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

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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. Yellow dwarf disease is caused by two related viruses within the Luteoviridae: Barley Yellow Dwarf Virus (BYDV, Luteovirus) and Cereal Yellow Dwarf Virus (CYDV, Polerovirus). High levels of yellow dwarf disease infection can result in yield losses of c. 20%, rising to 80% if infection is high. There are multiple B/CYDV species, some B/CYDV 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 B/CYDV transmission efficiency is synthesised and significant variation in B/CYDV transmission efficiency is detected between different populations for several vector species. Three biological mechanisms that potentially underpin this variation are proposed.

Barley/cereal 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 alone provides *25*% of daily calorific intake for the UK, 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 and 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 et al., 2003a; Perry et al., 2000). Yellow dwarf disease infection can result in yield losses of c. 20% (Kennedy and Connery, 2005; Liu et al., 2014; Perry et al., 2000), increasing to 80% if infection is high (Nancarrow et al., 2021).

Yellow dwarf disease is caused by two related viruses within the Luteoviridae: Barley Yellow Dwarf Virus (BYDV, *Luteovirus*) and Cereal Yellow Dwarf Virus (CYDV, *Polerovirus*). Yellow dwarf disease symptoms vary between cereal species, with stark symptomatic differences between oats and barley. Table 1 summarises the known yellow dwarf disease symptoms for the main cereal crops (wheat, barley, oats). However, it is important to note that there may be differences in symptoms between crop cultivars, the virus transmitted, and even between virus isolates within a virus species. Yellow dwarf disease is now 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 USA and potentially spread outwards from North America to China, Europe, and Australia, before spreading to additional countries (Malmstrom et al., 2007; Wei et al., 2023). Human activity 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 B/CYDV vectors of concern in agricultural systems (Plumb, 1974).

<u>Overview of the disease cycle</u>

Within the plant tissue, B/CYDV 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 (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. B/CYDV is a circulative, non-propagative, persistent virus (Ng and Perry, 2004). Essentially, this means: B/CYDV is able to circulate within and between the tissue and organs of the vector (Blanc et al., 2014; Gildow and Gray, 1993; Paliwal and Sinha, 1970); B/CYDV is unable to reproduce, or propagate, within the vector (Paliwal and Sinha, 1970); and B/CYDV remains present within the vector, and therefore the vector remains infective, for prolonged periods (Guo et al., 1997a; Paliwal and Sinha, 1970; Rochow, 1959).

B/CYDV can be present in the gut, haemolymph, and salivary glands of infected aphids (Gildow and Gray, 1993; Paliwal and Sinha, 1970), although it is only readily transmitted to plants when present in the salivary glands (Gildow and Gray, 1993). As a persistent virus, aphids infected with B/CYDV remain infective for long periods and the virus is not lost upon aphid moulting (Paliwal and Sinha, 1970; Rochow, 1959).

Table 1: Summary of the common yellow dwarf disease symptoms of barley, oat, and wheat

Crop	**Common symptom**				**References**
	Impact on above-ground crop physiology	**Impact on below-ground crop physiology**	**Impact on leaf discolouration**	**Impact on leaf anatomy**	
Barley	Crop stunting; delayed maturity; shrivelled grain; abortion of florets; excessive tillering in severe infection; lower transpiration; chlorosis	Reduced root mass; lower root:shoot ratio	Often turn chrome yellow	Leaf edges can become distorted, curled or serrated; reduced leaf area	(Agrios, 2005; Baltenberger et al., 1987; D'Arcy and Domier, 2000; Domier, 2008; Doodson and Saunders, 1970; Erion and Riedell, 2012; Hoffman and Kolb, 1997; Kojima et al., 1983; Liang et al., 2019; Moreno-Delafuente et al., 2020; Vandegeer et al., 2016)
Oat	Severe crop stunting; increased number of weak tillers; reduced tillering; interveinal chlorosis; abortion of florets; lower transpiration; chlorosis	Reduced root mass; lower root:shoot ratio	Often turn red, orange, or purple		
Wheat	Crop stunting; Increased number of undeveloped tillers; reduced tillering; delayed maturity; shrivelled grain; chlorosis	Reduced root length; lower root:shoot ratio; reduced root mass	Often turn yellow or red (especially flag leaf); leaf yellowing can vary between cultivars from minimal to severe with chlorosis.		

The main aphid vectors and virus species

There are several cereal aphid species that can vector BYDV and CYDV, and a summary is provided in Table 2. There is significant biological diversity within B/CYDV species, with multiple isolates described for each species. In total, there are around seven described BYDV species, two CYDV species, and three additional species that are unassigned to either genus (Aradottir and Crespo-Herrera, 2021). Multiple isolates for a given 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 *S. fragariae* are vectors of BYDV $^{\text{PAV}}$ and BYDV $^{\text{MAV}}$) whereas other species are primarily vectored by one or two aphid species (e.g., *R. maidis, M. dirhodum* and BYDV $^{\text{PAS}}$). This indicates that there are several compatible (competent) and incompatible (incompetent) vector-virus combinations within the aphid-B/CYDV system. The mechanism behind this vector-isolate specificity is believed to involve compatible and incompatible interactions between virus species and the basal lamina of the salivary gland, leading to selective uptake of the virus by the vector (Gildow and Gray, 1993); however, the evolutionary mechanism behind high specificity and selectivity, particularly within different isolates of a species, is unclear.

Table 2: Overview of the main vectors of each BYDV and CYDV species

Virus genus	Virus species	Main vectors (average transmission efficiency >10%)	References
BYDV	PAV	*R. padi,* *S. avenae,* *S. miscanthi,* *S. fragariae *,* *M. dirhodum,* *Sc. 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 et al., 1997a; Schliephake et al., 2013; Yu et al., 2022)
	MAV	*S. avenae,* *S. fragariae *,* *M. dirhodum,* *Sc. graminum* **	(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)
	PAS	*R. maidis *,* *R. padi *,* *S. avenae *,* *M. dirhodum **	(Jarošová et al., 2013)
	GAV	*Sc. graminum,* *S. avenae*	(Du et al., 2007)
	OYV	Vector not reported	(Bisnieks et al., 2004; Sõmera et al., 2021)
	ker-II	*R. padi **	(Svanella-Dumas et al., 2013)
	ker-III	*R. padi **	(Svanella-Dumas et al., 2013)
CYDV	RPV	*R. padi,* *Sc. graminum* *S. avenae* ***	(Creamer and Falk, 1989; Gray et al., 2007; Guo et al., 1997a; Halbert et al., 1992; Schliephake et al., 2013; Tamborindeguy et al., 2013)
	RPS	*R. padi **	(Minato et al., 2022)
Unassigned	GPV	*R. padi,* *S. avenae,* *Sc. graminum*	(Du et al., 2007; Wang et al., 2015)
	RMV	*R. maidis,* *R. padi,* *Sc. graminum*	(Gray et al., 2002; Halbert et al., 1992; Lucio-Zavaleta et al., 2001)
	SGV	*Sc. graminum* *R. padi* *S. avenae* *R. maidis* ***	(Halbert et al., 1992; Johnson and Rochow, 1972; Lei et al., 1995)

* Transmission or infection reported but no efficiency data; ** Competent clones identified for some aphid biotypes; *** Reported to transmit some isolates.

An overview of virus epidemiology

It is believed that different virus species dominate in different regions, for example in mainland Europe, The USA, China, Algeria, and Iran BYDV^{PAV} is thought to be the most abundant species 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 UK BYDV^{MAV} and BYDV^{PAV} occur at similar levels (Foster et al., 2004) and in Ireland BYDV^{MAV} is the dominant species (Kennedy and Connery, 2005). However, most monitoring surveys were only conducted over a relatively short time-period (1-3 growing seasons). Furthermore B/CYDV incidence is sporadic in nature and the prevalence and dominance of species can vary within regions (Dempster and 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 B/CYDV 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 nine 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 and BYDV^{MAV} is dominant in New South Wales (Milgate et al., 2016; Nancarrow et al., 2018). This sporadic nature of B/CYDV dominance, coupled with a lack of long-term epidemiological studies on B/CYDV prevalence, makes it difficult to state with confidence which species dominates in any given region. Indeed, the lack of long-term B/CYDV epidemiological studies is a significant knowledge gap that potentially restricts and limits the development of sustainable B/CYDV management practices.

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 and Holmes, 1995) and composition (Kendall et al., 1996) of common grassland species within the landscape, especially *Poa spp.* that can act as a BYDV source in agricultural systems (Masterman et al., 1994). 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 RT-PCR (Fabre et al., 2003b). These methodological variations in diagnostic detection can restrict survey impact.

Biological diversity within a vector species can influence transmission efficiency

Variation in transmission efficiency for a given B/CYDV species has been identified between competent vector species. Vector species have been ranked in terms of transmission efficiency (Halbert and Pike, 1985; Power et al., 1991) with *R. padi* often classified as the most efficient vector (Halbert and Pike, 1985). This highlights the importance of addressing the local composition of the aphid community when devising B/CYDV management plans as the local aphid population could greatly influence the B/CYDV 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,MAV} and CYDV^{RPV} amongst *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 et al., 1997a), *Schizaphis graminum* (Gray et al., 2007; Tamborindeguy et al., 2013), *R. 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, intra-species 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, inefficient transport of virions into the salivary glands, or ineffective transmission of virus particles from the aphid vector into the plant.

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

Aphid species (study)	**Aphid morph**	**Plant species**	**B/CYDV species**	**Number of clones examined**	**The range transmission efficiencies**	**Notes**
R. maidis (Saksena et al., 1964)	Apterous	Oat	Not specified	4	28 – 87%	Used one genotype/clone to examine vector transmission efficiency for multiple virus isolates in more detail.
R. maidis (Rochow and Eastop, 1966)	Mixed	Oat	MAV	2	0%	
			RPV		0%	
			RMV		83 – 100%	
			PAV		0 – 2%	
R. maidis (Gill, 1972)	Apterous	Oat	Not specified	3	3 – 18%	Compared two virus isolates.
	Nymph				38 – 58%	
R. maidis (Lucio-Zavaleta et al., 2001)	Nymph	Oat	RMV	2	0 – 95%	Compared ten virus isolates.
R. padi (Rochow and Eastop, 1966)	Mixed	Oat	MAV	2	0%	
			RPV		48 – 62%	
			RMV		2 – 21%	
			PAV		69 – 73%	
R. padi (Guo et al., 1996)	Apterous	Barley	PAV	6	11 – 96%	Compared three isolates.
	Alate				9 – 76%	
R. padi (Price et al., 1971)	Not stated	Oat	MAV	6	0 – 10%	
			PAV		100%	
			RPV		100%	

Aphid species (study)	**Aphid morph**	**Plant species**	**B/CYDV species**	**Number of clones examined**	**The range transmission efficiencies**	**Notes**
R. padi (Guo et al., 1997a)	Apterous	Barley	PAV	2	35 – 87%	Competent combination.
	Apterous		MAV		0 – 10%	Incompetent combination.
	Apterous		RPV		32 – 62%	Competent combination.
R. padi (Guo et al., 1997b)	Apterous	Barley	PAV	21	26 – 93%	Examined transmission efficiency in 20 *R. padi* clones collected from France and one clone collected from China.
R. padi (Sadeghi et al., 1997a)	Apterous	Barley	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.
R. padi (Sadeghi et al., 1997b)	Nymph	Barley	MAV	5	6 – 58%	Compared two isolates.
R. padi (Gray et al., 1998)	Mixed	Oat	PAV	2	99 – 100%	
			RPV		99 – 100%	
			RMV		10 – 73%	
			MAV		0 – 2%	
			SGV		0%	
R. padi (Habekuss et al., 1999)	Not stated	Barley	PAV	6	100%	
			RPV		80 – 100%	
			Mixed MAV/PAV		0 – 100%	

Aphid species (study)	**Aphid morph**	**Plant species**	**B/CYDV species**	**Number of clones examined**	**The range transmission efficiencies**	**Notes**
R. padi (Bencharki et al., 2000)	Not stated	Oat	PAV	10	20 – 38%	Used the most and least efficient clones to examine how acquisition access period affects transmission efficiency.
R. paidi (Lucio-Zavaleta et al., 2001)	Nymph	Oat	RMV	4	0 – 29%	Compared ten virus isolates.
R. padi (Du et al., 2007)	Not stated	Oat	PAV	19	50 – 100%	Used one genotype/clone to examine vector transmission efficiency for multiple virus isolates in more detail.
			GAV	19	0 – 53%	
			GPV	19	0-91%	
R. padi (Kern et al., 2022)	Apterous	Barley	PAV	3	53 – 90%	Examined aphid feeding behaviour and preference for BYDV-infected and uninfected plants; characterised volatile compounds in BYDV-infected and uninfected plants.
S. avenae (Rochow and Eastop, 1966)	Mixed	Oat	MAV	2	61 – 63%	
			RPV		0%	
			RMV		0%	
			PAV		9 – 15%	
S. avenae (Guo et al., 1996)	Apterous	Barley	PAV	5	7 – 76%	Compared three isolates.
	Alate				1 – 46%	
S. avenae (Guo et al., 1997b)	Apterous	Barley	PAV	21	13 - 76%	Examined transmission efficiency in 21 *S. avenae* clones collected from France.
S. avenae (Gray et al., 1998)	Mixed	Oat	PAV	2	79 – 100%	
			RPV		2 – 18%	
			RMV		2 – 13%	
			MAV		99 – 100%	

Aphid species (study)	**Aphid morph**	**Plant species**	**B/CYDV species**	**Number of clones examined**	**The range transmission efficiencies**	**Notes**
			SGV		0 – 1%	
S. avenae (Guo et al., 1997a)	Apterous	Barley	PAV	2	14 – 59%	Competent combination.
			MAV		35 – 57%	Competent combination.
			RPV		1 – 2%	Incompetent combination.
S. avenae (Bencharki et al., 2000)	Not stated	Oat	PAV	12	16 – 27%	Used the most and least efficient clones to examine how acquisition access period affects transmission efficiency.
S. avenae (Papura et al., 2002)	Nymph	Barley	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 isolates.
S. avenae (Dedryver et al., 2005)	Nymph	Barley	PAV	44	3 – 92%	Used a subset of clones to also examine transmission efficiency of other PAV isolates; developed F_1 progeny by crossing aphids with contrasting BYDV transmission phenotypes.
S. avenae (Du et al., 2007)	Not stated	Oat	PAV	12	11 – 68%	Used one genotype/clone to examine vector transmission efficiency for multiple virus isolates in more detail.
			GAV	12	50 – 100%	
			GPV	12	0 – 57%	
S. avenae (Yu et al., 2013)	Nymph	Wheat	PAV	14	23 – 66%	Compared two isolates.
S. avenae (Alkhedir et al., 2015)	Apterous	Wheat	PAV	4	0 – 8%	Compared different acquisition and inoculation periods. Also speculated on the potential role of endosymbionts in transmission success.
S. miscanthi (Yu et al., 2022)	Nymph	Wheat	PAV (Chinese isolate)	2	24 – 61%	Compared two isolates Examined effect removing endosymbionts had on the inhibition of virus transmission.
	Mixed	Oat	MAV	2	0%	

Aphid species (study)	**Aphid morph**	**Plant species**	**B/CYDV species**	**Number of clones examined**	**The range transmission efficiencies**	**Notes**
Sc. graminum (Rochow and Eastop, 1966)			RPV		33 – 38%	
			RMV		0 – 8%	
			PAV		8 – 12%	
Sc. graminum (Gray et al., 1998)	Nymph	Oat	PAV	2	3 – 36%	
			RPV		3 – 37%	
			RMV		16%	
			MAV		0 – 1%	
			SGV		3 – 88%	
Sc. graminum (Gray et al., 2002)	Adult	Oat	SGV	9	2 – 85%	Examined transmission efficiency in wild grass-adapted and agricultural crop-adapted biotypes.
			PAV		0 – 57%	
			MAV		0 – 38%	
			RMV		8 – 72%	
			RPV		0 – 87%	
Sc. graminum (Burrows et al., 2006; Burrows et al., 2007)	Adult	Oat	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).
			SGV	Multiple	0 – 80+%	Identified barriers preventing transmission in incompetent parent and non-vector progeny.
Sc. graminum (Gray et al., 2007)	Nymph	Wheat	PAV	2	2 – 35%	Produced 89 F1 *Sc. graminum* genotypes from parents with contrasting transmission efficiency to correlate genetic diversity with virus transmission efficiency.
	Nymph	Wheat	RPV		7 – 63%	
	Not stated	Oat	PAV	7	0 – 36%	

Aphid species (study)	**Aphid morph**	**Plant species**	**B/CYDV species**	**Number of clones examined**	**The range transmission efficiencies**	**Notes**
Sc. graminum (Du et al., 2007)			GAV		41 – 84%	Used one genotype/clone to examine vector transmission efficiency for multiple virus isolates in more detail.
			GPV		62 – 100%	
Sc. graminum (Yang et al., 2008)	Not stated	Barley	RPV	8	0 – 88%	Identified proteins associated with transmission success in competent aphid clones.
Sc. graminum (Cilia et al., 2011)	Not stated	Barley	RPV	10	0 – 100%	Identified barriers to CYDV transmission in incompetent clones.
Sc. graminum (Tamborindeguy et al., 2013)	Not stated	Oat	RPV	11	0 – 75%	Identified a vectoring allele associated with high transmission efficiency.

Potential mechanisms behind variable virus transmission efficiency

There is significant variation in B/CYDV transmission efficiency between clonal populations for the main B/CYDV vectors (Table 3). Variation in transmission efficiency was identified for different populations for *R. maidis* (four studies), *R. padi* (13 studies), *S. avenae* (ten studies), *S. miscanthi* (one study), and *Sc. graminum* (ten 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.

For the cereal aphid species that have been studied in more detail (*R. padi, R. maidis, S. avenae, Sc. graminum*) substantial variation in B/CYDV 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 (Fig. 1).

Mechanism one: Non-essential endosymbionts alter vector feeding behaviour to indirectly increase virus transmission

Aphids can form facultative (non-essential) relationships with a range of 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, Rickettsia spp. Ricketsiella spp, Aresnophonus spp, Serratia symbiotica, Spiroplasma spp.,* (Guo et al., 2019; Leybourne et al., 2020a; Leybourne et al., 2023; 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 non-essential endosymbionts are highly variable and generally range from *c.* 0-80%, depending on the endosymbiont and aphid species (Guo et al., 2019; Henry et al., 2015; Leybourne et al., 2020a; Leybourne et al., 2023; Zytynska et al., 2023).

Facultative endosymbionts can modulate the probing and feeding behaviour of cereal aphids (Leybourne et al., 2020b), 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 presence of the facultative endosymbiont, *H. defensa,* in *R. padi* can alter aphid feeding behaviour (Leybourne et al., 2020b). 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 (Fig. 1). The impact of endosymbiont-infection on virus acquisition, retention, and transmission of B/CYDV should be a key area of future research.

To date there has been limited examination of the influence these endosymbionts have on aphid-virus interactions: Only two studies have examined how endosymbionts influence aphid-BYDV interactions (Alkhedir et al., 2015; 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 *S. miscanthi*. By 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. However, in both study's the authors were unable to disentangle vector genotype effects from facultative endosymbiont effects, and neither study examined the potential role endosymbiont presence had on aphid feeding behaviour and the impact this had on BYDV^{PAV} transmission. Therefore, our proposed second 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)

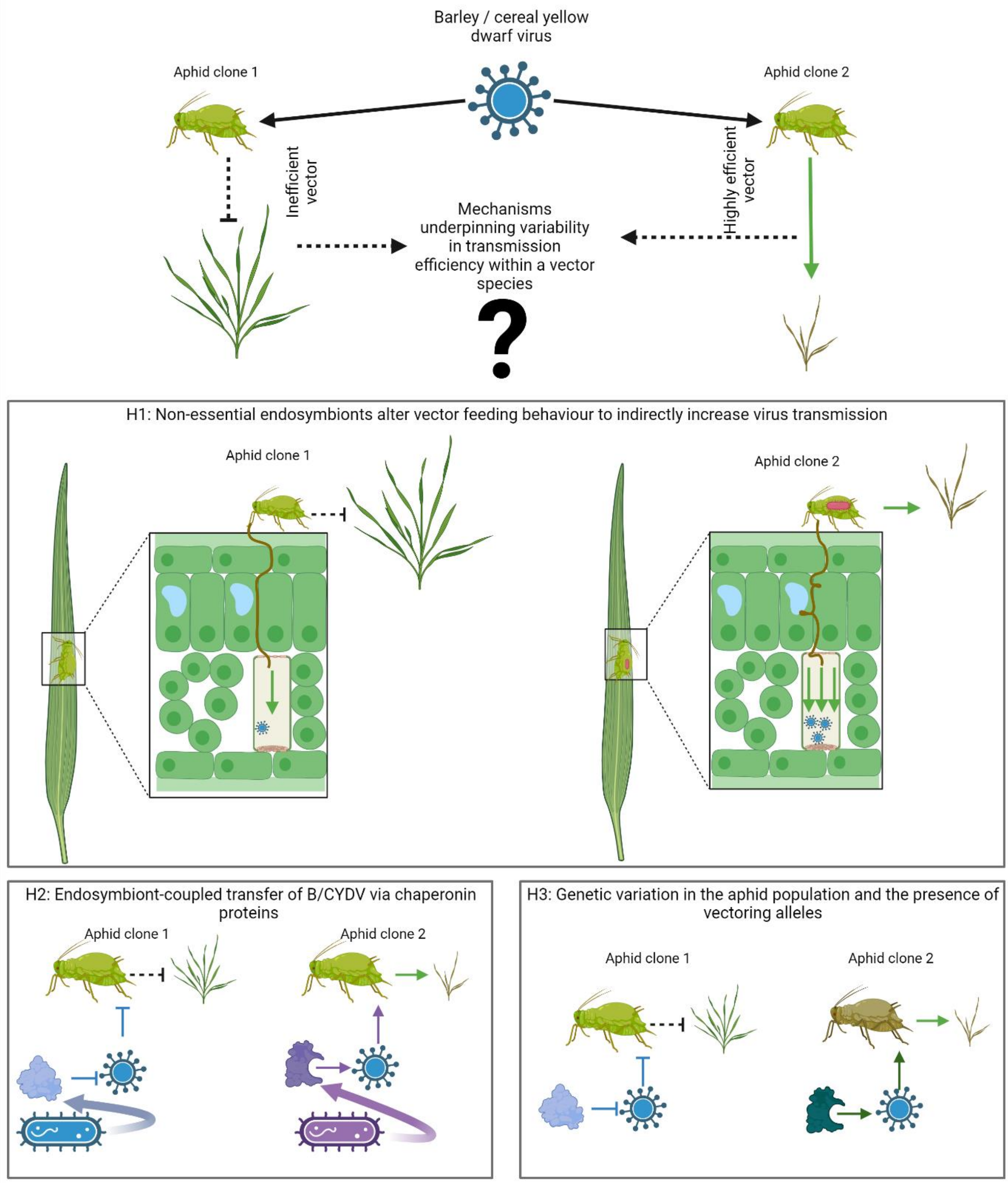

Fig. 1: Graphical representation of the three proposed mechanisms (hypotheses). H1: Non-essential endosymbionts alter vector feeding behaviour to indirectly increase virus transmission - Uninfected aphids display routine interactions with the host plant whereas aphids infected with a facultative endosymbiont show a greater number of cellular punctures and a increased of phloem ingestion (Leybourne et al., 2020b). H2: Endosymbiont-coupled transfer of B/CYDV via chaperonin proteins. H3: Genetic variation in aphid populations and the role of vectoring alleles. Image was created in bioRender – biorender.com; image is adapted from Leybourne (2019).

Mechanism two: Endosymbiont-coupled transfer of B/CYDV via chaperonin proteins

All aphids form an essential relationship with the obligate endosymbiont *Buchnera aphidicola* and 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 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. aphidciola*-chaperonins and plant viruses has been reported for several Luteoviridae, including BYDV (Filichkin et al., 1997), pea enation mosaic virus, beet western yellows virus (van den Heuvel et al., 1997), and potato leafroll virus. (van den Heuvel et al., 1994). Therefore, variation in B/CYDV 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, the potential role chaperonins derived from *B. aphidicola* play in B/CYDV-transmission is not consistent. Experiments using immunoblotting and immunocytochemistry in *R. padi* have found no direct evidence of binding or other potential interactions between B/CYDV 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 Luteoviridae (Filichkin et al., 1997; van den Heuvel et al., 1997). Li et al. (2001) identified alternative non-GroEL proteins that play an important role in binding BYDV^{MAV} in *S. avenae,* and Cilia et al. (2011) identified other *B. aphidicola*-derived factors that potentially influence transmission efficiency of CYDV^{RPV} in *Sc. graminum.* Therefore, genetic variation within *B. aphidicola* strains could alter the binding capacity of these factors and influence B/CYDV acquisition and transmission efficiency, although this needs to be examined.

One other potential symbiont-derived mechanism, that complements the mechanism proposed above, is the potential role of non-essential (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 B/CYDV 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 derive from GroEL of facultative endosymbionts, not the essential endosymbiont *B. aphidicola.* Facultative endosymbionts can contribute towards virus transmission in other sap-feeding plant virus vectoring species (Pinheiro et al., 2015), including transmission of tomato yellow leaf curl virus and cotton leaf curl virus 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: 1) Increased likelihood of B/CYDV acquisition and transmission in facultative endosymbiont-infected vectors through heightened interactions with the plant phloem by the aphid vector, and 2) Greater uptake of B/CYDV virions into the salivary gland in facultative endosymbiont-infected vectors via the chaperonins of facultative endosymbionts (Fig. 1). However, this requires further investigation.

Mechanism three: 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 B/CYDV transmission efficiency has been gained in *Sc. graminum* (Burrows et al., 2006; Burrows et al., 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 B/CYDV transmission efficiency (Cilia et al., 2011; Yang et al., 2008).

A “vectoring” allele of the cyclophilin gene has been identified as a key genetic trait driving variable BYDV transmission in *Sc. 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) propose that the protein facilitates CYDV^{RPV} transport across the aphid hindgut. Allelic variation in the cyclophilin gene could underpin variable B/CYDV transmission within 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 (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) propose that *F. occidentalis* cyclophilin facilitates ribonucleoprotein packing into tomato spotted wilt virus particles.

Vector-derived proteins can also restrict virus binding with vector tissue and influence virus transmission efficiency (Cilia et al., 2011). Several putative proteins have been identified, including CoA ligase, a cuticle protein, and Troponin-T (Cilia et al., 2011). Several of these proteins have been predicted to interact with the aphid hindgut or accessory salivary gland (Cilia 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 et al., 2011). Similar proteins were identified to interact with BYDV^{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 *Sc. graminum* (Cilia et al., 2011; Wang et al., 2015). Differential regulation and abundance of putative cuticular proteins in B/CYDV-infected aphids (Cilia 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 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 (Fig. 1).

Genetic diversity within vector populations could significantly contribute towards B/CYDV transmission efficiency. These insights primarily derive from one vector species, *Sc. 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 B/CYDV transmission efficiency in other vector-virus combinations is required. However, the work in

Sc. graminum has produced important insights that can be further explored in other vector-virus combinations, including:

i) 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).

ii) The impact barriers at the aphid hindgut and accessory salivary gland have on the uptake of B/CYDV virions and the role they play in transmission efficiency, especially in restricting virus acquisition and transmission in incompetent clones (Burrows et al., 2006; Burrows et al., 2007; Cilia et al., 2011).

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 B/CYDV transmission efficiency is synthesised and significant variation in B/CYDV transmission efficiency is detected in different populations for several vector species, including *R. padi, R. maidis, S. avenae,* and *Sc. graminum*. Other vector species, including *M. dirhodum, S. miscanthis,* and *S. fragariae* are, comparatively, understudied and underrepresented when compared with the other vector species. Aphid endosymbionts and genetic traits within vector populations are potential drivers behind this biological variation in transmission efficiency. 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: i) Non-essential endosymbionts alter vector feeding behaviour to indirectly increase virus transmission; ii) Endosymbiont-coupled transfer of B/CYDV via chaperonin proteins; iii) Genetic variation in aphid populations and the role of vectoring alleles.

Literature search method

The keywords “Barley OR Cereal” and “Yellow dwarf virus” and “Transmission” were used to search the Web of Science and Scopus databases. After excluding review articles, the search yielded 291 (Web of Science) and 210 (Scopus) articles. This database was used to compile information on variation in B/CYDV transmission efficiencies between clones, genotypes, or biotypes of a given vector species that was used to screen articles for inclusion in Table 3.

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

Declaration of competing interests

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