even between variants within a virus species. Yellow dwarf disease is a widespread crop disease of international importance and is of concern to cereal producers worldwide. A recent molecular evolution study has suggested that yellow dwarf disease originated from the United States and potentially spread outward from North America to China, Europe and Australia, before spreading to additional countries (Malmstrom et al., 2007; Wei et al., 2023). Human activity, for example via the movement of virus-carrying vectors or virus-infected plants, is the most likely mechanism behind this dispersal (Malmstrom et al., 2007; Wei et al., 2023; Yao et al., 2019). In Europe *R. padi*, *S. avenae* and *M. dirhodum* are the main YDV vectors of concern in agricultural systems (McNamara et al., 2020), and vector demographics and immigration are key foci for ongoing research efforts (Holland et al., 2021; Morales-Hojas et al., 2020).

1.1 | Overview of the disease cycle

YDV is a circulative, non-propagative, persistent virus (Ng & Perry, 2004). Essentially, this means YDV is able to circulate within and between the tissue and organs of the vector (Blanc et al., 2014; Gildow & Gray, 1993; Paliwal & Sinha, 1970); YDV is unable to reproduce, or propagate, within the vector (Paliwal & Sinha, 1970); and YDV remains present within the vector, and therefore the vector remains infective, for prolonged periods (Guo et al., 1997a; Paliwal & Sinha, 1970; Rochow, 1959). YDV can be present in the gut, hemolymph and salivary glands of virus-carrying aphids (Gildow & Gray, 1993; Paliwal & Sinha, 1970), although the virus is only transmitted to plants when present in the salivary glands (Gildow & Gray, 1993). As a persistent virus, aphids carrying YDV remain infective for long periods and the virus is not lost upon aphid moulting (Paliwal & Sinha, 1970; Rochow, 1959).

Virus particles are acquired from virus-infected plants during aphid ingestion of the plant phloem. Following ingestion from infected phloem cells, the viral particles traverse the food canal and foregut into the mid- and hindgut where they are transported across gut epithelial cells into the hemocoel (Li et al., 2001). Virions circulate in the hemolymph and are then selectively taken up by accessory salivary gland cells (Gildow & Gray, 1993). Salivary gland selectivity is thought to be modulated, to a certain extent, by the basal lamina of the accessory salivary gland (Gildow & Gray, 1993). The capsid proteins of the virus are also key determinants of viral selectivity and movement across the epithelial barriers, and as such the capsid proteins of the virus are thought to contribute toward vector specificity.

Virus particles are inoculated into the phloem of uninfected plants during salivation by virus-carrying aphids (Gildow & Gray, 1993; Jiménez et al., 2020; Ng & Perry, 2004; Prado & Tjallingii, 1994). The length of time required for successful transmission is highly variable (Power et al., 1991; Watson & Mulligan, 1960) and transmission success increases with infestation time (Power et al., 1991). Until recently it was believed that successful YDV transmission required a prolonged period of phloem contact, with seminal research indicating that YDV transmission can occur after 2 h of aphid infestation, increasing gradually to a plateau of transmission efficiency around 24 h (Lowles et al., 1996). However, recent observations have indicated that YDV can be successfully transmitted following brief contact between the stylet of an infected aphid and a sieve element cell (Jiménez et al., 2020). In terms of transmission efficiency (i.e., the percentage of plants infected with B/CYDV), Jiménez et al. (2020) found a transmission efficiency of around 15% following brief intracellular probe of a sieve element cell with the aphid stylet and a transmission efficiency of 33% following a period of brief salivation into a probed sieve element cell. The highest transmission efficiency (c. 56%) occurred after a sustained period of salivation into the phloem (Jiménez et al., 2020).

Within the plant tissue, YDV is phloem-limited (Esau, 1957; Jensen, 1969), although occasional secondary infection of adjacent vascular tissue (xylem and parenchyma) has been observed after necrosis of neighbouring phloem cells (Esau, 1957). Viral particles reduce meristematic activity in the vascular tissue of infected plants

TABLE 1 Summary of the common yellow dwarf disease symptoms of barley, oat, and wheat.

Crop	Common symptom			
	Impact on aboveground crop physiology	Impact on below-ground crop physiology	Impact on leaf discolouration	Impact on leaf anatomy
Barley (*Hordeum vulgare*)	Crop stunting[1,2,6,7,10]; delayed maturity[1]; shrivelled grain[1,7]; abortion of florets and sterile flowers[1]; excessive tillering in severe infection[1]; lower transpiration[2]; chlorosis[6,10]	Reduced root mass[1,10]; lower root:shoot ratio[2]	Often turn chrome yellow[1,2,6,7,10]	Leaf edges can become distorted, curled or serrated[1]; reduced leaf area[1,7]
Oat (*Avena sativa*)	Severe crop stunting[2,6,7]; increased number of weak tillers; reduced tillering[1]; abortion of florets and sterile flowers[1]; lower transpiration[2]; chlorosis[2,6]	Reduced root mass[1]; lower root:shoot ratio[2]	Often turn red, orange or purple[1,2,6,7]	
Wheat (*Triticum aestivum*)	Crop stunting[5,6,8]; increased number of undeveloped tillers[5]; abortion of florets and sterile flowers[1,9]; reduced tillering[1,4,9]; delayed maturity[5]; shrivelled grain[9]; chlorosis[6]; reduced chlorophyll content[5]	Reduced root length[3]; lower root:shoot ratio[3]; reduced root mass[1,4]	Often turn yellow or red (especially flag leaf)[1,6,7,8]; leaf yellowing can vary between cultivars from minimal to severe with chlorosis	

[1]Agrios (2005).
[2]Erion and Riedell (2012).
[3]Hoffman and Kolb (1997).
[4]Vandegeer et al. (2016).
[5]Moreno-Delafuente et al. (2020).
[6]Baltenberger et al. (1987), Kojima et al. (1983).
[7]Doodson and Saunders (1970).
[8]Liang et al. (2019).
[9]Smith and Sward (1982).
[10]Kiesling (1985).

(Esau, 1957), which can disrupt differentiation and development of cellular organelles in infected phloem cells (Jensen, 1969), resulting in stunted growth and eventual necrosis of infected cells (Esau, 1957), culminating in the symptoms detailed in Table 1. Persistent infestation with virus-carrying vectors can increase the severity of disease observed (Liang et al., 2019).

1.2 | The aphid vectors and virus species of economic importance

There are many cereal aphid species that can vector YDV, and a summary of the species of economic importance is provided in Table 2. There is significant biological diversity within YDV species, with multiple variants described for each species. In total, there are around seven described BYDV species, two CYDV species, one MYDV species, one WYDV species, and a related species that is currently unassigned a genus (Aradottir & Crespo-Herrera, 2021). Multiple variants for a given virus species can also exist, adding a further level of biological complexity. Furthermore, some virus species are vectored by multiple aphid species (e.g., *R. padi*, *S. avenae*, *M. dirhodum*, and *Sitobion. fragariae* are vectors of BYDV-PAV and BYDV-MAV) whereas other species are primarily vectored by one or two aphid species (e.g., *Schizaphis graminum*, *S. avenae*, and BYDV-GAV). This indicates that there are several compatible (competent or efficient) and incompatible (incompetent or inefficient) vector–virus combinations within the aphid–YDV system. The mechanisms behind this vector–variant specificity are believed to involve compatible and incompatible interactions between different virus variants and the basal lamina of the salivary gland of a given vector species, leading to selective uptake of the virus by the vector (Gildow & Gray, 1993); selectivity can also occur in the midgut and hindgut (Gray et al., 2014). Specific proteins are also thought to aid virus uptake and retention and contribute toward transmission efficiency (Cilia, Howe, et al., 2011; Wang et al., 2015). Vector (aphid) and host (plant) proteins can also interact to influence virus uptake and transmission (Cilia et al., 2012). However, the evolutionary mechanism behind high specificity and selectivity, particularly within different variants of a virus species, is unclear.

Note that the International Committee on Taxonomy of Viruses (ICTV) is currently reassigning and renaming multiple virus species (Walker et al., 2022), including many plant viruses. Several YDV species have been updated, and where taxonomy has been recently revised the new genus and species name are provided in Table 2.

TABLE 2 Overview of the main vectors of each yellow dwarf virus species.

Virus species	Virus strain (updated name, if applicable)	Main vectors (average transmission efficiency >10%)	References
Barley yellow dwarf virus (*Tombusviridae*, *Luteovirus*)	BYDV-PAV (*Luteovirus pavhordei*)	*Rhopalosiphum padi*, *Sitobion avenae*, *Sitobion miscanthi*, *Sitobion fragariae*,[a] *Metapolophium dirhodum*, *Schizaphis graminum*	Bencharki et al. (2000), Creamer and Falk (1989), Farrell and Sward (1989), Guo et al. (1996), Papura et al. (2002), Parizoto et al. (2013), Quillec et al. (1995), Sadeghi, Dedryver, and Gauthier (1997), Schliephake et al. (2013), Yu et al. (2022)
	BYDV-MAV (*Luteovirus mavhordei*)	*S. avenae*, *S. fragariae*,[a] *M. dirhodum*, *S. graminum*[b]	Creamer and Falk (1989), Farrell and Sward (1989), Gray et al. (2002), Guo et al. (1997a), Halbert et al. (1992), Quillec et al. (1995), Schliephake et al. (2013)
	BYDV-PAS (*Luteovirus pashordei*)	*Rhopalosiphum maidis*,[a] *R. padi*,[a] *S. avenae*,[a] *M. dirhodum*[a]	Jarošová et al. (2013)
	BYDV-GAV	*S. graminum*, *S. avenae*	Du et al. (2007)
	BYDV-OYV	Vector not reported	Bisnieks et al. (2004), Sõmera et al. (2021)
	ker-II (*Luteovirus kerbihordei*)	*R. padi*[a]	Svanella-Dumas et al. (2013)
	ker-III (*Luteovirus kertrihordei*)	*R. padi*[a]	Svanella-Dumas et al. (2013)
Cereal yellow dwarf virus (*Solemoviridae*, *Polerovirus*)	CYDV-RPV	*R. padi*, *S. graminum*, *S. avenae*[c]	Creamer and Falk (1989), Gray et al. (2007), Guo et al. (1997a), Halbert et al. (1992), Schliephake et al. (2013), Tamborindeguy et al. (2013)
	CYDV-RPS	*R. padi*[a]	Minato et al. (2022)
Maize yellow dwarf virus (*Solemoviridae*, *Polerovirus*)	MYDV-RMV	*R. maidis*, *R. padi*, *S. graminum*	Gray et al. (2002), Halbert et al. (1992), Lucio-Zavaleta et al. (2001)
Wheat yellow dwarf virus (*Solemoviridae*, genus unassigned)	WYDV-GPV	*R. padi*, *S. avenae*, *S. graminum*	Du et al. (2007), Wang et al. (2015)
Unassigned (*Solemoviridae*)	SGV	*S. graminum*, *R. padi*, *S. avenae*, *R. maidis*[c]	Halbert et al. (1992), Johnson and Rochow (1972), Lei et al. (1995)
Barley virus G (*Solemoviridae*, *Polerovirus*)	BVG	*R. maidis*	Erickson et al. (2023)
Wheat leaf yellowing-associated virus (*Solemoviridae*, *Polerovirus*)	WLYaV	Vector not reported	Zhang et al. (2017)

[a]Transmission or infection reported but no efficiency data.
[b]Competent clones identified for some aphid biotypes.
[c]Reported to transmit some variants.

1.3 | An overview of virus epidemiology

It is believed that different virus species dominate in different regions, for example in mainland Europe, the United States, China, Algeria and Iran BYDV-PAV is thought to be the most abundant species infecting cereals and is therefore considered to be the most agriculturally important (Adhikari et al., 2020; Boubetra et al., 2023; Liu et al., 2019; Pakdel et al., 2010), whereas in the United Kingdom BYDV-MAV and BYDV-PAV occur at similar levels (Foster et al., 2004) and in Ireland BYDV-MAV is the dominant species (Kennedy & Connery, 2005). However, most monitoring surveys were only conducted over a relatively short time-period (up to three growing seasons) and more up-to-date information for some regions is lacking. Furthermore, YDV incidence is sporadic in nature and the prevalence and dominance of species can vary within regions (Dempster & Holmes, 1995; Henry et al., 1993; Liu et al., 2019), fluctuate between monitoring years (Bisnieks et al., 2006; Liu et al., 2019) and be further influenced by the divergence of new YDV species (Bisnieks et al., 2004; Sõmera et al., 2021). Shifts in the dominance of a given species within a region have also been reported, for example in China BYDV-GAV was the dominant strain for 9 years before BYDV-PAV became predominant (Liu et al., 2019). The dominance of a given species can also vary spatially within a region, for example in Australia, BYDV-PAV is dominant in Victoria but BYDV-MAV is dominant in New South Wales (Milgate et al., 2016; Nancarrow et al., 2018).

This sporadic nature of YDV dominance, coupled with a lack of long-term epidemiological studies on YDV prevalence, makes it difficult to state with confidence which species dominates in any given region. Indeed, the lack of long-term YDV epidemiological studies is a significant knowledge gap that potentially restricts and limits the development of sustainable YDV management practices. There are also methodological constraints in virus monitoring that need to be considered. Some diagnostic methods are less sensitive than others, which can lead to an underestimation of risk. Transmission tests are thought to be less sensitive than ELISA (Torrance et al., 1986), which is in turn less sensitive than real-time PCR (Fabre, Kervarrec, et al., 2003). These methodological variations in diagnostic detection can restrict survey impact.

There are multiple factors that could explain the observed variation in species dominance between different regions, including the host-range and prevalence of the main aphid vector, variation in agricultural practices between regions, and the presence (Dempster & Holmes, 1995) and composition (Kendall et al., 1996) of common grassland species within the landscape, especially *Poa* species. An increased proportion of grassland in the landscape can act as a YDV source for migrating aphids (Holland et al., 2021) and increase the risk of YDV infection during the growing season (Rashidi et al., 2020).

2 | BIOLOGICAL DIVERSITY WITHIN A VECTOR SPECIES CAN INFLUENCE TRANSMISSION EFFICIENCY

Variation in transmission efficiency for a given YDV species has been identified between competent vector species. Vector species have been ranked in terms of transmission efficiency (Halbert & Pike, 1985; Power et al., 1991), with *R. padi* often classified as the most efficient vector (Halbert & Pike, 1985). This highlights the importance of addressing the composition of the aphid community present within the field when devising YDV management plans, as the local aphid population (or species of aphid that migrates into the field) could greatly influence the YDV risk of a given crop.

There is also evidence that biological diversity within a given vector species can significantly impact virus transmission efficiency. Several studies have reported variation in virus transmission efficiency between clones, genotypes or biotypes of a given aphid vector species (Guo et al., 1997a; Kern et al., 2022; Lucio-Zavaleta et al., 2001). This includes variation in transmission efficiency for BYDV-PAV, BYDV-MAV and CYDV-RPV among *R. padi* and *S. avenae* clones (Guo et al., 1997a). Further variation in transmission efficiency between aphid clones has also been reported for *R. padi* (Bencharki et al., 2000; Guo et al., 1997a; Kern et al., 2022; Sadeghi, Dedryver, & Gauthier, 1997), *S. graminum* (Gray et al., 2007; Tamborindeguy et al., 2013), *Rhopalosiphum maidis* (Lucio-Zavaleta et al., 2001) and *S. avenae* (Bencharki et al., 2000; Guo et al., 1997a). Table 3 provides an overview of the studies that describe variable transmission efficiency between aphid clones or genotypes of a given species. Interestingly, intraspecies diversity appears to also influence the success of incompetent vector–virus interactions. For example, *R. padi* is supposedly an inefficient, or incompetent, vector of BYDV-GAV. However, a study examining transmission efficiencies in multiple *R. padi* populations found one clone with high transmission efficiency (52%) and three clones with moderate transmission efficiency (18%–33%) for BYDV-GAV, with 15 additional *R. padi* genotypes unable to transmit BYDV-GAV (Du et al., 2007).

It is unclear what biological factors drive this variation in transmission efficiency. From a biological perspective, variation in transmission efficiency is likely related to either inefficient uptake of the virus by the aphid vector and limited transport across the gut barrier, inefficient transport of virions into the salivary glands, or ineffective transmission of virus particles from the aphid vector into the plant.

3 | POTENTIAL MECHANISMS BEHIND VARIABLE VIRUS TRANSMISSION EFFICIENCY

There is significant variation in YDV transmission efficiency between clonal populations for the main YDV vectors (Table 3). Variation in transmission efficiency was identified for different populations for *R. maidis* (5 studies), *R. padi* (15 studies), *S. avenae* (12 studies), *S. miscanthi* (1 study) and *S. graminum* (10 studies). Vectoring efficiency has rarely been examined for *M. dirhodum* or *S. fragariae*, and these two species, alongside *S. miscanthi*, are significantly understudied when compared with the other vectors. Some virus species are also more widely studied than others; both BVG and WLYaV are significantly understudied when compared with the other YDV species. No comparative transmission studies were found for BVG or WLYaV.

For the cereal aphid species that have been studied in more detail (*R. padi*, *R. maidis*, *S. avenae* and *S. graminum*), substantial variation in YDV transmission efficiency between populations within each aphid species was identified. This included variation in transmission efficiency for competent (e.g., *R. padi* and BYDV-PAV; 50%–100%; Du et al., 2007) and incompetent (e.g., *R. padi* and BYDV-GAV; 0%–53%; Du et al., 2007) vector–virus combinations. Below, three mechanisms that potentially drive this variation in transmission efficiency between aphid clones within a given aphid species are proposed (Figure 1).

3.1 | Mechanism 1: Nonessential endosymbionts alter vector feeding behaviour to indirectly increase virus transmission

Aphids can form facultative (nonessential) relationships with a range of bacterial endosymbionts that confer a diverse range of traits to the aphid (Zytynska et al., 2021). Multiple facultative endosymbionts have been described to associate with aphids, and eight of these endosymbiont species have been detected in cereal aphids: *Fukatsuia symbiotica*, *Hamiltonella defensa*, *Regiella insecticola*,

TABLE 3 Overview of the variation in transmission efficiency between clones of a given aphid species.

Aphid species	Study	Aphid morph	Plant species	YDV species	Number of clones examined	The range of transmission efficiencies (%)	Notes
Rhopalosiphum maidis	Saksena et al. (1964)	Apterous	Oat	Not specified	4	28–87	Used one genotype/clone to examine vector transmission efficiency for multiple virus variants in more detail
	Brumfield et al. (1992)	Not specified	Oat	MYDV-RMV	5	19–77	Compared four virus variants
				CYDV-RPV	4	0	
				BYDV-MAV	4	0–2	
				BYDV-PAV	4	0	
				SGV	4	0	
	Rochow and Eastop (1966)	Mixed	Oat	BYDV-MAV	2	0	
				CYDV-RPV		0	
				MYDV-RMV		83–100	
				BYDV-PAV		0–2	
	Gill (1972)	Apterous	Oat	Not specified	3	3–18	Compared two virus variants
		Nymph				38–58	
	Lucio-Zavaleta et al. (2001)	Nymph	Oat	MYDV-RMV	2	0–95	Compared 10 virus variants
Rhopalosiphum padi	Rochow and Eastop (1966)	Mixed	Oat	BYDV-MAV	2	0	
				CYDV-RPV		48–62	
				MYDV-RMV		2–21	
				BYDV-PAV		69–73	
	Guo et al. (1996)	Apterous	Barley	BYDV-PAV	6	11–96	Compared three variants
		Alate				9–76	
	Price et al. (1971)	Not specified	Oat	BYDV-MAV	6	0–10	
				BYDV-PAV		100	
				CYDV-RPV		100	
	Guo et al. (1997a)	Apterous	Barley	BYDV-PAV	2	35–87	Competent combination
		Apterous		BYDV-MAV		0–10	Incompetent combination
		Apterous		CYDV-RPV		32–62	Competent combination
	Guo et al. (1997b)	Apterous	Barley	BYDV-PAV	21	26–93	Examined transmission efficiency in 20 *R. padi* clones collected from France and one clone collected from China

TABLE 3 (Continued)

Aphid species	Study	Aphid morph	Plant species	YDV species	Number of clones examined	The range of transmission efficiencies (%)	Notes
	Sadeghi, Dedryver, and Gauthier (1997)	Apterous	Barley	BYDV-PAV	20	45–80	48 h acquisition; 6 h inoculation
						80–100	48 h acquisition; 120 h inoculation
						0–10	6 h acquisition; 6 h inoculation.
						0–40	6 h acquisition; 24 h inoculation
						50–85	6 h acquisition; 120 h inoculation
	Sadeghi, Dedryver, Riault, et al. (1997)	Nymph	Barley	BYDV-MAV	5	6–58	Compared two variants
	Gildow and D'Arcy (1988)	Not specified	Oat	CYDV-RPV	2	75–100	Examined the impact infection with the aphid virus, Rhopalosiphum padi virus (RhPV) had on YDV transmission efficiency; assessed how aphid abundance affected transmission efficiency. Data presented in the table represent the range across RhPV-uninfected aphids
				MYDV-RMV		0	
				BYDV-MAV		0	
				BYDV-PAV		50–100	
	Gray et al. (1998)	Mixed	Oat	BYDV-PAV	2	99–100	
				CYDV-RPV		99–100	
				MYDV-RMV		10–73	
				BYDV-MAV		0–2	
				SGV		0	
	Habekuss et al. (1999)	Not stated	Barley	BYDV-PAV	6	100	
				CYDV-RPV		80–100	
				Mixed BYDV-MAV/PAV		0–100	
	Bencharki et al. (2000)	Not stated	Oat	BYDV-PAV	10	20–38	Used the most and least efficient clones to examine how acquisition access period affects transmission efficiency
	Smyrnioudis et al. (2001)	Apterous	Wheat	BYDV-PAV	7	39–61	Compared efficiencies over a temperature range: 5°C
						62–80	Compared efficiencies over a temperature range: 10°C
						80–86	Compared efficiencies over a temperature range: 15°C
	Lucio-Zavaleta et al. (2001)	Nymph	Oat	MYDV-RMV	4	0–29	Compared 10 virus variants

(Continues)

TABLE 3 (Continued)

Aphid species	Study	Aphid morph	Plant species	YDV species	Number of clones examined	The range of transmission efficiencies (%)	Notes
	Du et al. (2007)	Not stated	Oat	BYDV-PAV	19	50–100	Used one genotype/clone to examine vector transmission efficiency for multiple virus variants in more detail
				BYDV-GAV	19	0–53	
				WYDV-GPV	19	0–91	
	Kern et al. (2022)	Apterous	Barley	BYDV-PAV	3	53–90	Examined aphid feeding behavior and preference for BYDV-infected and uninfected plants; characterized volatile compounds in BYDV-infected and uninfected plants
Sitobion avenae	Rochow and Eastop (1966)	Mixed	Oat	BYDV-MAV	2	61–63	
				CYDV-RPV		0	
				MYDV-RMV		0	
				BYDV-PAV		9–15	
	Guo et al. (1996)	Apterous	Barley	BYDV-PAV	5	7–76	Compared three variants
		Alate				1–46	
	Guo et al. (1997b)	Apterous	Barley	BYDV-PAV	21	13–76	Examined transmission efficiency in 21 *S. avenae* clones collected from France
	Gray et al. (1998)	Mixed	Oat	BYDV-PAV	2	79–100	
				CYDV-RPV		2–18	
				MYDV-RMV		2–13	
				BYDV-MAV		99–100	
				SGV		0–1	
	Guo et al. (1997a)	Apterous	Barley	BYDV-PAV	2	14–59	Competent combination
				BYDV-MAV		35–57	Competent combination
				CYDV-RPV		1–2	Incompetent combination
	Bencharki et al. (2000)	Not stated	Oat	BYDV-PAV	12	16–27	Used the most and least efficient clones to examine how acquisition access period affects transmission efficiency
	Smyrnioudis et al. (2001)	Apterous	Wheat	BYDV-PAV	5	6–13	Compared efficiencies over a temperature range: 5°C
						15–30	Compared efficiencies over a temperature range: 10°C
						21–32	Compared efficiencies over a temperature range: 15°C

TABLE 3 (Continued)

Aphid species	Study	Aphid morph	Plant species	YDV species	Number of clones examined	The range of transmission efficiencies (%)	Notes
	Papura et al. (2002)	Nymph	Barley	BYDV-PAV	39	0–88	Produced F_1 clones by selfing a clone with poor transmission efficiency; used a subset of clones to examine transmission efficiency of other PAV variants
	Dedryver et al. (2005)	Nymph	Barley	BYDV-PAV	44	3–92	Used a subset of clones to also examine transmission efficiency of other PAV variants; developed F_1 progeny by crossing aphids with contrasting BYDV transmission phenotypes
	Du et al. (2007)	Not stated	Oat	BYDV-PAV	12	11–68	Used one genotype/clone to examine vector transmission efficiency for multiple virus variants in more detail
				BYDV-GAV	12	50–100	
				WYDV-GPV	12	0–57	
	Yu et al. (2013)	Nymph	Wheat	BYDV-PAV	14	23–66	Compared two variants
	Alkhedir et al. (2015)	Apterous	Wheat	BYDV-PAV	4	0–8	Compared different acquisition and inoculation periods. Also speculated on the potential role of endosymbionts in transmission success
Sitobion miscanthi	Yu et al. (2022)	Nymph	Wheat	BYDV-PAV	2	2–61	Compared two variants. Examined effect removing endosymbionts had on the inhibition of virus transmission
Schizaphis graminum	Rochow and Eastop (1966)	Mixed	Oat	BYDV-MAV	2	0	
				CYDV-RPV		33–38	
				MYDV-RMV		0–8	
				BYDV-PAV		8–12	
	Gray et al. (1998)	Nymph	Oat	BYDV-PAV	2	3–36	
				CYDV-RPV		3–37	
				MYDV-RMV		16	
				BYDV-MAV		0–1	
				SGV		3 88	
	Gray et al. (2002)	Adult	Oat	SGV	9	2–85	Examined transmission efficiency in wild grass-adapted and agricultural crop-adapted biotypes
				BYDV-PAV		0–57	
				BYDV-MAV		0–38	
				MYDV-RMV		8–72	
				CYDV-RPV		0–87	

(Continues)

TABLE 3 (Continued)

Aphid species	Study	Aphid morph	Plant species	YDV species	Number of clones examined	The range of transmission efficiencies (%)	Notes
	Burrows et al. (2006, 2007)	Adult	Oat	CYDV-RPV	Multiple	0–80+	Compared transmission efficiencies between a competent clone, an incompetent clone, and subsequent progeny generated by crossing these clones (F_1 and F_2). Identified barriers preventing transmission in incompetent parent and nonvector progeny
				SGV	Multiple	0–80+	
	Gray et al. (2007)	Nymph	Wheat	BYDV-PAV	2	2–35	Produced 89 F_1 *S. graminum* genotypes from parents with contrasting transmission efficiency to correlate genetic diversity with virus transmission efficiency
		Nymph	Wheat	CYDV-RPV		7–63	
	Du et al. (2007)	Not stated	Oat	BYDV-PAV	7	0–36	Used one genotype/clone to examine vector transmission efficiency for multiple virus variants in more detail
				BYDV-GAV		41–84	
				WYDV-GPV		62–100	
	Yang et al. (2008)	Not stated	Barley	CYDV-RPV	8	0–88	Identified proteins associated with transmission success in competent aphid clones
	Cilia, Tamborindeguy, et al. (2011)	Not stated	Barley	CYDV-RPV	10	0–100	Identified barriers to CYDV transmission in incompetent clones
	Tamborindeguy et al. (2013)	Not stated	Oat	CYDV-RPV	11	0–75	Identified a vectoring allele associated with high transmission efficiency

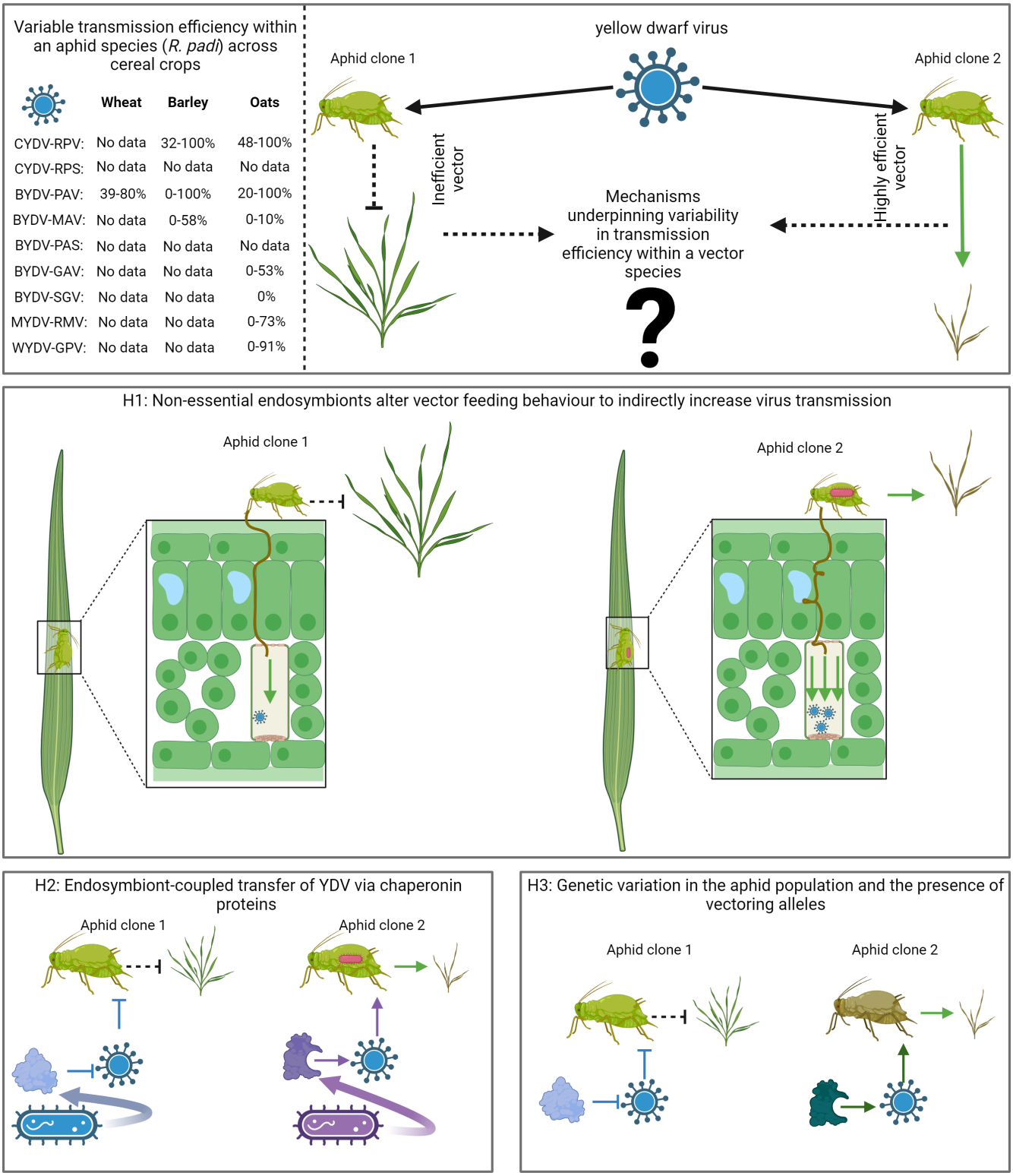

FIGURE 1 Graphical representation of the three proposed mechanisms (hypotheses) underpinning variability in virus transmission efficiency. H1: Nonessential (facultative) endosymbionts alter vector feeding behaviour to indirectly increase virus transmission. Uninfected aphids display routine interactions with the host plant whereas aphids infected with a facultative endosymbiont show a greater number of cellular punctures and an increase in phloem ingestion (Leybourne, Valentine, et al., 2020). H2: Endosymbiont-coupled transfer of YDV via chaperonin proteins. H3: Genetic variation in the aphid population and the presence of vectoring alleles. Image was created in bioRender (biorender.com).

Rickettsia spp., *Ricketsiella* spp., *Aresnophonus* spp., *Serratia symbiotica* and *Spiroplasma* spp. (Guo et al., 2019; Leybourne et al., 2023; Leybourne, Bos, et al., 2020; Zytynska et al., 2023). In cereal aphids these endosymbionts can occur individually or co-occur alongside other endosymbionts in a range of multi-infections (Leybourne et al., 2023; Zytynska et al., 2023). Infection frequencies of these nonessential endosymbionts are highly variable and generally range from 0% to 80%, depending on the endosymbiont and aphid species (Guo et al., 2019; Henry et al., 2015; Leybourne et al., 2023; Leybourne, Bos, et al., 2020; Zytynska et al., 2023). When present, facultative endosymbionts can have a significant impact on aphid phenology, providing beneficial traits that include protection against parasitism (Leybourne, Bos, et al., 2020). Facultative endosymbionts occasionally confer fitness consequences to the host aphid, including lower fecundity (Zytynska et al., 2021) and reduced growth (Leybourne, Bos, et al., 2020).

Facultative endosymbionts can also modulate the probing and feeding behaviour of cereal aphids (Leybourne, Valentine, et al., 2020), with potential consequences for virus acquisition and transmission. Previous research using the electrical penetration graph (EPG) technique to monitor aphid probing and feeding behaviour has shown that the presence of a facultative endosymbiont, *H. defensa*, in *R. padi* can alter aphid feeding behaviour (Leybourne, Valentine, et al., 2020). This included altering behavioural traits that are involved in virus transmission, such as phloem contact. These behaviours could increase the vectoring capacity of endosymbiont-infected aphids by making them more efficient at acquiring and transmitting the virus (Figure 1).

Due to this observation, the impact of endosymbiont infection on virus acquisition, retention and transmission of YDV should be a key area of future research. However, to date there has been limited examination of the influence facultative endosymbionts have on aphid–virus interactions; only three studies have examined how endosymbionts influence aphid–YDV interactions (Alkhedir et al., 2015; Chirgwin et al., 2024; Yu et al., 2022). Yu et al. (2022) provide anecdotal evidence that suggests the endosymbiont *Rickettsia* spp. is important for efficient BYDV-PAV transmission in *Sitobion miscanthi*. By selectively removing facultative endosymbionts, including *Rickettsia* spp., from aphid clones through antibiotic treatment, Yu et al. (2022) showed that the vectoring capacity of two *S. miscanthi* populations was reduced. Alkhedir et al. (2015) examined BYDV-PAV transmission efficiency in four *S. avenae* clones with differing levels of genetic and endosymbiotic diversity, and Chirgwin et al. (2024) show that *R. padi* harbouring *Rickettsiella viridis* have a higher BYDV-PAV density than aphids that lack *R. viridis*. However, in these studies, the authors were unable to disentangle vector genotype effects from facultative endosymbiont effects, and no study examined the potential role endosymbiont presence had on aphid feeding behaviour and the impact of this on BYDV transmission. Therefore, the proposed first mechanism remains purely hypothetical and requires experimental examination. Studies have examined endosymbiont–aphid–virus interactions in other aphid–virus systems (Angelella et al., 2018; Sanches et al., 2023), including for another persistent plant virus, the pea enation mosaic virus, where facultative endosymbionts were implemented in the modulation of plant–aphid–virus interactions including increased virus transmission in *H. defensa*-infected aphids (Sanches et al., 2023).

3.2 | Mechanism 2: Endosymbiont-coupled transfer of YDV via chaperonin proteins

All aphids form an essential relationship with the obligate endosymbiont *Buchnera aphidicola*. *B. aphidicola* is retained in specialized cells, bacteriocytes, within the aphid tissue (Braendle et al., 2003). The obligate nature of the aphid–*B. aphidicola* relationship stems from the provision of essential amino acids, particularly those often lacking in the phloem sap, to the aphid from *B. aphidicola* (Wilson et al., 2010). Several studies have suggested that *B. aphidicola* plays a pivotal role in virus–vector interactions. Specifically, it has been suggested that *B. aphidicola* facilitates the retention of *Tombusviridae* (previously classified as *Luteoviridae*) within vector populations via coupling of virus particles to the *B. aphidicola*-derived chaperonin proteins GroEL (van den Heuvel et al., 1997) or SymL (Filichkin et al., 1997). This coupling between *B. aphidicola* chaperonins and plant viruses has been reported for several viruses previously classified as *Luteoviridae*, including BYDV-PAV (Filichkin et al., 1997), pea enation mosaic virus (*Solemoviridae*, *Enamovirus*), beet western yellows virus (*Solemoviridae*, *Polerovirus*; van den Heuvel et al., 1997), and potato leafroll virus (*Solemoviridae*, *Polerovirus*; van den Heuvel et al., 1994). Therefore, variation in YDV transmission efficiency between aphid clones within a given aphid species could be associated with variability in *B. aphidicola* titre between the aphid clones, with a greater *B. aphidicola* titre resulting in greater chaperonin production that increases the acquisition, and indirectly the transmission, efficiency of the vector.

However, evidence of the potential role *B. aphidicola*-derived chaperonins play in YDV transmission is not consistent. Experiments using immunoblotting and immunocytochemistry in *R. padi* have found no direct evidence of binding or other potential interactions between YDV and *B. aphidicola*-derived GroEL (Bouvaine et al., 2011) and BYDV-MAV did not bind to GroEL homologues identified in *S. avenae* (Li et al., 2001). This is in contrast with earlier observations of GroEL–virus interactions with other viruses (Filichkin et al., 1997; van den Heuvel et al., 1997). Li et al. (2001) identified alternative non-GroEL proteins of *B. aphidicola* that play an important role in binding BYDV-MAV in *S. avenae*, and Cilia, Tamborindeguy, et al. (2011) identified other *B. aphidicola*-derived factors that potentially influence transmission efficiency of CYDV-RPV in *S. graminum*. Therefore, genetic variation within *B. aphidicola* strains could alter the binding capacity of these factors and influence YDV acquisition and transmission efficiency, although this needs to be examined.

One other potential symbiont-derived mechanism, which complements the mechanism proposed above, is the potential role of nonessential (facultative) endosymbionts and chaperonin proteins derived from these endosymbionts. There is evidence for this in

other plant virus vectors (Rana et al., 2012; Su et al., 2013) and this has been proposed for YDV vectors (Bouvaine et al., 2011) but not directly explored. Bouvaine et al. (2011) proposed an alternative GroEL mechanism whereby differential interactions between BYDV and bacterial GroEL derived from facultative endosymbionts, not the essential endosymbiont *B. aphidicola*. Facultative endosymbionts can contribute toward virus transmission in other virus vectors (Pinheiro et al., 2015), including transmission of tomato yellow leaf curl virus (*Geminiviridae*, *Begomovirus*) and cotton leaf curl virus (*Geminiviridae*, *Begomovirus*) in the whitefly *Bemisia tabaci* (Rana et al., 2012; Su et al., 2013). This could be an endosymbiont-derived mechanism that increases transmission efficiency via a combination of (a) increased likelihood of YDV acquisition and transmission in facultative endosymbiont-infected vectors through heightened interactions with the plant phloem by the aphid vector, and (b) greater uptake of YDV virions into the salivary gland in facultative endosymbiont-infected vectors via the chaperonins of facultative endosymbionts (Figure 1). However, this requires further investigation.

3.3 | Mechanism 3: Genetic variation in aphid populations and the role of vectoring alleles

An observation made in *S. avenae* found that transmission efficiency (BYDV-PAV; 3%–92%) varied between aphid genotypes, with the high transmission phenotype found to have a high level of heritability (Dedryver et al., 2005). The molecular mechanisms underpinning this genotype-driven variation in transmission efficiency are unclear; however, significant insight into potential genetic traits that influence YDV transmission efficiency has been gained in *S. graminum* (Burrows et al., 2006, 2007; Gray et al., 2007; Tamborindeguy et al., 2013; Yang et al., 2008). This has primarily been achieved by crossing low (incompetent) and highly efficient (competent) parents to generate F_1 and F_2 populations (Gray et al., 2007; Tamborindeguy et al., 2013) and supplementing these observations with comparative quantitative proteomics to identify key biological drivers determining YDV transmission efficiency (Cilia, Tamborindeguy, et al., 2011; Yang et al., 2008).

A "vectoring" allele of the cyclophilin gene has been identified as a key genetic trait driving variable YDV transmission in *S. graminum* (Tamborindeguy et al., 2013). Cyclophilin proteins are involved in multiple cellular and biological processes, including cell signalling, immune response and protein trafficking. Cyclophilin proteins also play an important, and diverse, role in virus–host and virus–vector interactions. Cyclophilin A was shown to directly interact with CYDV-RPV (Tamborindeguy et al., 2013; Yang et al., 2008). Although the direct role of cyclophilin A is unknown, Tamborindeguy et al. (2013) proposed that the protein facilitates CYDV-RPV transport across the aphid hindgut. Allelic variation in the cyclophilin gene could underpin variable YDV transmission between aphid clones in other vector species; however, this would require direct examination for each vector species. Similar interactions between vector-derived cyclophilin proteins and plant viruses have been described in other plant virus vectors, including the western flower thrips, *Frankliniella occidentalis*, where cyclophilin interacts with a structural glycoprotein of tomato spotted wilt virus (*Bunyaviridae*, *Orthotospovirus*; Badillo-Vargas et al., 2019). This glycoprotein is thought to facilitate virus entry into vector cells, including interaction with the thrips gut (Montero-Astúa et al., 2014; Whitfield et al., 2007). Badillo-Vargas et al. (2019) proposed that *F. occidentalis* cyclophilin facilitates ribonucleoprotein packing into tomato spotted wilt virus particles. It should be noted that tomato spotted wilt virus is capable of propagating within the host, whereas YDVs cannot; therefore, the exact interactions between the virus and the vector could differ.

Vector-derived proteins can also restrict virus binding with vector tissue and influence virus transmission efficiency (Cilia, Tamborindeguy, et al., 2011). Several proteins have been identified that are thought to interact with YDV virions, including CoA ligase, a cuticle protein and Troponin-T (Cilia, Tamborindeguy, et al., 2011). Several of these proteins have been predicted to interact with the aphid hindgut or accessory salivary gland (Cilia, Tamborindeguy, et al., 2011), with binding of these proteins to the hindgut proposed to act as a barrier against virus acquisition and binding to the aphid accessory salivary gland acting as a barrier against virus transmission (Burrows et al., 2006; Cilia, Tamborindeguy, et al., 2011). Similar proteins were identified to interact with WYDV-GPV in *R. padi* (Wang et al., 2015), and putative cuticle proteins were identified as differentially abundant in viruliferous and nonviruliferous aphids in *R. padi* and *S. graminum* (Cilia, Tamborindeguy, et al., 2011; Wang et al., 2015). Differential regulation and abundance of putative cuticular proteins in YDV-carrying aphids (Cilia, Tamborindeguy, et al., 2011; Wang et al., 2015) suggests that these proteins are potentially involved in facilitating virus interactions with vector tissue, as proposed by Wang et al. (2015). Additional molecular drivers include several proteins detected to be differentially regulated between competent and incompetent clones, including putative proteins present in the gut and the accessory salivary gland (Cilia, Tamborindeguy, et al., 2011). Similar work using an F_1 population in *S. avenae* highlighted analogous proteins potentially involved in variable transmission efficiency of BYDV-PAV (Papura et al., 2002). Therefore, structural changes to these proteins (potentially via allelic variation within these genes, as reported for cyclophilin) could interfere with vector–virus interactions and influence virus uptake into vector tissue (Figure 1).

Genetic diversity within vector populations could significantly contribute toward YDV transmission efficiency. These insights primarily derive from one vector species, *S. graminum*, with supporting evidence in *R. padi* (Wang et al., 2015) and *S. avenae* (Papura et al., 2002). Further exploration of the underlying genetic factors that drive variable YDV transmission efficiency in other vector–virus combinations is required. However, the work in *S. graminum* has produced important insights that can be further explored in other vector–virus combinations, including (a) the presence of genetic loci and alleles that influence and determine transmission efficiencies, including cyclophilin vectoring alleles (Gray et al., 2007; Tamborindeguy et al., 2013; Yang et al., 2008) and (b) the impact barriers at the aphid

hindgut and accessory salivary gland have on the uptake of YDV virions and the role they play in transmission efficiency, especially in restricting virus acquisition and transmission in incompetent clones (Burrows et al., 2006, 2007; Cilia, Tamborindeguy, et al., 2011).

4 | CONCLUSIONS

Understanding how biological variation in vector populations influences virus transmission efficiency can help to identify biological traits that underpin successful virus transmission in competent vector populations. Here, the available literature on YDV transmission efficiency is synthesized and significant variation in YDV transmission efficiency is detected in different populations for several vector species, including *R. padi*, *R. maidis*, *S. avenae* and *S. graminum*. Other vector species including *M. dirhodum*, *S. miscanthi* and *S. fragariae* are, comparatively, understudied and under-represented when compared with the other vector species. There are also significant knowledge gaps for transmission efficiency for each vector–virus combination across the main crop species (Table 3), as visualized for *R. padi* in Figure 1. Aphid endosymbionts and genetic traits within vector populations are potential drivers behind this biological variation in transmission efficiency, and recent modelling studies have attempted to disentangle these complex relationships (Enders & Hefley, 2023). Three biological mechanisms are proposed that potentially drive these variations in virus transmission efficiency within these vector populations, and it is recommended that these are investigated in future studies: (a) nonessential endosymbionts alter vector feeding behaviour to indirectly increase virus transmission, (b) endosymbiont-coupled transfer of YDV via chaperonin proteins, and (c) genetic variation in aphid populations and the role of vectoring alleles.

5 | LITERATURE SEARCH METHOD

The keywords "Barley OR Cereal" and "Yellow dwarf virus" and "Transmission" were used to search for BYDV and CYDV studies; the keywords "Maize" and "Yellow dwarf virus" and "Transmission" were used to search for MYDV studies; "Wheat" and "Yellow dwarf virus" and "Transmission" were used to search for WYDV studies; the search term for BVG comprised "Barley Virus G" and "Transmission"; and WLYV studies were searched for using the terms "Wheat leaf yellow virus" and "Transmission". The Web of Science and Scopus databases were used to conduct the literature search, with review articles and book chapters excluded. Duplicates were identified and removed by screening article titles and doi's in R (v. 4.3.0) using the R package revtools (v. 0.4.1) (Westgate, 2019). This filtered dataset was checked manually and any further duplicates were removed. This process yielded 392 articles. Of these articles, 278 described a YDV study with 81 reporting on YDV transmission. This database was used to compile information on variation in YDV transmission efficiencies between clones, genotypes or biotypes of a given vector species that was used to screen articles for inclusion in Table 3. A full list of studies is provided in Table S1.

ACKNOWLEDGEMENTS

The author thanks Dr Sacha White (RSK ADAS Ltd.) for helpful feedback on earlier versions of the manuscript. D.J.L. received support from the Royal Commission for the Exhibition of 1851 through a Research Fellowship (RF-2022-100004).

CONFLICT OF INTEREST STATEMENT

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

ORCID

Daniel J. Leybourne https://orcid.org/0000-0001-5836-3849

REFERENCES

Adhikari, A., Lockhart, B.E., Ganiger, M., Byamukama, E., Tande, C., Smith, M.J. et al. (2020) Barley yellow dwarf virus-PAV is the dominant species causing barley yellow dwarf disease in South Dakota and Minnesota. *Crop Protection*, 134, 105171.

Agrios, G.N. (2005) Plant diseases caused by viruses. In: Agrios, G.N. (Ed.) *Plant pathology*, 5th edition. San Diego: Academic Press, pp. 723–824.

Alkhedir, H., Habekuss, A., Schliephake, E., Mashaly, A.M. & Vidal, S. (2015) Do secondary bacterial endosymbionts of aphids affect the vector specificity or transmission efficiency of plant viruses? *African Entomology*, 23, 356–360.

Angelella, G., Nalam, V., Nachappa, P., White, J. & Kaplan, I. (2018) Endosymbionts differentially alter exploratory probing behavior of a nonpersistent plant virus vector. *Microbial Ecology*, 76, 453–458.

Aradottir, G.I. & Crespo-Herrera, L. (2021) Host plant resistance in wheat to barley yellow dwarf viruses and their aphid vectors: a review. *Current Opinion in Insect Science*, 45, 59–68.

Armand, T., Souquet, M., Korn, L., Gauthier, K. & Jacquot, E. (2023) Asymmetric interactions between barley yellow dwarf virus-PAV and wheat dwarf virus in wheat. *Frontiers in Plant Science*, 14, 1194622.

Badillo-Vargas, I.E., Chen, Y., Martin Kathleen, M., Rotenberg, D. & Whitfield, A.E. (2019) Discovery of novel thrips vector proteins that bind to the viral attachment protein of the plant bunyavirus tomato spotted wilt virus. *Journal of Virology*, 93, 1128.

Baltenberger, D.E., Ohm, H.W. & Foster, J.E. (1987) Reactions of oat, barley, and wheat to infection with barley yellow dwarf virus isolates. *Crop Science*, 27, 195–198.

Bencharki, B., Yamani, M.E. & Zaoui, D. (2000) Assessment of transmission ability of barley yellow dwarf virus-PAV isolates by different populations of *Rhopalosiphum padi* and *Sitobion avenae*. *European Journal of Plant Pathology*, 106, 455–464.

Bisnieks, M., Kvarnheden, A., Sigvald, R. & Valkonen, J.P.T. (2004) Molecular diversity of the coat protein-encoding region of barley yellow dwarf virus-PAV and barley yellow dwarf virus-MAV from Latvia and Sweden. *Archives of Virology*, 149, 843–853.

Bisnieks, M., Kvarnheden, A., Turka, I. & Sigvald, R. (2006) Occurrence of barley yellow dwarf virus and cereal yellow dwarf virus in pasture

grasses and spring cereals in Latvia. *Acta Agriculturae Scandinavica Section B Soil and Plant Science*, 56, 171–178.
Blanc, S., Drucker, M. & Uzest, M. (2014) Localizing viruses in their insect vectors. *Annual Review of Phytopathology*, 52, 403–425.
Boubetra, S., Yahiaoui, B., Lehad, A., Mokhtari, M., Boudchicha, R.H., Mohammedi, F. et al. (2023) Occurrence and diversity of barley yellow dwarf virus in Algeria. *Acta Phytopathologica et Entomologica Hungarica*, 58, 139–148.
Bouvaine, S., Boonham, N. & Douglas, A.E. (2011) Interactions between a luteovirus and the GroEL chaperonin protein of the symbiotic bacterium *Buchnera aphidicola* of aphids. *Journal of General Virology*, 92, 1467–1474.
Braendle, C., Miura, T., Bickel, R., Shingleton, A.W., Kambhampati, S. & Stern, D.L. (2003) Developmental origin and evolution of bacteriocytes in the aphid–*Buchnera* symbiosis. *PLoS Biology*, 1, e21.
Brumfield, S., Carroll, T.W. & Gray, S.M. (1992) Biological and serological characterization of three Montana RMV-like isolates of *barley yellow dwarf virus*. *Plant Disease*, 76, 33–39.
Burrows, M.E., Caillaud, M.C., Smith, D.M., Benson, E.C., Gildow, F.E. & Gray, S.M. (2006) Genetic regulation of *Polerovirus* and *Luteovirus* transmission in the aphid *Schizaphis graminum*. *Phytopathology*, 96, 828–837.
Burrows, M.E., Caillaud, M.C., Smith, D.M. & Gray, S.M. (2007) Biometrical genetic analysis of *Luteovirus* transmission in the aphid *Schizaphis graminum*. *Heredity*, 98, 106–113.
Chirgwin, E., Yang, Q., Umina, P.A., Thia, J.A., Gill, A., Song, W. et al. (2024) Barley yellow dwarf virus influences its vector's endosymbionts but not its thermotolerance. *Microorganisms*, 12, 10.
Cilia, M., Howe, K., Fish, T., Smith, D., Mahoney, J., Tamborindeguy, C. et al. (2011) Biomarker discovery from the top down: protein biomarkers for efficient virus transmission by insects (Homoptera: Aphididae) discovered by coupling genetics and 2-D DIGE. *Proteomics*, 11, 2440–2458.
Cilia, M., Peter, K.A., Bereman, M.S., Howe, K., Fish, T., Smith, D. et al. (2012) Discovery and targeted LC-MS/MS of purified *Polerovirus* reveals differences in the virus–host interactome associated with altered aphid transmission. *PLoS One*, 7, e48177.
Cilia, M., Tamborindeguy, C., Fish, T., Howe, K., Thannhauser, T.W. & Gray, S. (2011) Genetics coupled to quantitative intact proteomics links heritable aphid and endosymbiont protein expression to circulative *Polerovirus* transmission. *Journal of Virology*, 85, 2148–2166.
Creamer, R. & Falk, B.W. (1989) Characterization of a nonspecifically aphid-transmitted CA-RPV isolate of barley yellow dwarf virus. *Phytopathology*, 79, 942–946.
Dedryver, C.-A., Le Ralec, A. & Fabre, F. (2010) The conflicting relationships between aphids and men: a review of aphid damage and control strategies. *Comptes Rendus Biologies*, 333, 539–553.
Dedryver, C.A., Riault, G., Tanguy, S., Gallic, J.F.L., Trottet, M. & Jacquot, E. (2005) Intra-specific variation and inheritance of BYDV-PAV transmission in the aphid *Sitobion avenae*. *European Journal of Plant Pathology*, 111, 341–354.
Dempster, L.C. & Holmes, S.J.I. (1995) The incidence of strains of barley yellow dwarf virus in perennial ryegrass crops in south-west and central Scotland. *Plant Pathology*, 44, 710–717.
Doodson, J.K. & Saunders, P.J.W. (1970) Some effects of barley yellow dwarf virus on spring and winter cereals in field trials. *Annals of Applied Biology*, 66, 361–374.
Du, Z.Q., Li, L., Liu, L., Wang, X.F. & Zhou, G. (2007) Evaluation of aphid transmission abilities and vector transmission phenotypes of barley yellow dwarf viruses in China. *Journal of Plant Pathology*, 89, 251–259.
Enders, L. & Hefley, T. (2023) Modeling host–microbiome interactions to improve mechanistic understanding of aphid vectored plant pathogens. *Frontiers in Ecology and Evolution*, 11, 1251165.
Erickson, A., Jiang, J., Kuo, Y.-W. & Falk, B.W. (2023) Construction and use of an infectious cDNA clone to identify aphid vectors and susceptible monocot hosts of the polerovirus barley virus G. *Virology*, 579, 178–185.
Erion, G.G. & Riedell, W.E. (2012) Barley yellow dwarf virus effects on cereal plant growth and transpiration. *Crop Science*, 52, 2794–2799.
Esau, K. (1957) Phloem degeneration in Gramineae affected by the barley yellow-dwarf virus. *American Journal of Botany*, 44, 245–251.
Fabre, F., Dedryver, C.A., Leterrier, J.L. & Plantegenest, M. (2003) Aphid abundance on cereals in autumn predicts yield losses caused by barley yellow dwarf virus. *Phytopathology*, 93, 1217–1222.
Fabre, F., Kervarrec, C., Mieuzet, L., Riault, G., Vialatte, A. & Jacquot, E. (2003) Improvement of barley yellow dwarf virus-PAV detection in single aphids using a fluorescent real time RT-PCR. *Journal of Virological Methods*, 110, 51–60.
Farrell, J.A. & Sward, R.J. (1989) Barley yellow dwarf virus serotypes and their vectors in Canterbury, New Zealand. *Australasian Plant Pathology*, 18, 21–23.
Filichkin, S.A., Brumfield, S., Filichkin, T.P. & Young, M.J. (1997) In vitro interactions of the aphid endosymbiotic SymL chaperonin with barley yellow dwarf virus. *Journal of Virology*, 71, 569–577.
Foster, G.N., Blake, S., Tones, S.J., Barker, I. & Harrington, R. (2004) Occurrence of barley yellow dwarf virus in autumn-sown cereal crops in the United Kingdom in relation to field characteristics. *Pest Management Science*, 60, 113–125.
Gildow, F.E. & D'Arcy, C.J.D. (1988) Barley and oats as reservoirs for an aphid virus and the influence on barley yellow dwarf virus transmission. *Phytopathology*, 78, 811–816.
Gildow, F.E. & Gray, S.M. (1993) The aphid salivary gland basal lamina as a selective barrier associated with vector-specific transmission of barley yellow dwarf luteoviruses. *Phytopathology*, 83, 1293–1302.
Gill, C.C. (1972) Further studies on the transmission of certain isolates of barley yellow dwarf virus by nymphs and adults of *Rhopalosiphum maidis*. *Canadian Journal of Plant Science*, 52, 107–109.
Gray, S.M., Caillaud, M.C., Burrows, M. & Smith, D.M. (2007) Transmission of two viruses that cause barley yellow dwarf is controlled by different loci in the aphid, *Schizaphis graminum*. *Journal of Insect Science*, 7, 25.
Gray, S.M., Chapin, J.W., Smith, D.M., Banerjee, N. & Thomas, J.S. (1998) Barley yellow dwarf luteoviruses and their predominant aphid vectors in winter wheat grown in South Carolina. *Plant Disease*, 82, 1328–1333.
Gray, S.M., Cilia, M. & Ghanim, M. (2014) Circulative, "nonpropagative" virus transmission: an orchestra of virus-, insect-, and plant-derived instruments. *Advances in Virus Research*, 89, 141–199.
Gray, S.M., Smith, D.M., Barbierri, L. & Burd, J. (2002) Virus transmission phenotype is correlated with host adaptation among genetically diverse populations of the aphid *Schizaphis graminum*. *Phytopathology*, 92, 970–975.
Guo, J.Q., Lapierre, H. & Moreau, J.P. (1997a) Vectoring ability of aphid clones of *Rhopalosiphum padi* (L.) and *Sitobion avenae* (Fabr.) and their capacity to retain barley yellow dwarf virus. *Annals of Applied Biology*, 131, 179–188.
Guo, J.Q., Lapierre, H. & Moreau, J.P. (1997b) Clonal variations and virus regulation by aphids in transmission of a French PAV-type isolate of barley yellow dwarf virus. *Plant Disease*, 81, 570–575.
Guo, J.Q., Liu, X., Poncelet, N., He, K., Francis, F. & Wang, Z. (2019) Detection and geographic distribution of seven facultative endosymbionts in two *Rhopalosiphum* aphid species. *Microbiology Open*, 8, e00817.
Guo, J.Q., Moreau, J.P. & Lapierre, H. (1996) Variability among aphid clones of *Rhopalosiphum padi* L. and *Sitobion avenae* Fabr. (Homoptera: Aphididae) in transmission of three PAV isolates of barley yellow dwarf viruses. *The Canadian Entomologist*, 128, 209–217.
Habekuss, A., Leistner, H.U. & Schliephake, E. (1999) Characterization of *Rhopalosiphum padi* genotypes differing in the geographical

origin by transmission efficiency of barley yellow dwarf viruses and molecular markers. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*, 106, 437–443.

Halbert, S.E., Connelly, B.J., Bishop, G.W. & Blackmer, J.L. (1992) Transmission of barley yellow dwarf virus by field collected aphids (Homoptera: Aphididae) and their relative importance in barley yellow dwarf epidemiology in southwestern Idaho. *Annals of Applied Biology*, 121, 105–121.

Halbert, S.E. & Pike, K.S. (1985) Spread of barley yellow dwarf virus and relative importance of local aphid vectors in central Washington. *Annals of Applied Biology*, 107, 387–395.

Henry, L.M., Maiden, M.C.J., Ferrari, J. & Godfray, H.C.J. (2015) Insect life history and the evolution of bacterial mutualism. *Ecology Letters*, 18, 516–525.

Henry, M., George, S., Arnold, G.M., Dedryver, C.A., Kendall, D.A., Robert, Y. et al. (1993) Occurrence of barley yellow dwarf virus (BYDV) isolates in different farmland habitats in western France and south-west England. *Annals of Applied Biology*, 123, 315–329.

Hoffman, T.K. & Kolb, F.L. (1997) Effects of barley yellow dwarf virus on root and shoot growth of winter wheat seedlings grown in aeroponic culture. *Plant Disease*, 81, 497–500.

Holland, J.M., McHugh, N.M. & Salinari, F. (2021) Field specific monitoring of cereal yellow dwarf virus aphid vectors and factors influencing their immigration within fields. *Pest Management Science*, 77, 4100–4108.

Jarošová, J., Chrpová, J., Šíp, V. & Kundu, J.K. (2013) A comparative study of the barley yellow dwarf virus species PAV and PAS: distribution, accumulation and host resistance. *Plant Pathology*, 62, 436–443.

Jensen, S.G. (1969) Occurrence of virus particles in the phloem tissue of BYDV-infected barley. *Virology*, 38, 83–91.

Jiménez, J., Arias-Martín, M., Moreno, A., Garzo, E. & Fereres, A. (2020) Barley yellow dwarf virus can be inoculated during brief intracellular punctures in phloem cells before the sieve element continuous salivation phase. *Phytopathology*, 110, 85–93.

Johnson, R.A. & Rochow, W.F. (1972) An isolate of barley yellow dwarf virus transmitted specifically by *Schizaphis graminum*. *Phytopathology*, 62, 921–925.

Kendall, D.A., George, S. & Smith, B.D. (1996) Occurrence of barley yellow dwarf viruses in some common grasses (Gramineae) in southwest England. *Plant Pathology*, 45, 29–37.

Kennedy, T.F. & Connery, J. (2005) Grain yield reductions in spring barley due to barley yellow dwarf virus and aphid feeding. *Irish Journal of Agricultural and Food Research*, 44, 111–128.

Kern, M., Meiners, T., Schliephake, E., Habekuss, A., Ordon, F. & Will, T. (2022) Infection of susceptible/tolerant barley genotypes with barley yellow dwarf virus alters the host plant preference of *Rhopalosiphum padi* clones depending upon their ability to transmit BYDV. *Journal of Pest Science*, 95, 215–229.

Kidanemariam, D. & Abraham, A. (2023) Luteoviruses. In: Gaur, R.K., Patil, B.L. & Selvarajan, R. (Eds.) *Plant RNA viruses*. London: Academic Press, pp. 57–77.

Kiesling, R.L. (1985) The diseases of barley. In: Rasmusson, D.C. (Ed.) *Barley*, Vol. 26. Hoboken, NJ: Wiley Online Library, pp. 269–312.

Kojima, M., Matsubara, A., Yanase, S. & Toriyama, S. (1983) The occurrence of barley yellow dwarf disease in Japan. *Japanese Journal of Phytopathology*, 49, 338–346.

Lei, C.H., Lister, R.M., Vincent, J.R. & Karanjkar, M.N. (1995) SGV serotype isolates of barley yellow dwarf virus differing in vectors and molecular relationships. *Phytopathology*, 85, 820–826.

Leybourne, D.J., Bos, J.I.B., Valentine, T.A. & Karley, A.J. (2020) The price of protection: a defensive endosymbiont impairs nymph growth in the bird cherry-oat aphid, *Rhopalosiphum padi*. *Insect Science*, 27, 69–85.

Leybourne, D.J., Melloh, P. & Martin, E.A. (2023) Common facultative endosymbionts do not influence sensitivity of cereal aphids to pyrethroids. *Agricultural and Forest Entomology*, 25, 344–354.

Leybourne, D.J., Valentine, T.A., Bos, J.I.B. & Karley, A.J. (2020) A fitness cost resulting from *Hamiltonella defensa* infection is associated with altered probing and feeding behaviour in *Rhopalosiphum padi*. *Journal of Experimental Biology*, 223, jeb207936.

Li, C., Cox-Foster, D., Gray, S.M. & Gildow, F. (2001) Vector specificity of barley yellow dwarf virus (BYDV) transmission: identification of potential cellular receptors binding BYDV-MAV in the aphid, *Sitobion avenae*. *Virology*, 286, 125–133.

Liang, X., Rashidi, M., Rogers, C.W., Marshall, J.M., Price, W.J. & Rashed, A. (2019) Winter wheat (*Triticum aestivum*) response to barley yellow dwarf virus at various nitrogen application rates in the presence and absence of its aphid vector, *Rhopalosiphum padi*. *Entomologia Experimentalis et Applicata*, 167, 98–107.

Liu, X.-F., Hu, X.-S., Keller, M.A., Zhao, H.-Y., Wu, Y.-F. & Liu, T.-X. (2014) Tripartite interactions of barley yellow dwarf virus, *Sitobion avenae* and wheat varieties. *PLoS One*, 9, e106639.

Liu, Y., Khine, M.O., Zhang, P., Fu, Y. & Wang, X. (2019) Incidence and distribution of insect-transmitted cereal viruses in wheat in China from 2007 to 2019. *Plant Disease*, 104, 1407–1414.

Lowles, A.J., Tatchell, G.M., Harrington, R. & Clark, S.J. (1996) The effect of temperature and inoculation access period on the transmission of barley yellow dwarf virus by *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.). *Annals of Applied Biology*, 128, 45–53.

Lucio-Zavaleta, E., Smith, D.M. & Gray, S.M. (2001) Variation in transmission efficiency among barley yellow dwarf virus-RMV isolates and clones of the normally inefficient aphid vector, *Rhopalosiphum padi*. *Phytopathology*, 91, 792–796.

Malmstrom, C.M., Ruijie, S., Eric, W.L., Linsey, A.N. & Meridith, A.C. (2007) Barley yellow dwarf viruses (BYDVs) preserved in herbarium specimens illuminate historical disease ecology of invasive and native grasses. *Journal of Ecology*, 95, 1153–1166.

Marshall, A., Cowan, S., Edwards, S., Griffiths, I., Howarth, C., Langdon, T. et al. (2013) Crops that feed the world 9. Oats—a cereal crop for human and livestock feed with industrial applications. *Food Security*, 5, 13–33.

McNamara, L., Gauthier, K., Walsh, L., Thébaud, G., Gaffney, M. & Jacquot, E. (2020) Management of yellow dwarf disease in Europe in a post-neonicotinoid agriculture. *Pest Management Science*, 76, 2276–2285.

Milgate, A., Adorada, D., Chambers, G. & Terras, M.A. (2016) Occurrence of winter cereal viruses in New South Wales, Australia, 2006 to 2014. *Plant Disease*, 100, 313–317.

Miller, W.A. & Lozier, Z. (2022) Yellow dwarf viruses of cereals: taxonomy and molecular mechanisms. *Annual Review of Phytopathology*, 60, 121–141.

Minato, N., Hatori, S., Okawa, A., Nakagawa, K. & Hironaka, M. (2022) Manipulation of insect vectors' host selection behavior by barley yellow dwarf virus is dependent on the host plant species and viral co-infection. *Life*, 12, 644.

Montero-Astúa, M., Rotenberg, D., Leach-Kieffaber, A., Schneweis, B.A., Park, S., Park, J.K. et al. (2014) Disruption of vector transmission by a plant-expressed viral glycoprotein. *Molecular Plant–Microbe Interactions*, 27, 296–304.

Morales-Hojas, R., Sun, J., Alvira Iraizoz, F., Tan, X. & Chen, J. (2020) Contrasting population structure and demographic history of cereal aphids in different environmental and agricultural landscapes. *Ecology and Evolution*, 10, 9647–9662.

Moreno-Delafuente, A., Viñuela, E., Fereres, A., Medina, P. & Trębicki, P. (2020) Simultaneous increase in CO_2 and temperature alters wheat growth and aphid performance differently depending on virus infection. *Insects*, 11, 459.

Mottaleb, K.A., Kruseman, G. & Snapp, S. (2022) Potential impacts of Ukraine-Russia armed conflict on global wheat food security: a quantitative exploration. *Global Food Security*, 35, 100659.

Nancarrow, N., Aftab, M., Freeman, A., Rodoni, B., Hollaway, G. & Trębicki, P. (2018) Prevalence and incidence of yellow dwarf viruses

across a climatic gradient: a four-year field study in southeastern Australia. *Plant Disease*, 102, 2465–2472.

Nancarrow, N., Aftab, M., Hollaway, G., Rodoni, B. & Trębicki, P. (2021) Yield losses caused by barley yellow dwarf virus-PAV infection in wheat and barley: a three-year field study in south-eastern Australia. *Microorganisms*, 9, 645.

Newton, A.C., Flavell, A.J., George, T.S., Leat, P., Mullholland, B., Ramsay, L. et al. (2011) Crops that feed the world 4. Barley: a resilient crop? Strengths and weaknesses in the context of food security. *Food Security*, 3, 141–178.

Ng, J.C.K. & Perry, K.L. (2004) Transmission of plant viruses by aphid vectors. *Molecular Plant Pathology*, 5, 505–511.

Pakdel, A., Afsharifar, A., Niazi, A., Almasi, R. & Izadpanah, K. (2010) Distribution of cereal luteoviruses and molecular diversity of BYDV-PAV isolates in central and southern Iran: proposal of a new species in the genus *Luteovirus*. *Journal of Phytopathology*, 158, 357–364.

Paliwal, Y.C. & Sinha, R.C. (1970) On the mechanism of persistence and distribution of barley yellow dwarf virus in an aphid vector. *Virology*, 42, 668–680.

Papura, D., Jacquot, E., Dedryver, C.A., Luche, S., Riault, G., Bossis, M. et al. (2002) Two-dimensional electrophoresis of proteins discriminates aphid clones of *Sitobion avenae* differing in BYDV-PAV transmission. *Archives of Virology*, 147, 1881–1898.

Parizoto, G., Rebonatto, A., Schons, J. & Lau, D. (2013) Barley yellow dwarf virus-PAV in Brazil: seasonal fluctuation and biological characteristics. *Tropical Plant Pathology*, 38, 11–19.

Perry, K.L., Kolb, F.L., Sammons, B., Lawson, C., Cisar, G. & Ohm, H. (2000) Yield effects of barley yellow dwarf virus in soft red winter wheat. *Phytopathology*, 90, 1043–1048.

Pinheiro, P.V., Kliot, A., Ghanim, M. & Cilia, M. (2015) Is there a role for symbiotic bacteria in plant virus transmission by insects? *Current Opinion in Insect Science*, 8, 69–78.

Power, A.G., Seaman, A.J. & Gray, S.M. (1991) Aphid transmission of barley yellow dwarf virus: inoculation access periods and epidemiological implications. *Phytopathology*, 81, 545–548.

Prado, E. & Tjallingii, W.F. (1994) Aphid activities during sieve element punctures. *Entomologia Experimentalis et Applicata*, 72, 157–165.

Price, R.D., Muller, I. & Rochow, W.F. (1971) Variation in transmission of an isolate of barley yellow dwarf virus by *Rhopalosiphum padi*. *Phytopathology*, 61, 753–754.

Quillec, F.L.-L.E., Tanguy, S. & Dedryver, C.A. (1995) Aerial flow of barley yellow dwarf viruses and of their vectors in western France. *Annals of Applied Biology*, 126, 75–90.

Rana, V.S., Singh, S.T., Priya, N.G., Kumar, J. & Rajagopal, R. (2012) *Arsenophonus* GroEL interacts with CLCuV and is localized in midgut and salivary gland of whitefly *B. tabaci*. *PLoS One*, 7, e42168.

Rashidi, M., Cruzado, R.K., Hutchinson, P.J.S., Bosque-Pérez, N.A., Marshall, J.M. & Rashed, A. (2020) Grassy weeds and corn as potential sources of barley yellow dwarf virus spread into winter wheat. *Plant Disease*, 105, 444–449.

Rochow, W.F. (1959) Transmission of strains of barley yellow dwarf virus by 2 aphid species. *Phytopathology*, 49, 744–748.

Rochow, W.F. & Eastop, V.F. (1966) Variation within *Rhopalosiphum padi* and transmission of barley yellow dwarf virus by clones of four aphid species. *Virology*, 30, 286–296.

Sadeghi, E., Dedryver, C.A. & Gauthier, J.P. (1997) Role of acquisition and inoculation time in the expression of clonal variation for BYDV-PAV transmission in the aphid species *Rhopalosiphum padi*. *Plant Pathology*, 46, 502–508.

Sadeghi, E., Dedryver, C.A., Riault, G. & Gauthier, J.P. (1997) Variation in transmission of two BYDV-MAV isolates by multiple clones of *Rhopalosiphum padi* L. *European Journal of Plant Pathology*, 103, 515–519.

Saksena, K.N., Singh, S.R. & Sill, W.H., Jr. (1964) Transmission of barley yellow-dwarf virus by four biotypes of the corn leaf aphid, *Rhopalosiphum maidis*. *Journal of Economic Entomology*, 57, 569–571.

Sanches, P., De Moraes, C.M. & Mescher, M.C. (2023) Endosymbionts modulate virus effects on aphid–plant interactions. *The ISME Journal*, 17, 2441–2451.

Schliephake, E., Habekuss, A., Scholz, M. & Ordon, F. (2013) Barley yellow dwarf virus transmission and feeding behaviour of *Rhopalosiphum padi* on *Hordeum bulbosum* clones. *Entomologia Experimentalis et Applicata*, 146, 347–356.

Shiferaw, B., Smale, M., Braun, H.-J., Duveiller, E., Reynolds, M. & Muricho, G. (2013) Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. *Food Security*, 5, 291–317.

Smith, P.R. & Sward, R.J. (1982) Crop loss assessment studies on the effects of barley yellow dwarf virus in wheat in Victoria. *Australian Journal of Agricultural Research*, 33, 179–185.

Smyrnioudis, I.N., Harrington, R., Hall, M., Katis, N. & Clark, S.J. (2001) The effect of temperature on variation in transmission of a BYDV PAV-like isolate by clones of *Rhopalosiphum padi* and *Sitobion avenae*. *European Journal of Plant Pathology*, 107, 167–173.

Sõmera, M., Massart, S., Tamisier, L., Sooväli, P., Sathees, K. & Kvarnheden, A. (2021) A survey using high-throughput sequencing suggests that the diversity of cereal and barley yellow dwarf viruses is underestimated. *Frontiers in Microbiology*, 12, 673218.

Su, Q., Pan, H., Liu, B., Chu, D., Xie, W., Wu, Q. et al. (2013) Insect symbiont facilitates vector acquisition, retention and transmission of plant virus. *Scientific Reports*, 3, 1367.

Svanella-Dumas, L., Candresse, T., Hullé, M. & Marais, A. (2013) Distribution of barley yellow dwarf virus-PAV in the sub-Antarctic Kerguelen Islands and characterization of two new *Luteovirus* species. *PLoS One*, 8, e67231.

Tamborindeguy, C., Bereman, M.S., DeBlasio, S., Igwe, D., Smith, D.M., White, F. et al. (2013) Genomic and proteomic analysis of *Schizaphis graminum* reveals cyclophilin proteins are involved in the transmission of cereal yellow dwarf virus. *PLoS OneN*, 8, e71620.

Torrance, L., Plumb, R.T., Lennon, E.A. & Gutteridge, R.A. (1986) Comparison of ELISA with transmission tests to detect barley yellow dwarf virus-carrying aphids. In: Jones, R.A.C. & Torrance, L. (Eds.) *Developments and applications in virus testing*. Association of Applied Biologists: Wellesbourne, pp. 165–176.

van den Heuvel, J.F., Bruyère, A., Hogenhout, S.A., Ziegler-Graff, V., Brault, V., Verbeek, M. et al. (1997) The N-terminal region of the luteovirus readthrough domain determines virus binding to *Buchnera* GroEL and is essential for virus persistence in the aphid. *Journal of Virology*, 71, 7258–7265.

van den Heuvel, J.F.J.M., Verbeek, M. & van der Wilk, F. (1994) Endosymbiotic bacteria associated with circulative transmission of potato leafroll virus by *Myzus persicae*. *Journal of General Virology*, 75, 2559–2565.

van Emden, H. & Harrington, R. (2007) *Aphids as crop pests*. Wallingford: CABI.

Vandegeer, R.K., Powell, K.S. & Tausz, M. (2016) Barley yellow dwarf virus infection and elevated CO_2 alter the antioxidants ascorbate and glutathione in wheat. *Journal of Plant Physiology*, 199, 96–99.

Walker, P.J., Siddell, S.G., Lefkowitz, E.J., Mushegian, A.R., Adriaenssens, E.M., Alfenas-Zerbini, P. et al. (2022) Recent changes to virus taxonomy ratified by the International Committee on Taxonomy of Viruses (2022). *Archives of Virology*, 167, 2429–2440.

Wang, H., Wu, K., Liu, Y., Wu, Y. & Wang, X. (2015) Integrative proteomics to understand the transmission mechanism of barley yellow dwarf virus-GPV by its insect vector *Rhopalosiphum padi*. *Scientific Reports*, 5, 10971.

Watson, M.A. & Mulligan, T. (1960) The manner of transmission of some barley yellow-dwarf viruses by different aphid species. *Annals of Applied Biology*, 48, 711–720.

Wei, S., Chen, G., Yang, H., Huang, L., Gong, G., Luo, P. et al. (2023) Global molecular evolution and phylogeographic analysis of barley yellow dwarf virus based on the CP and MP genes. *Virology Journal*, 20, 130.

Westgate, M.J. (2019) Revtools: an R package to support article screening for evidence synthesis. *Research Synthesis Methods*, 10, 606–614.

Whitfield, A.E., Kumar, N.K.K., Rotenberg, D., Ullman, D.E., Wyman, E.A., Zietlow, C. et al. (2007) A soluble form of the tomato spotted wilt virus (TSWV) glycoprotein GN (GN-S) inhibits transmission of TSWV by *Frankliniella occidentalis*. *Phytopathology*, 98, 45–50.

Wilson, A.C.C., Ashton, P.D., Calevro, F., Charles, H., Colella, S., Febvay, G. et al. (2010) Genomic insight into the amino acid relations of the pea aphid, *Acyrthosiphon pisum*, with its symbiotic bacterium *Buchnera aphidicola*. *Insect Molecular Biology*, 19, 249–258.

Yang, X., Thannhauser, T.W., Burrows, M., Cox-Foster, D., Gildow, F.E. & Gray, S.M. (2008) Coupling genetics and proteomics to identify aphid proteins associated with vector-specific transmission of *Polerovirus* (*Luteoviridae*). *Journal of Virology*, 82, 291–299.

Yao, S.M., Hung, T.H., Huang, Y.F. & Yang, J.I. (2019) First report of barley yellow dwarf virus-PAV infecting oats (*Avena sativa*) in Taiwan. *Plant Disease*, 103, 1796.

Yu, W., Bosquée, E., Fan, J., Liu, Y., Bragard, C., Francis, F. et al. (2022) Proteomic and transcriptomic analysis for identification of endosymbiotic bacteria associated with BYDV transmission efficiency by *Sitobion miscanthi*. *Plants*, 11, 3352.

Yu, W., Xu, Z., Francis, F., Liu, Y., Cheng, D., Bragard, C. et al. (2013) Variation in the transmission of barley yellow dwarf virus-PAV by different *Sitobion avenae* clones in China. *Journal of Virological Methods*, 194, 1–6.

Zhang, P., Liu, Y., Liu, W., Cao, M., Massart, S. & Wang, X. (2017) Identification, characterization and full-length sequence analysis of a novel *Polerovirus* associated with wheat leaf yellowing disease. *Frontiers in Microbiology*, 8, 1689.

Zhao, F., Lim, S., Yoo, R.H., Igori, D., Kim, S.-M., Kwak, D.Y. et al. (2016) The complete genomic sequence of a tentative new polerovirus identified in barley in South Korea. *Archives of Virology*, 161, 2047–2050.

Zytynska, S.E., Sturm, S., Hawes, C., Weisser, W.W. & Karley, A. (2023) Floral presence and flower identity alter cereal aphid endosymbiont communities on adjacent crops. *Journal of Applied Ecology*, 60, 1409–1423.

Zytynska, S.E., Tighiouart, K. & Frago, E. (2021) Benefits and costs of hosting facultative symbionts in plant-sucking insects: a meta-analysis. *Molecular Ecology*, 30, 2483–2494.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Leybourne, D.J. (2024) How does vector diversity influence the transmission efficiency of yellow dwarf virus? Perspectives from a review. *Plant Pathology*, 00, 1–18. Available from: https://doi.org/10.1111/ppa.13871