Review

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Identifying drivers of spatio-temporal dynamics in barley yellow dwarf virus epidemiology as a critical factor in disease control

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Abstract

Barley yellow dwarf virus (BYDV) is one of the most important viral diseases of small grains worldwide. An understanding of its epidemiology is crucial to control this disease in a sustainable way. The virus moves through the agricultural landscape via cereal aphids as vectors. Understanding movement of these aphids in space and time is of key importance and in doing so, the spatial and temporal variables that influence BYDV epidemiology can be identified. The presence of summer hosts, crop rotation, crop diversity, agricultural practices and climate variables are crucial. Through digitalization, spatial (e.g. land-use) and temporal (e.g. weather) information is becoming more readily available. Including this information into a prediction model could improve decision support systems that will rationalize the decision-making process towards a more integrated control of the disease.

Supporting information may be found in the online version of this article.

Keywords: BYDV; cereal aphids; spatio-temporal influences; epidemiology; IPM; decision support systems

1 INTRODUCTION

Barley yellow dwarf virus (BYDV) is one of the most important viral diseases in small grains, in terms of both worldwide distribution and economic significance. Yield losses of 13–45 kg ha^{-1} for each 1% increase in BYDV incidence are reported, and can result in a total yield reduction of 80% in wheat. The virus restricts photosynthate transportation and causes phloem degeneration within the plant, resulting in leaf discoloration, dwarfism, reduced numbers of tillers, kernels per spike, kernel weight and root growth.[1]

The virus is transmitted by cereal aphids in a persistent and non-propagative manner. This means it remains infectious within the body of the aphid for a long time, but does not multiply within the vector.[1] Ten virus species cause the disease symptoms known as barley yellow dwarf. They are all part of the *Luteoviridae* family and are spread over two genera. Within the genus *Luteovirus* the following species are recognized: BYDV-PAV, BYDV-MAV, BYDV-PAS, BYDV-KerII and BYDV-KerIII. The genus *Polerovirus* incorporates the species CYDV-RPV, CYDV-RPS and MYDV-RMV. The species BYDV-GPV and BYDV-SGV are not yet classified within a genus.[2] All species are further addressed as BYDV, unless the species is specified. Knowledge of these different species is important for the epidemiology for two main reasons. First, the severity of symptoms can depend on the species. For example, the BYDV-PAS induces more severe symptoms than BYDV-PAV in spring varieties of oat and barley. Moreover, a mixed infection of BYDV-PAV with CYDV-RPV aggravates the symptoms of the disease.[3] A second reason is that the transmission efficiency of a species varies with the vector species. Table 1 summarizes research on transmission efficiencies for different cereal aphid and BYDV species. This efficiency can differ from 0% to 100% between different combinations of vector and BYDV species. Consequently, knowledge about the prevailing aphid species in a certain region, period or crop gives information about BYDV species occurring and disease severity.

This review focuses on the situation in temperate climate regions. The most important cereal aphid species transferring the virus in this region are *Rhopalosiphum padi*, *Metopolophium dirhodum*, *Sitobion avenae* and *Schizaphis graminum*.[4] Because the virus is not transferred from infected aphids to their progeny, the latter can only acquire the virus from feeding on infected plants. When no infected plants are available, BYDV cannot persist

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Table 1. Overview of the specificity of the vectors of the different barley yellow dwarf virus (BYDV) species

	Luteovirus[a]				*Polerovirus*			Unassigned	
Species	PAV	MAV	PAS	KerII	RPV	RPS	RMV	GPV	SGV
Rhopalosiphum padi	XXX	—	O	O	XXX	O	X	XX	—
Sitobion avenae	XX	XXX	O		—		—	X	—
Metopolophium dirhodum	XX	XXX	O		—				
Schizaphis graminum	X	—			XX		X	XXX	XXX
Rhopalosiphum maidis	—	—	O		—		XXX		—

XXX, vector species transfers the BYDV species very efficiently and is the main vector species (75–100%); XX, transfers the BYDV species efficiently but is not the main vector species (25–75%); X, does not transfer the BYDV species very efficiently, but more than rarely (5–25%); —,does not transfer, or rarely transfers the BYDV species (0–5%); O, species is known to transfer the BYDV species but there is no information on transmission efficiency. Empty cells indicate that there is no information on the transmission of this vector and BYDV species. Based on different studies summarized in detail in Table S1.

[a] Species *Luteovirus kerIII* was not included in the table because no information is available on the vector species.

within the aphid population.[3] Consequently, because crops naturally perish, BYDV inoculum has to move multiple times a year within the agricultural landscape to alternative hosts. This is accomplished by cereal aphids that act as mobile vectors and hence determine where infection appears, which BYDV species is present and how it spreads. Therefore, to understand the epidemiology of the virus, an understanding of the life-cycle and movements of cereal aphids is crucial.

During autumn, alate (i.e. winged) aphids colonize newly sown winter small grains, where they infect the seedlings and spread BYDV within the crop.[5] The temperature threshold for cereal aphid flight is 14–15 °C. However, this temperature threshold is not a firm limit, and humidity and wind speed also affect aphid take-off and flight. Studies show mixed results on the effect of humidity, but a maximum wind speed threshold of 8 km h^{-1} is generally accepted.[6] The main immigrating aphid species in autumn is *R. padi* and on average 7% of aphids carry the virus, but this varies between years and locations from 0% to 33% (Table S2). Generally, aphid infestation of winter small grains in autumn is seen as the primary determinant of virus infection and subsequent yield loss.[7]

Within winter small grains, reproduction during autumn is parthenogenetic and individuals are mostly wingless, which enables fast population growth.[8] No virus transmission from aphids to plants occurs when temperatures drop below 12 °C and aphid development stops below 5 °C.[1,9] As winter approaches, winged individuals develop within these populations and migrate to their primary host plant. Within the life-cycle of aphids, the primary host is the plant species upon which they lay their eggs. For *S. avenae* the primary hosts are Poaceae species, whereas *R. padi* and *M. dirhodum* migrate to woody primary hosts *Prunus padus* L. and *Rosa* spp., respectively. Here, sexual reproduction takes place, resulting in eggs. These eggs are more resistant to cold temperatures than adult aphids, which increases the survival rate in severe winters.[9] However, winter survival of these aphids and the conditions for egg development and hatching have been investigated only poorly. In spring, the eggs hatch and after a few generations on the primary host, winged individuals recolonize small grains. The woody primary hosts of *R. padi* and *M. dirhodum* are not hosts for BYDV and the emigrating aphids from these plants are therefore virus-free.[10] Virus-free cereal aphids have a preference for BYDV-infected host plants and quickly acquire the virus in infected small grain fields. After becoming viruliferous they show no preference between BYDV-infected or non-infected host plants and spread BYDV within the small grain fields.[8]

When winter temperatures are mild and primary hosts are scarce, the positive effects of sexual reproduction may not make up for the demographic disadvantages incurred by the production of males and eggs.[11] Consequently, some individuals of all three species can overwinter anholocyclically (without eggs) on small grains. The proportion of anholocyclic individuals usually increases in more southern regions, where winters are warmer.[7] Consequently, with winter temperatures expected to rise in temperate regions due to climate change, an increased amount of anholocyclic survival is expected. Moreover, the increased temperatures caused by climate change will result in more efficient virus transmission from vector to plant throughout the year.[8] Persistent populations remain in small grain fields as living aphids and can continue their parthenogenetic reproduction each time temperatures rise above the 5 °C threshold for aphid development. They do not have the day-degree requirement for egg hatching and recolonization of small grains like holocyclic populations.[9] Thus, these populations expand in the crop much earlier after winter, when plants are still small and susceptible to virus infection, and virus spread is increased.[12]

Small grains mature and ripen in summer. At the same time, winged individuals colonize summer hosts: maize, (weed) grasses and volunteer small grain plants.[13] All of these are good hosts for BYDV and can act as a source of virus carrying aphids in the following autumn.[10,14] These summer hosts act as the green bridge between two winter small grain growing seasons. Figure 1 shows the different hosts for cereal aphids in the agricultural landscape and the times of aphid migration between them. When a sufficient temporal gap occurs in the succession of these host crops, the continuity of BYDV epidemics is disturbed. However, the perennial hosts always remain as a background virus and aphid reservoir.

This introduction demonstrates how cereal aphids and BYDV move in both space and time within the agricultural landscape. These landscapes are diverse in space and change over time.[15] Therefore, the influences of spatial diversity, temporal change and their interactions on BYDV epidemiology are complex. This review identifies key spatial and temporal variables that influence BYDV epidemiology and how they can be used to improve disease management. Most of the research in this review is carried out in the absence of insecticides. Studies that incorporate the interaction between spatio-temporal influences and insecticide use is lacking.

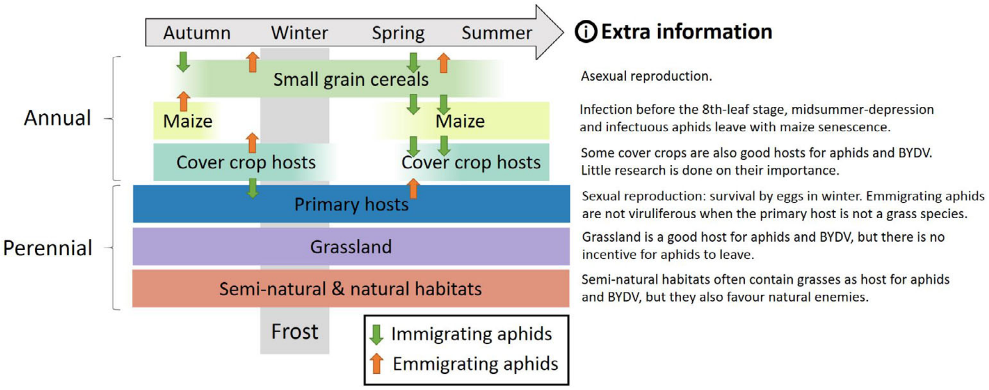

Figure 1. Overview of the hosts of cereal aphids throughout the year. At different times these cereal aphids migrate from one host to another. The green and red arrows show when aphids enter and leave a certain host crop, respectively. When a sufficient temporal gap occurs in the succession of these host crops, the continuity of barley yellow dwarf virus (BYDV) epidemics are disturbed.

2 STRUCTURE AND COMPOSITION OF AGRICULTURAL LANDSCAPES

2.1 Summer hosts

BYDV and cereal aphids survive on alternative hosts over the summer. Consequently, these summer hosts play an important role in BYDV epidemiology as a reservoir for both aphids and BYDV that can infest and infect winter small grains during autumn (Fig. 1). There are four main groups of hosts within Poaceae present during this period in agricultural landscapes: grassland, maize, volunteer plants of small grains and Poaceae cover crops.[5,13] In southern Europe, maize is the main source of migrating aphids in autumn. In northern Europe, the main source is believed to be grassland.[16]

2.1.1 Maize

BYDV is able to infect most maize genotypes and replicate within the plant. Sometimes symptoms become visible, red bands at the edge of the leaves and interveinal yellowing of leaves, but yield losses are generally low or non-existent. The variation in symptom severity seen in different maize populations can be explained by the high natural variation in BYDV tolerance in maize. Some resistance genes stop BYDV infection in maize and could consequently reduce infections in small grains.[17] However, because problems with the virus in maize are small, there is currently no incentive for maize breeders to incorporate these genes into their varieties.

Maize plants are most susceptible to BYDV infection when they are young, especially before the eight-leaf stage. The decrease in infection at later stages is most likely due to the expression of resistance of matured plants to virus replication.[18] Generally, cereal aphids appear early in the growing season of maize. *S. avenae* and *M. dirhodum* populations usually reach their maxima in July and disappear in August. In autumn, populations of these species are either absent or low. *R. padi* has a longer period of development on maize, which may result in an autumn outbreak.[18,19] These populations are the basis of the *R. padi* individuals immigrating into small grain fields, as discussed further below.

In Italy, studies found up to 68% of maize plants were colonized by aphids.[20] The reported proportion of infected maize plants with BYDV ranges from 9% to 80%.[18,20] Moreover, emerging *R. padi* populations in autumn are able to acquire the virus from infected maize plants and transmit it to small grain plants.[18] This has led to the assumption that maize is an important source of viruliferous aphids in autumn. Recent research confirms this by employing two new techniques: isotopic analysis and geographic information systems (GIS), as discussed below.

Isotopic analysis is based on the difference in abundance ratios of natural carbon isotopes (δ^{13}C ratios) between plants with a different photosynthetic pathway (C_3 or C_4 type). These differences are transmitted to the next trophic level, which makes it possible to distinguish insects that fed on either C_3 or C_4 plants. Isotopic analysis was performed on immigrant *R. padi* individuals on small grains in autumn, in France. Eighty five per cent originated from C_4 plants. Maize (97% of the area) and sorghum (3% of the area) are the only crop species that have a C_4 photosynthetic pathway and C_4 host weeds are rare in this area. This led to the conclusion that most of these aphids originated from maize.[5] When maize is harvested later in autumn, the origin of the immigrating aphids shifts to C_3 plants. All alate *S. avenae* individuals caught in suction traps in France before 21 September originated from C_4 plants. In October, 39% of *S. avenae* individuals landing on wheat came from C_4 plants, whereas in November, colonizers originated exclusively from C_3 plants.[13] The latter were most likely emigrants from other small grain fields or from grassland.

Large amounts of spatial data can be linked to field observations using GIS. This allows the influence of the presence of maize within an area on aphid populations in small grains to be analyzed.[5] The effect of maize in a 1-km radius around small grain fields on the colonization rate by aphids was significantly positive. It was suggested that better results could be obtained by increasing the radius beyond 1 km, as better models were obtained when increasing the buffer size from 0.25 to 1 km. However, as buffers from the observed fields start to overlap, statistical independence decreases, complicating analysis of larger buffer sizes.

The proportion of viruliferous cereal aphids increases with the ratio of the area sown with small grains compared to maize in a 50-km region. This might be explained by the fact that even though maize is a good reservoir of aphid vectors, it does seem to harbour a smaller virus concentration than small grains, and is therefore a poorer source for virus acquisition.[14] It was suggested that maize is an important source of vectors for BYDV, but a poor virus reservoir, whereas grassland could be a source of vectors and viruses.[5]

2.1.2 Grassland

The size of the aphid populations on pastures is very low compared with those on maize.[19,21] However, in grassland, up to

80% of the plants can be infected with BYDV, especially in perennial grasslands that accumulate infections over multiple years.[21,22] An extensive list of all grass species found to be susceptible to BYDV infection has been published.[10] This list contains, among others, all the economically important grass species (*Lolium* spp., *Phleum pratense*, *Festuca arundinaceae*, etc.). Even though BYDV is not seen as a problem in grassland, some studies reveal effects on grass growth. In ryegrass species (*Lolium* spp.), a reduction in root yield was reported, although foliar symptoms are rare.[23]

The effects of grassland area in the landscape on aphid abundance are diverse and often contradicting. In the study mentioned earlier,[5] researchers found a negative effect of the amount of grassland at a radius of 1 km around small grains on the colonization by aphids in autumn. A possible explanation put forward is the reluctance of aphids to leave a perennial resource, and the higher predation and parasitism pressures exerted in grasslands, resulting in lower aphid densities. Other studies show a positive relation between the proportion of area covered with grassland in a 3.2-km radius and aphid abundance in small grain fields.[24] Moreover, increasing BYDV infection in grassland is found with increasing proportion of area covered with small grains in a 1-km radius.[22]

2.1.3 *Volunteer plants*

Seeds of small grains that fall to the ground at harvest and sprout as volunteer seedlings are evidently good green bridges for aphids and BYDV between harvest and newly sown small grains. They are generally attractive to cereal aphids and susceptible to BYDV with efficient transmission rates.[14] The presence of a field with small grain volunteers significantly increases aphid infestation on plants placed next to these fields.[5] However, the area covered with volunteers plants of small grains is many times smaller than that covered by maize crops or grassland, and the infection rate of these volunteer seedlings can differ from low to very high.[25,26] Little research is available on the importance of small grain volunteers for autumn infection in winter small grains. We believe volunteers can be an important source at a local scale, but the few locally present volunteers cannot provide viruliferous aphids for a wider landscape. More research is needed to quantify the importance of volunteers in BYDV epidemiology.

2.1.4 *Cover crops*

Some cover crops or green manure crops are also good hosts for cereal aphids and BYDV. Temporary grassland as a cover crop is discussed above (Section 2.1.2). Some other important cover crop hosts are lopsided oat (*Avena strigosa*), spring oat (*Avena sativa*), winter rye (*Secale cereale*) and Sudan grass (*Sorghum sudanense*).[10,27,28] These cover crops are similar to the economically important small grains, but are often sown earlier, making them good hosts in late summer until sowing of the latter. However, no research is currently available on the importance of these crops in the landscape on cereal aphid population or BYDV in small grains. Within the lopsided oat and rye populations, some traits for resistance against BYDV are known, but this does not mean the virus cannot multiply within these populations and spread to susceptible small grain fields.[27,28]

2.2 Crop rotation and agricultural landscape change

On a year-to-year timeframe, agricultural landscapes change because of crop rotations. On a larger time-scale they change more extensively. In Europe, past decades have led to an increase in the size of individual fields, due to land consolidation, and a decrease in crop diversity. These changes have a profound effect on crop pests and their natural enemies.[15] The effects on cereal aphids, their natural enemies and BYDV epidemiology are discussed below.

2.2.1 *Link with dispersal abilities*

Pest species with high dispersal abilities are only influenced by the current landscape composition and not by changes in landscape composition, because they have the ability to move to more suitable habitats when the landscape changes negatively.[29] The dispersal abilities of cereal aphids depend upon the situation and the time of year. They can be divided into long-range migration and short-range 'appetitive' dispersal or secondary dispersal. Short-range dispersal is most important when aphids migrate from summer hosts to autumn-sown small grains.[30] There is also evidence that alate aphids show wing muscle autolysis within 2–3 days after moulting. This means they can fly only during those few days, leaving just a little window for migration. Recent studies agree that alate aphids tend to move mainly short distances over their lifetime, in the order of 20 m in favourable habitats and 100 m in poor habitats.[6] Moreover, dispersal is an extremely vulnerable stage for cereal aphids. In the case of *R. padi*, an estimated 99.4% of alate aphids die during autumn migration and even when aphids survive dispersal, it comes with a fitness cost. Both resistance to infection and fecundity are reduced with increases in dispersal distance.[31] This suggests that cereal aphids have rather limited dispersal abilities making them prone to changes in local crop patterns due to annual succession of crops.

2.2.2 *Semi-natural habitats as a refuge*

Semi-natural habitats are usually defined as woodlots, hedges, field margins, fallow land and pasture (Table S3). These landscape components are stable over time and can act as a permanent link in the landscape for both crop pests and their natural enemies through temporal changes of the landscape.[15]

To understand the effect on cereal aphids and their natural enemies, the available literature (Table S3) is summarized in Fig. 2. Here, the effect of semi-natural habitats within different distances from a small grain field on cereal aphid and natural enemy abundance within the field is visualized for different growth stages of winter wheat. All this research is conducted on winter wheat in spring. Most research finds a positive effect of semi-natural habitats within 0.2–0.5 km on cereal aphid and natural enemy abundance early in the season. Within larger distances (0.6 –2.5 km), the same is true for cereal aphids, but no effect is found on the abundance of natural enemies. From flowering to grain-filling, all research found either negative or no effects on cereal aphid abundance from semi-natural habitats close to the field (0.2–0.5 km). The results for natural enemy abundance differ for this distance. At 0.6–2.5 km the effects are predominantly positive on both cereal aphid and natural enemy abundance during these growth stages. At even greater distances, the effects on cereal aphid populations remain positive, whereas no effects on natural enemy abundance are found. It can be concluded that more semi-natural habitats in the landscape generally lead to higher cereal aphid densities. Only for semi-natural habitats close to the small grain field can the effect on aphid abundance be negative later in the growing season. Possibly, the constant influx of migrating aphids during the migration period cancels out the biological control effects of natural enemies during early growth stages. Because viruses are most damaging during the early growth stages of a plant, the late arrival of natural enemies at the time of flowering might not help sufficiently against BYDV infection

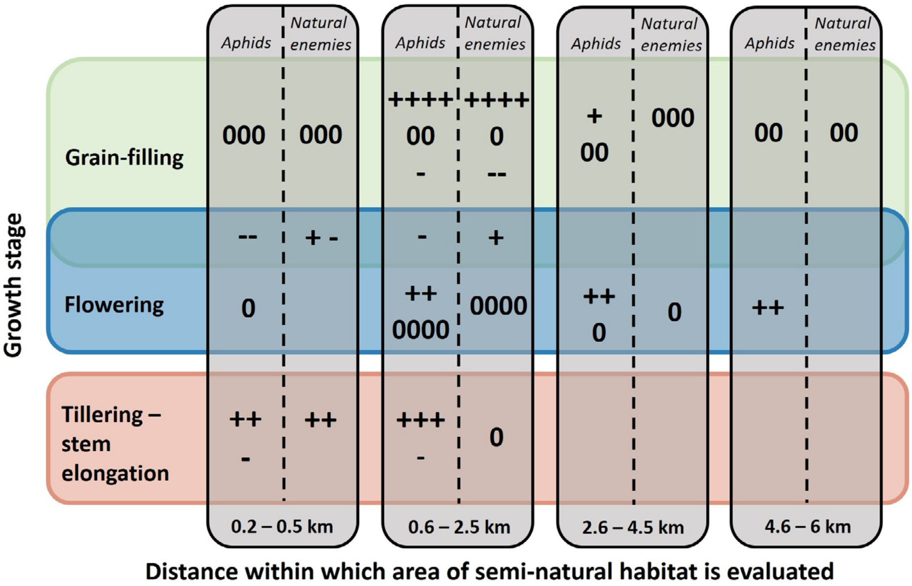

Figure 2. Overview of the effect of the area of semi-natural habitats within different distances around wheat fields on cereal aphid and natural enemy abundance within these wheat fields depending on the growth stage of the wheat plants. This figure is based on research summarized in Table S3. +, study found a significant positive effect; −, study found a significant negative effect; 0, study found no significant effect.

in spring.[3] One could argue for an increase in the amount of semi-natural habitats close to the small grain fields, but whether this is enough to compensate for the influx from semi-natural habitats at larger distances is uncertain and remains to be investigated.

There is no inverse relation between the effect on aphid population and natural enemy abundance. Positive effects on natural enemy abundance are often associated with a positive effect on cereal aphid abundance. This is counterintuitive as one would expect higher natural enemy abundance to be associated with lower pest density. Possibly, larger aphid populations allow for larger natural enemy populations. Little research is available about the effects of semi-natural habitats on cereal aphid and natural enemy abundance in autumn.

It is clear that the expansion of semi-natural habitats is not a universal solution for the suppression of all crop pests.[32] For BYDV specifically, the number of immigrating aphids might be more important than aphid densities later in the season, as they bring the first inoculum to these fields of small grains that can be spread further. Research on how the presence of semi-natural habitats influences the proportion of viruliferous aphids is lacking but is needed to evaluate whether these semi-natural habitats have a positive or negative effect, specifically on the spread of BYDV infection.

2.2.3 *Dilution and crowding hypothesis*

The dilution and crowding hypothesis is a classic theory in ecology that could explain the effect of interannual landscape change on pest densities. When the host crop area of a pest decreases, the crowding hypothesis states that pest density on the remaining host area increases. Pest dilution occurs when local pest abundance decreases with increasing host area.[15] For cereal aphids, this hypothesis is fortified by research. Aphid densities were determined at 23 locations between 5 and 25 May in three consecutive years. The change in wheat crop coverage was determined within a 0.5-km radius. Aphid densities generally declined with increasing wheat field area on a year-to-year basis. Densities of specialist predators decreased with increasing wheat crop coverage in two consecutive years.[33] Generalist predators did not respond to changes in wheat crop coverage. Specialist predators are dependent on the cereal aphid population, whereas generalist predators can feed on other insect species or food sources as well, which makes the generalist population more stable in an environment where the cereal aphid populations are changing.

2.3 Crop and agricultural landscape diversity

2.3.1 *Resource concentration and enemies hypothesis*

Spatial crop heterogeneity is described by its configuration and composition. Two hypotheses were suggested to understand the effect of these two elements on crop pests and their natural enemies: the resource concentration hypothesis for configurational crop heterogeneity (field border density and field size) and the enemies hypothesis for compositional crop heterogeneity (crop diversity).[15]

The resource concentration hypothesis predicts that specialist herbivorous insects reach higher densities in large patches of host plants, because insects are more likely to find and stay longer in those patches. Studies have shown that the lowest aphid densities occur in small fields (< 1 ha), but also in the largest fields (> 31 ha). Highest aphid densities were found in fields between 2 and 4 ha.[34] Moreover, on a landscape instead of an individual field level, the results also contradict the resource concentration hypothesis. The proportion of wheat in areas with a scale of 0.5–2 km has a significant negative effect on cereal aphid abundances.[35] In other research, arable land consisting mostly of small grains in a range of 1–6 km, also had a negative effect on cereal aphid abundances.[36] However, this effect was significant only at the wheat flowering stage and not at wheat milk ripening. The effect at early growth stages, before winter when BYDV infection is most important, was not studied. In a study carried out in autumn, the proportion of wheat in an area up to 3.2 km around a wheat field did not have a significant effect on cereal aphid abundance. Significant negative effects of the proportion of wheat on *Lysiphlebus testaceipes* abundance did occur in autumn. This species is known as a natural enemy of cereal aphids.[24] These results contradict the resource concentration hypothesis for cereal aphid populations. Another component of configurational crop heterogeneity is the field border density. Landscapes with higher field border densities have lower aphid and natural enemy abundance if the density of grassy borders is high. If the grassy border density is low, aphid abundance increases and natural enemy abundance is not affected.[15]

The enemies hypothesis states that natural enemies may be more attracted by polycultures than monocultures due to better possibilities for shelter, and more stable and diverse prey resources, leading to higher predation and thus lower herbivorous insect densities.[15] Note that this hypothesis does not necessarily contradict the dilution and crowding hypothesis because the latter specifically applies to a changing landscape over time. When evaluated at up to 0.5 km, increased crop diversity has a strong positive effect on biological control and predator densities. At spatial scales > 2 km a positive effect of crop diversity on parasitoid abundance is also found.[32] Research on naturally occurring aphid populations revealed higher parasitism rates in more complex landscapes, but aphid densities were also higher.[37] Other studies showed significantly fewer aphids occurred in areas with a higher crop diversity, but only if aphid hosts decreased in comparison with the previous year. When the number of aphid hosts increased in comparison with the previous year, aphid densities increased in areas with a higher crop diversity.[15] Moreover, at the time of colonization, parasitism and aphid abundance might be strongly influenced by landscape variables, although this is much less the case later in the growing season when these are then more influenced by within field population dynamics.[24] Different research shows how natural enemies are present earlier in the field in more complex landscapes, making early biocontrol much more efficient.[24,38]

Figure 3 summarizes the effects discussed above, assuming the agricultural landscape did not change in comparison with the previous year and that the total host crop area is equal between the different landscapes.

2.4 Agricultural practices

Field-specific agricultural practices have an effect on aphid abundance. The sowing date of winter small grains has a large and well-known effect on cereal aphid immigration. Early sowing increases the duration of exposure to cereal aphids migrating from their summer host, leading to higher abundances of cereal aphids in these fields.[39] Preferences of cereal aphids for certain varieties are also reported and these preferences seem to differ between the different small grain species.[40] Moreover, some resistance genes have been reported against aphids for both barley and wheat, and there are some resistance genes against BYDV that are commercially used in varieties today. However, most are actually tolerances, as the virus can still multiply within the plant, but the plant does not show symptoms or reduced yield.[41] From an epidemiological point of view, this is important as fields sown with BYDV-tolerant varieties can still be a source of viruliferous aphids for fields with non-tolerant varieties.

Nitrogen fertilization increases the amino acid content in the phloem sap, which in turn can increase the aphid population growth.[42] This is observed for *M. dirhodum*, whereas *S. avenae* seems to be negatively influenced or indifferent to nitrogen fertilization.[43] This might be explained by the fact that *M. dirhodum* feeds on the leaves, whereas *S. avenae* feeds mostly on the ears. When nitrogen is a limiting factor, the plant will translocate nitrogen from the leaves to the ears, reducing the effect of low nitrogen fertilization on *S. avenae*.[42] This theory is supported by observations of *R. padi*. This species feeds on the leaves as well as on the ears of mature plants.[44] When the plant is young (three-leaf to three-tiller stage), this species has no choice other than to feed on the leaves and during this time, nitrogen fertilizer has a positive effect on the population growth.[45] However, nitrogen fertilizer has no effect as the plant matures, because the aphids then feed on the ears where the effect of low nitrogen fertilization is reduced.[43]

3 CLIMATE AND WEATHER VARIABLES

As ectothermic organisms, aphid population growth is closely linked to weather variables. Immediate effects of weather conditions on aphid populations and BYDV transmission are discussed in the Introduction. More information can also be found in research on decision support systems (DDSs) with weather variable inputs, as listed in Table S4. However, weather conditions

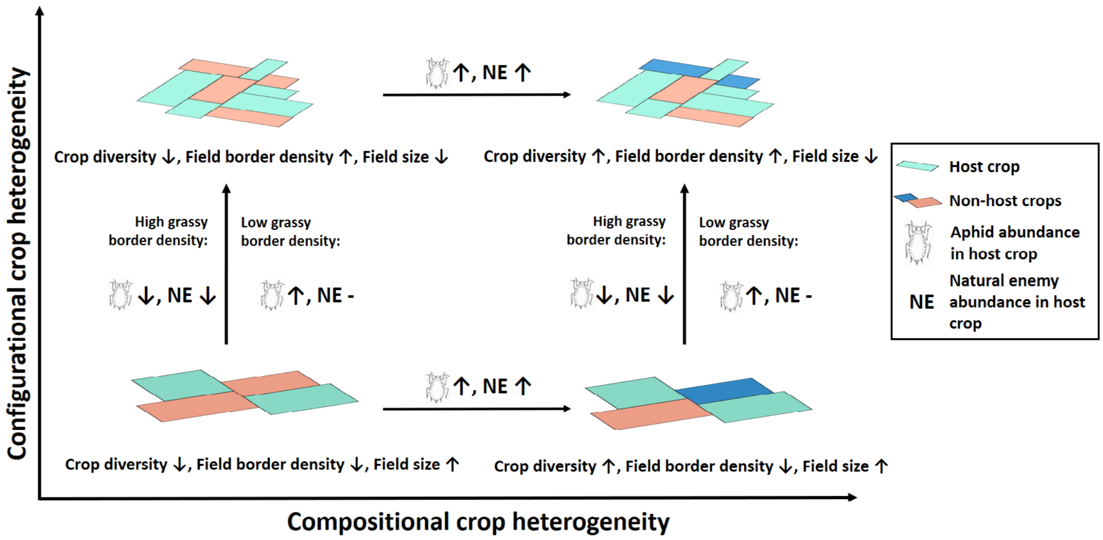

Figure 3. Schematic overview of the effect of compositional and configurational crop heterogeneity on cereal aphid and natural enemy abundance on host crops. It is assumed that the agricultural landscape did not change in comparison with the previous year and that the total host crop area is equal between the different presented landscapes.

long before cereal aphid colonization can also be predictive of population dynamics during and after colonization. Two weather-related factors are known to increase the number of cereal aphids in the following autumn: a lack of severe frosts in the previous winter and spring, and abundant precipitation in early spring. The effect of a mild winter would not be surprising if it also had a positive effect on the summer peak population, but this is not the case. However, the lack of severe frosts in late winter and early spring does prolong the summer migration, which in turn can increase the size of the subsequent autumn migration.[46] Warmer temperatures in spring results in an earlier onset of summer aphid migration,[47] and the earlier migration starts, the longer the total migration length, which in turn leads to a more abundant autumn migration.[46] Cold temperatures in winter and spring delay summer migration, especially in holocyclic populations as this delays the egg hatching.[47] Temperatures at 50–80 and 90–110 days before the beginning of the aphid season in spring have a strong positive effect on aphid densities in spring.[9] Moreover, the warmer the period from January to August, the higher the proportion of viruliferous aphids in the following autumn. The increased rate of population growth in this period increases the virus spread in the landscape, resulting in a higher proportion of viruliferous aphids.[14]

The positive effect of early spring precipitation on autumn populations is explained by the fact that precipitation at this time of the year is usually in the form of snow that insulates the aphid eggs from severe frost damage and protects them from predators.[46]

4 MODELLING

DSSs are especially useful to control diseases with sporadic prevalence that varies greatly from year to year and from field to field, such as BYDV. The annual average cost of BYDV disease and control can be reduced by 36% by adopting a model-based strategy instead of a preventative spraying strategy.[7] Over the years, many DSSs have been developed for cereal aphid infestations. Only a few incorporate the effect of BYDV (Table S4). Inputs for these DSSs are often based on initial aphid populations, the sowing date of the small grains or weather-related variables (Table S4). Many of the spatio-temporal influences described in this review are ignored. However, increasing digitalization in agriculture offers opportunities. Through GIS, spatio-temporal information about the agricultural landscape is readily available. This makes it faster and easier to implement these into DSSs. Moreover, weather observations and weather predictions are now available with more spatial and temporal detail.

There is still a lack of information about the parameters that influence the proportion of viruliferous aphids in a certain year and at a certain location. From Table S2 it is clear that the proportion of viruliferous aphids can vary significantly between years and locations, which evidently has a large effect on the risk of aphid infestations in a small grain crop. An extensive detection network for viruliferous aphids can increase knowledge on this subject. DSSs on cereal aphids can then be extended to BYDV control, and more precision and accurate predictions will be possible.

To date, all the DSSs presented in Table S4 are based on mechanistic or statistical models. Machine learning has the potential to incorporate the large amount of spatio-temporal data currently available to improve the prediction accuracy.[48]

5 CONCLUDING REMARKS

As temperatures are expected to rise in the temperate region due to climate change, problems with cereal aphids and consequently BYDV are expected to increase.[8] Moreover, use of conventional insecticides is under pressure from both society and regulations. Therefore, a more efficient and sustainable method of control is necessary. Reduction in preventative insecticide spraying will reduce the economic and ecological costs.[7] A model-based strategy in the form of a DSS that is readily accessible to farmers can help to accomplish this. Understanding the key drivers of spatio-temporal dynamics in BYDV epidemiology is the first step towards a prediction model that can help rationalize the decision-making process.

It is clear that the spatio-temporal influences are a complex and intertwined set of influences that are hard to completely understand and implement into a general prediction model. The larger the spatial and temporal scale this model has to cover, the more observations are needed to identify the effect of every factor and the interaction effects between the different factors. This review can act as a guide to select the independent variables that have to be observed to increase efficiency in the building of such a model. This review concludes:

- with increasing numbers of summer hosts in the landscape, the aphid and BYDV pressure increases;
- semi-natural habitats in the landscape result in higher aphid pressures;
- an interannual increase in host plants results in a dilution effect, reducing aphid densities and thus BYDV infection density;
- with increasing configurational crop heterogeneity, aphid density is reduced if the landscape has a high grassy border density – the opposite is true with a low grassy border density;
- with increasing compositional crop heterogeneity, aphid density is increased;
- sowing earlier results in larger aphid infestations;
- nitrogen fertilization can increase aphid population growth;
- weather conditions that increase winter survival rate (warmer temperatures and insulating precipitation such as snow), result in higher aphid densities later in the year.

To date, DSSs have been based on mechanistic and statistical modelling with very few inputs and inputs that require a significant effort (e.g. aphid population monitoring). Machine learning models, based on the different spatio-temporal influences described in this review, have the potential to increase the accuracy of the predictions.

Much of the research presented in this review was carried out in spring. Knowledge about the effects in autumn remains scarce but is needed to evaluate the effect on BYDV epidemiology. Moreover, most of the conclusions presented here deal with the effect of the discussed spatio-temporal influences on cereal aphid population densities. However, knowledge of how these spatio-temporal factors influence the proportion of cereal aphids that carry BYDV is still lacking. More research is needed to understand and include these influences in DSSs, which will enable us to predict the full pathology and make better decisions in control of the disease.

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SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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