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Dispersal responses of cereal aphids to wheat cultivar and planting configuration

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Abstract

Cultivar mixtures are advocated as an agroecological strategy for suppressing cereal aphid vectors and reducing barley yellow dwarf virus (BYDV) transmission, yet their effects on within-crop dispersal remain largely untested, particularly across vector species and virus infection states. We quantified the walking dispersal of *Sitobion avenae* and both BYDV-PAV-viruliferous and non-viruliferous *Rhopalosiphum padi* through wheat stands comprising a 1970s cultivar (Maris Huntsman) and a *Bdv2*-carrying BYDV-resistant cultivar (RGT Wolverine), arranged as monocultures, alternating-row intercropping and randomised mixtures. Dispersal responses were species-specific, cultivar-dependent and fundamentally altered by virus infection status. *S. avenae* colonised non-source plants at comparable rates across all treatments. Non-viruliferous *R. padi* showed strong cultivar-mediated responses as colonisation on Maris Huntsman monocultures was 67%–69% lower than on Wolverine, with a steep distance-decay gradient (64% decline per unit distance) indicating rapid arrestment on the preferred host. Within randomised mixtures, *R. padi* preferentially colonised Maris Huntsman, but the presence of Wolverine plants disrupted arrestment and produced spatially uniform dispersal resembling that on Wolverine monocultures. Source plant cultivar, rather than surrounding planting configuration, was the primary driver of *R. padi* dispersal in mixtures. Critically, BYDV-PAV infection eliminated all cultivar-specific responses in *R. padi* as viruliferous aphids dispersed uniformly regardless of cultivar arrangement, consistent with virus-induced behavioural manipulation overriding host-acceptance cues. These findings demonstrate that this cultivar combination does not provide consistent associational resistance and can create associational susceptibility for non-viruliferous *R. padi*, indicating that species-specific vector ecology and virus-mediated behavioural modification must be integrated into the design of cultivar diversification strategies for BYDV management in cereals.

KEYWORDS
associational resistance, barley yellow dwarf virus, cultivar mixtures, host plant resistance, *Rhopalosiphum padi*, *Sitobion avenae*, vector manipulation hypothesis, walking dispersal

1 | INTRODUCTION

Barley yellow dwarf virus (BYDV) is the most economically important viral disease of cereals worldwide, with yield losses ranging from 5% to 80% in wheat depending on cultivar susceptibility, infection timing and vector pressure (Aradottir & Crespo-Herrera, 2021; Nancarrow et al., 2021). In Europe, the species of greatest concern has been reported to be BYDV-PAV (Tombusviridae: *Luteovirus pavhordei*) (Foster et al., 2004). Field studies have demonstrated that even moderate infection incidence can reduce grain yield by approximately 0.9% for each 1% increase in natural BYDV-PAV infection (Nancarrow et al., 2021), while early seedling-stage infections can reduce yields by up to 84% in wheat under severe pressure (Nancarrow et al., 2021). In temperate cereal-growing regions, BYDV is transmitted in a persistent, circulative manner by several aphid species (Hemiptera: Aphididae), of which *Rhopalosiphum padi* L. (bird cherry–oat aphid) and *Sitobion avenae* Fabricius (English grain aphid) are the principal vectors in European wheat production systems (Aradottir & Crespo-Herrera, 2021; Dedryver et al., 2010; Jarošová et al., 2019). Autumn-sown cereals are particularly vulnerable as viruliferous alate aphids colonise crops in autumn and subsequent apterous dispersal within the crop during mild periods drives secondary spread that can determine epidemic severity (Fabre et al., 2006; Thackray et al., 2009). The restriction of neonicotinoid seed treatments across the European Union in 2018 (Commission Implementing Regulations (EU) 2018/783–785), with all outdoor uses now prohibited following a 2023 Court of Justice ruling confirming that no emergency derogations may be granted, has removed the principal prophylactic tool for early-season aphid management (Jactel et al., 2019). With pyrethroid-based foliar sprays now the sole chemical option for many growers, and with target-site resistance to pyrethroids already documented in *S. avenae* populations across the UK (Foster et al., 2014; Walsh et al., 2020), there is an urgent need for non-chemical strategies that reduce vector-mediated virus transmission in autumn-sown cereals.

Cultivar mixtures using the simultaneous cultivation of two or more genotypes of the same crop species within a single field are increasingly advocated as an agroecological approach to pest and disease suppression (Barot et al., 2017; Finckh et al., 2000; Mundt, 2002). The theoretical basis for mixture efficacy draws on the resource concentration hypothesis, which predicts that specialist herbivores should be less abundant in genotypically diverse plantings due to reduced host-finding efficiency and increased emigration (Andow, 1991; Root, 1973), and the framework of associational resistance, whereby the proximity of non-host or resistant genotypes reduces herbivore colonisation of susceptible neighbours (Barbosa et al., 2009). The evidence for cultivar mixture benefits is good for fungal pathogens. Mixtures reduce disease severity through dilution of inoculum, barrier effects and induced resistance, with meta-analyses reporting yield advantages of 4–6% in winter wheat mixtures relative to component monocultures (Kiær et al., 2009; Mundt, 2002; Wolfe, 1985). For arthropod pests, however, the evidence is unclear (Tooker & Frank, 2012). Reviews and field studies have highlighted that herbivore suppression in cultivar mixtures is inconsistent and depends on the specific pest species, crop and cultivar combination, with some mixtures producing associational susceptibility rather than resistance (Hambäck et al., 2014; Mansion-Vaquié et al., 2019). Recent field experiments in winter wheat have found that combining intra- and interspecific diversification did not outperform individual practices in reducing cereal aphid populations, and that cultivar mixtures were sometimes more infested than the least susceptible component cultivar (Fandos et al., 2023; Mansion-Vaquié et al., 2019). The mechanisms by which cultivar mixtures might suppress aphid vectors specifically, and thereby reduce virus transmission, remain poorly understood.

Host plant resistance offers a complementary approach to BYDV management. The *Bdv2* gene, introgressed from *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey into hexaploid wheat, confers resistance to BYDV-PAV by restricting viral replication within the plant and has been deployed in several commercial cultivars, including RGT Wolverine (Aradottir & Crespo-Herrera, 2021; Banks et al., 1995). Beyond effects on virus titre, BYDV-resistant cultivars may also influence vector behaviour directly. *Bdv2*-carrying genotypes have been reported to affect aphid settling and feeding responses, raising the possibility that resistance genes could exert both antibiotic effects on the virus and behavioural effects on the vector (Aradottir & Crespo-Herrera, 2021; Leandro et al., 2025). However, the extent to which such effects translate into meaningful reductions in vector dispersal and secondary virus spread within crop stands has not been experimentally tested. Moreover, host plant resistance operates within a broader context of aphid–plant interactions that are species-specific as *S. avenae* is predominantly an ear- and upper-leaf feeder with comparatively broad cultivar acceptance (Gianoli, 2000; Watt, 1979), whereas *R. padi* typically colonises basal plant parts and exhibits stronger cultivar-specific responses in both settling and reproduction (Hesler et al., 1999; Leather & Dixon, 1984). These species-specific differences in host utilisation suggest that cultivar-based management strategies may not be equally effective against all vectors.

A further complication arises from the capacity of persistently transmitted viruses to modify the behaviour of their vectors. The Vector Manipulation Hypothesis (VMH) proposes that plant viruses have evolved to alter vector behaviour in ways that enhance their own transmission (Ingwell et al., 2012; Mauck et al., 2018). For BYDV, Ingwell et al. (2012) demonstrated that virus acquisition switches the host preference of *R. padi* as non-viruliferous aphids preferentially settle on BYDV-infected plants, facilitating virus acquisition, whereas viruliferous aphids prefer uninfected plants, facilitating inoculation. This behavioural switch implies that the dispersal phenotype of the vector may differ fundamentally depending on its infection status. Chesnais et al. (2020) extended this framework by showing that aphids carrying turnip yellows virus (TuYV), another persistently transmitted polerovirus, exhibited enhanced locomotor activity and dispersal capacity relative to non-viruliferous individuals, with post-acquisition effects on vector behaviour exceeding plant-mediated pre-acquisition effects. Subsequent molecular studies have begun to elucidate the mechanisms underlying these changes, with TuYV

shown to suppress host plant defence responses to aphid feeding, thereby facilitating vector performance and onward transmission (Krieger et al., 2023). If viruliferous aphids exhibit a restless, exploratory dispersal phenotype that overrides the host-acceptance cues normally governing cultivar-specific settling, then the efficacy of cultivar-based management strategies, including cultivar mixtures, may be substantially reduced under the conditions most relevant to virus spread, namely when vectors are actively transmitting.

Most studies of cultivar mixture effects on aphid populations have assessed abundance or fecundity at the field scale, with limited attention to the dispersal processes that determine how aphids move among plants within a stand. Yet apterous ambulatory dispersal (i.e., walking movement between neighbouring plants) is the primary mode of secondary spread for both aphids and aphid-vectored viruses within established crops (Fabre et al., 2006; Irwin & Thresh, 1990). The spatial dynamics of walking dispersal determine how rapidly viruliferous aphids encounter and inoculate new hosts following initial colonisation by alates and are therefore central to the epidemiology of BYDV (Thackray et al., 2009). Whether cultivar arrangement can constrain this ambulatory dispersal, and whether such effects are modified by the virus infection status of the vector, has not been experimentally addressed. Furthermore, volatile organic compound (VOC)-mediated interactions between neighbouring cultivars can influence aphid host acceptance independently of direct plant–aphid contact. Ninkovic et al. (2002) demonstrated that exposure to volatiles from certain barley cultivars reduced *R. padi* acceptance of neighbouring plants, and subsequent work has shown that these allelobiotic effects are cultivar-combination-specific, with only particular pairings producing the 'right neighbour' effect that enhances resistance in the receiving plant (Dahlin et al., 2018; Glinwood et al., 2007; Kheam et al., 2023; Pettersson et al., 1999). Whether such VOC-mediated effects extend to wheat cultivar mixtures, and whether they are robust to virus-induced changes in vector behaviour, remains unknown.

The deployment of cultivar mixtures for BYDV management therefore rests on three largely untested assumptions: (1) that genotypic diversity will constrain aphid dispersal within the crop; (2) that this effect will be consistent across vector species with different host utilisation strategies; and (3) that the behavioural responses of non-viruliferous aphids will predict the behaviour of viruliferous vectors responsible for secondary virus spread. This study addresses these assumptions directly by quantifying the walking dispersal of *S. avenae* as well as BYDV-PAV viruliferous and non-viruliferous *R. padi* through wheat stands comprising two cultivars, a 1970s cultivar without known BYDV resistance and a modern cultivar carrying *Bdv2*, arranged as monocultures, alternating-rows of cultivars but referred to here as intercropping, and randomised mixtures. We measured colonisation extent, spatial gradients of dispersal, cultivar preference within mixtures, nymph production and the influence of source plant cultivar identity on subsequent dispersal. Specifically, we tested the hypotheses that: (1) cultivar mixtures reduce aphid colonisation relative to the poorer-performing monoculture; (2) dispersal responses are consistent between *S. avenae* and *R. padi*; and (3) BYDV-PAV infection alters the dispersal phenotype of *R. padi*, overriding the cultivar-specific responses observed in non-viruliferous individuals and producing a dispersal pattern consistent with virus-mediated behavioural manipulation.

2 | MATERIALS AND METHODS

2.1 | Aphid populations and age-synchronised cohorts

Polyclonal populations of *Sitobion avenae* and *Rhopalosiphum padi* were established by collecting 10 mixed-age individuals per species from cereal fields at Harper Adams University (52°46′33.1″N 2°25′42.9″W). Aphids were placed onto potted spring barley (*Hordeum vulgare* L., cv. Planet) sown 1 cm deep into 9 × 9 cm pots (Teku, Poeppelmann GmbH, Lohne, Germany) filled with peat-free John Innes No. 2 compost (Sylva Grow®, Melcourt, Tetbury, UK) and grown to growth stage 10–11 (BBCH scale) prior to infestation. Infested plants were maintained in insect-rearing cages (47.5 × 47.5 × 47.5 cm; Bugdorm-4, Taichung, Taiwan), one cage per species, in a controlled environment chamber (20°C; 60% RH; L:D 16:8; Fitotron, Weiss Technik, Loughborough, UK). Fresh barley plants were added weekly and half of the previous week's pots removed to ensure continuous availability of young host material. After 12 weeks of population establishment, aphids were screened for barley yellow dwarf virus (BYDV-PAV, BYDV-MAV and BYDV-RPV) using a commercial DAS-ELISA kit (BIOREBA AG, Switzerland), which confirmed BYDV-PAV infection in the *R. padi* population. A virus-free *R. padi* population was subsequently established by transferring 10 adults from the infected population to clean potted barley in a separate cage and removing adults after 24 h, retaining only first-instar nymphs that had not acquired the virus. From this point, three populations were maintained in separate controlled environment chambers under identical conditions to prevent cross-contamination: BYDV-negative *S. avenae*, BYDV-negative *R. padi* and BYDV-PAV-positive *R. padi*. Viral status was confirmed monthly by DAS-ELISA. Before each block of the experiment began, age-synchronised cohorts were produced to ensure homogeneity in aphid age and to minimise potential confounding effects of crowding or feeding on heavily infested plants. Adults from stock populations were transferred onto clean barley plants and allowed to larviposit for 24 h, after which they were removed, leaving only first-instar nymphs. Nymphs were maintained under the same conditions as stock populations and monitored daily until they reached adulthood, which was approximately 7–8 days for *S. avenae* and 8–9 days for *R. padi*. Newly moulted adults were collected for experiments as soon as sufficient numbers were available.

2.2 | Plant material

Winter wheat (*Triticum aestivum* L.) plants were grown to the two-leaf stage (BBCH growth stage 12) in 35-cell plant trays (35 cm × 45 cm;

Yard, China) arranged as 7 rows (A–G) × 5 columns (1–5), with one plant per cell (4.5 cm cell spacing). Plants were grown in peat-free John Innes No. 2 compost (Sylva Grow®, Melcourt, Tetbury, UK) under glasshouse conditions (mean temperature: 20 ± 5°C day/10 ± 5°C night; 16:8 h L:D photoperiod). Trays were sub-irrigated using water-filled saucers checked every 2 days. Two cultivars were selected for use in experiments: (1) RGT Wolverine (R.A.G.T. Seeds Ltd., Saffron Walden, UK), a modern cultivar carrying the *Bdv2* gene conferring resistance to BYDV-PAV, and Maris Huntsman (released in 1972 by Plant Breeding Institute PBI, Cambridge, UK) a cultivar without known BYDV resistance and historically associated with high aphid infestations. RGT Wolverine seed was supplied by the breeder while Maris Huntsman seed was originally sourced from the Germplasm Resources Unit at John Innes Centre, UK, then maintained as part of a breeding programme and teaching resource at Harper Adams University.

Each 35-cell tray was assigned to one of four planting configurations prior to sowing, representing different crop management strategies: (1) Huntsman monoculture where all cells were sown with Maris Huntsman; (2) Wolverine monoculture where all cells were sown with RGT Wolverine; (3) Random mixture where both cultivars were distributed randomly within each tray in an approximate 1:1 ratio, with randomisation at the row level using R v4.4.0 to minimise clustering of a single cultivar; and (4) Intercropping where both cultivars were arranged in alternating rows within the tray. In the intercropping treatment, the cultivar identity of the central source plant (position D3, the release point) alternated between Maris Huntsman and RGT Wolverine across replicates to control for source plant identity effects. In the random mixture treatment, source plant cultivar identity varied according to the randomisation.

2.3 | Experimental design

Three separate experiments were completed to investigate the effects of crop genetic diversity and the spatial arrangement of cultivars on the walking dispersal of: (1) non-viruliferous *S. avenae*; (2) non-viruliferous *R. padi*; and (3) BYDV-PAV-viruliferous *R. padi*. Experiments were run sequentially; consequently, comparisons across experiments are qualitative only and no cross-experiment statistical tests were carried out. Each experiment followed a complete randomised block design with four blocks. Within each block, each of the four planting configurations was represented by three replicate trays, yielding 12 trays per block and 48 trays per experiment. At the start of each experiment, trays were transferred from the glasshouse to a polytunnel under semi-field conditions. Custom experimental cages were constructed from 60 L transparent plastic storage boxes (Wham Crystal, What More UK; 60 × 40 × 33 cm). Four 20 × 20 cm ventilation openings were cut into the sides of each box and covered with 680 µm polyester mesh to allow airflow while preventing aphid escape. Cages were inverted over plant trays with the open base positioned downward, enabling rapid removal and replacement without disturbing the experimental setup.

2.4 | Aphid release and monitoring

Wingless adult aphids were collected from age-synchronised cohorts using a fine paintbrush (size 000). Groups of 10 adults were released onto the central source plant (cell D3) and immediately isolated from the rest of the tray by inverting a clear plastic cup (12 cm height, 6 cm diameter at top, 4 cm diameter at base) over the plant. The base of the cup was removed and replaced with a fine-mesh organza bag (18 × 13 cm) secured with a rubber band to allow ventilation. Trays were enclosed under cages and left undisturbed for 24 h to allow aphids to settle on the central plant. Following this acclimation period, the plastic cups were removed from the central cell, enabling aphid dispersal across the tray. Aphid colonisation and dispersal were assessed at 1, 3, 5 and 7 days after release by carefully removing the cage and counting the aphids. Care was taken to not disturb the aphids and to minimise the time with the cage removed. We did not observe any aphid movement during this process. At each census, the number of adult aphids and nymphs on each of the 35 plants in the tray was recorded. The source plant (D3) was included in counts but excluded from dispersal analyses.

2.5 | Confirmation of viral status

At the end of each experimental block, DAS-ELISA was used to confirm the assigned BYDV status of aphid and plant samples from each tray. For monoculture trays, three leaves from different plants were collected per tray. For intercropping and random mixture trays, six leaves were collected per tray, comprising three leaves from each cultivar. Leaves were not necessarily restricted to aphid-occupied plants. Before plant sampling, 20–30 aphids of mixed ages were collected from each tray. For each ELISA plate, samples from the laboratory aphid populations and the positive and negative controls supplied with the kit were included. These assays were used to confirm tray-level aphid population status and plant infection status, rather than to determine the infection status of every individual plant. Plant samples were processed by grinding tissue at a 1:10 weight-to-volume ratio with extraction buffer prepared according to the manufacturer's specifications. Aphid samples were homogenised in extraction buffer, and plant and aphid extracts were aliquoted into ELISA microplates at 100 µL per well. Analysis was carried out following the manufacturer's protocol (BIOREBA, Reinach, Switzerland).

2.6 | Statistical analysis

All analyses were carried out in R v. 4.4.0 (R Core Team, 2024) using the glmmTMB package for generalised linear mixed models (GLMMs) (Brooks et al., 2017), the car package for Type II Wald χ^2 tests (Fox & Weisberg, 2019), the emmeans package for estimated marginal means (EMMs) and pairwise comparisons (Lenth & Piaskowski, 2025) and the DHARMa package for residual diagnostics (Hartig, 2024). Each experiment was analysed independently because experiments were carried

out sequentially; no cross-experiment statistical analyses were performed. Four complementary analyses were carried out to characterise treatment effects on dispersal extent, spatial gradients of colonisation, cultivar preference and nymph production. Planting configuration was treated as a fixed factor with four levels: Maris Huntsman monoculture, RGT Wolverine monoculture, intercropping and random mixture. Census day was treated as a fixed categorical factor with four post-release levels: 1, 3, 5 and 7 d.

The proportion of non-source plants colonised by at least one adult aphid was modelled at the tray level. The central source plant was excluded, resulting in 34 non-source plants per tray. The response was fitted as a two-column matrix of colonised and uncolonised plants using binomial or beta-binomial GLMMs with a logit link. Fixed effects comprised planting configuration, census day and their interaction. Random effects included block and tray identity, with tray identity included to account for repeated measurements of the same tray across census days. Where the beta-binomial model with both random effects failed to converge, a reduced model retaining only block as a random effect, or a standard binomial model with tray identity as a random effect, was fitted. All converged candidate models were compared by Akaike information criterion (AIC) and the best-fitting model was selected for inference. Overdispersion and distributional assumptions were assessed using DHARMa residual simulations with 1000 iterations.

To test whether planting configuration modified the spatial decay of colonisation from the source plant, a plant-level binomial GLMM was fitted with the presence or absence of adult aphids on each non-source plant as the response variable. Euclidean distance from the source plant, cell D3, was calculated from the grid coordinates and included as a continuous predictor. Fixed effects comprised planting configuration, distance from source, their interaction and census day as an additive effect. Random effects were block and tray identity, with tray identity included because plants were subsamples within trays and trays were repeatedly censused. The planting configuration × distance interaction was the key test; a significant interaction ($p < 0.05$, Wald test) indicated that the rate at which colonisation probability declined with distance differed among planting configurations. Distance-decay slopes on the logit scale were estimated for each planting configuration using the *emtrends* function. Slope contrasts were evaluated using unadjusted Wald tests. An extended model including a census day × distance interaction was fitted to test whether spatial gradients changed over the assessment period.

Cultivar preference was assessed within the random mixture treatment to avoid the cultivar–position confound inherent in the intercropping arrangement. A plant-level binomial GLMM was fitted with adult presence or absence as the response. Fixed effects comprised plant cultivar identity, census day and their interaction, with distance from source included as a covariate and source plant cultivar identity included as a factor. Random effects were block and tray identity. A supplementary analysis of the intercropping treatment was conducted for comparison, noting that cultivar identity was partially confounded with row position in this arrangement. Distance from source was omitted from the intercropping cultivar-preference model owing to collinearity with cultivar arrangement.

Nymph production on non-source plants was analysed at the tray level. Total nymph counts across the 34 non-source plants in each tray were modelled using negative binomial GLMMs with NB2 parameterisation (modelling variance quadratically rather than linearly (NB1) in terms of the mean) and a log link. Fixed effects comprised planting configuration, census day and their interaction, with block and tray identity included as random effects. DHARMa residual simulations were used to assess dispersion, uniformity and zero inflation. Zero inflation was assessed using *testZeroInflation*, which compares the observed number of zeros with the number expected under the fitted model. Where significant zero inflation was detected, a zero-inflated negative binomial model was fitted for comparison, and the model with the lower AIC was retained for inference if convergence and Hessian checks were satisfactory.

To determine whether treatment effects on nymph production reflected differences in the number of plants colonised or differences in aphid density on occupied plants, plant-level density summaries were calculated at the tray level. Source plants and non-source plants were summarised separately because the central source plant was included in the census counts but excluded from the dispersal analyses. For each tray and census day, we calculated the number of adults and nymphs on the source plant, the number of adult-occupied and nymph-bearing non-source plants, adults per adult-occupied non-source plant, nymphs per nymph-bearing non-source plant, nymphs per non-source plant, and whole-tray nymph abundance including the source plant. These summaries were calculated at the tray level to retain tray as the experimental unit and are reported as raw tray means ± SE.

Focused assessments were used to assess whether the lower non-source nymph counts observed in Maris Huntsman monocultures reflected lower nymph density on occupied plants. These analyses were restricted to BYDV-negative *R. padi* in Maris Huntsman and RGT Wolverine monocultures at days 5 and 7, because the treatment difference in non-source nymph production was evident from day 5 onwards and earlier census days contained too few nymph-bearing non-source plants for stable estimation of density on occupied plants. Source-plant nymph counts were analysed using a negative binomial GLMM with cultivar, census day and their interaction as fixed effects, block as a fixed effect and tray identity as a random effect. Nymph density on occupied non-source plants was assessed by modelling total non-source nymph counts with the log number of nymph-bearing non-source plants fitted as an offset, retaining tray as the experimental unit. Trays with no nymph-bearing non-source plants were excluded from this offset model because the density denominator was zero. Models were used for inference only where convergence, finite AIC, finite fixed-effect estimates and positive-definite Hessian checks were satisfied.

In mixture treatments, the cultivar onto which aphids were released varied across trays. To assess whether source plant identity influenced subsequent dispersal, the dispersal extent model was re-fitted for each experiment using only the random mixture and

intercropping treatments, with source plant cultivar included as an additional fixed-effect factor. This restriction avoided aliasing between source cultivar and planting configuration in monoculture trays. Model fit with and without this factor was compared by AIC, and the significance of the planting-configuration effect was re-evaluated after adjustment for source cultivar.

Inference focused on planned comparisons aligned with the experimental hypotheses, particularly Maris Huntsman versus RGT Wolverine monocultures, mixture treatments versus monocultures, and source-cultivar effects in mixture trays. EMMs and contrasts were calculated on the response scale where appropriate. Contrasts were evaluated using unadjusted Wald tests, with no multiple-comparison adjustment applied. For all GLMMs, Type II Wald χ^2 tests were used to test fixed effects. As there were only four blocks, the dispersal extent model was also re-fitted for each experiment with block treated as a fixed (taking up 3 degrees of freedom, df) rather than a random effect (1 df), retaining tray identity as a random effect.

3 | RESULTS

3.1 | Confirmation of BYDV status by DAS-ELISA

DAS-ELISA confirmed that aphid population status matched the assigned experimental treatments. Aphid samples from BYDV-PAV-positive *R. padi* treatments tested positive, whereas aphid samples from BYDV-negative *S. avenae* and *R. padi* treatments tested negative. Plant assays were consistent with cultivar resistance status. BYDV-PAV was detected in susceptible Maris Huntsman tissue from BYDV-positive treatments, while no BYDV-PAV was detected in RGT Wolverine tissue irrespective of aphid population status. Plant samples from BYDV-negative treatments tested negative.

3.2 | Colonisation of non-source plants

The proportion of non-source plants colonised by adult aphids increased over time in all three experiments (Figure 1). For *S. avenae*, colonisation was unaffected by planting configuration ($\chi^2_3 = 1.01$, $p = 0.80$, Wald test), reaching 12–15% of non-source plants by day 7 across all treatments (Figure 1a). BYDV-negative *R. padi* showed a different response, with planting configuration significantly affecting colonisation ($\chi^2_3 = 11.57$, $p = 0.009$, Wald test; Figure 1b). Averaged across post-release census days, colonisation on Huntsman monocultures (2.0%) was approximately one-third that on Wolverine monocultures (6.0%; OR = 0.31, $p = 0.003$, Wald test) and intercropping (5.8%; OR = 0.32, $p = 0.005$, Wald test), equivalent to a 67–69% reduction relative to these treatments. This difference widened over time: by day 5, colonisation on Wolverine (7.3%) was 5.5-fold that on Huntsman (1.3%; $p < 0.001$, Wald test), representing an 82%

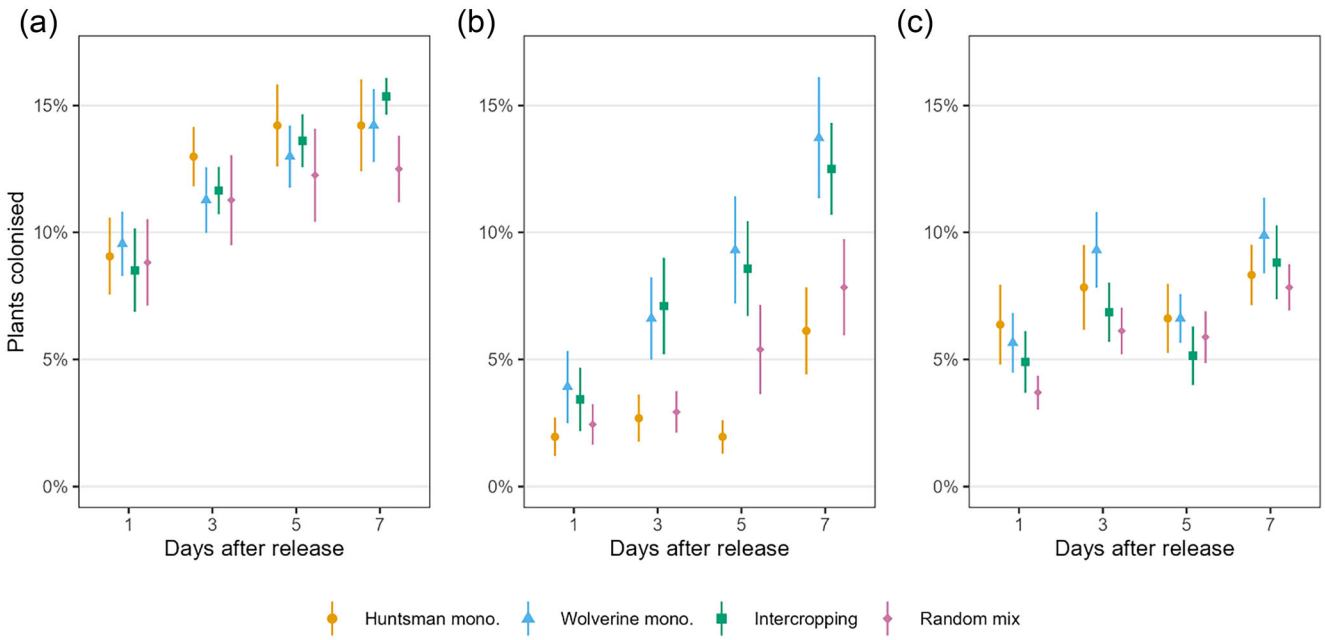

FIGURE 1 Effect of planting treatment on the proportion of non-source plants colonised by adult cereal aphids over time. Aphids were released onto a single central plant in 7 × 5 cell trays (35 plants per tray) containing wheat cultivars Maris Huntsman and RGT Wolverine arranged as monocultures, alternating-row intercropping, or randomised mixtures. Points show treatment means and vertical bars show ±1 SE of the proportion of non-source plants ($n = 34$ per tray) on which at least one adult was recorded at each census day ($n = 12$ trays per treatment per time point). Colonisation was analysed using beta-binomial or binomial GLMMs with treatment, day and treatment × day as fixed effects, and block and tray as random effects; model selection was based on AIC. (a) *Sitobion avenae* (non-viruliferous), (b) *Rhopalosiphum padi* (non-viruliferous), (c) *R. padi* (BYDV-PAV viruliferous). Experiments were conducted sequentially; y-axes are shared to facilitate qualitative comparison across species and virus status.

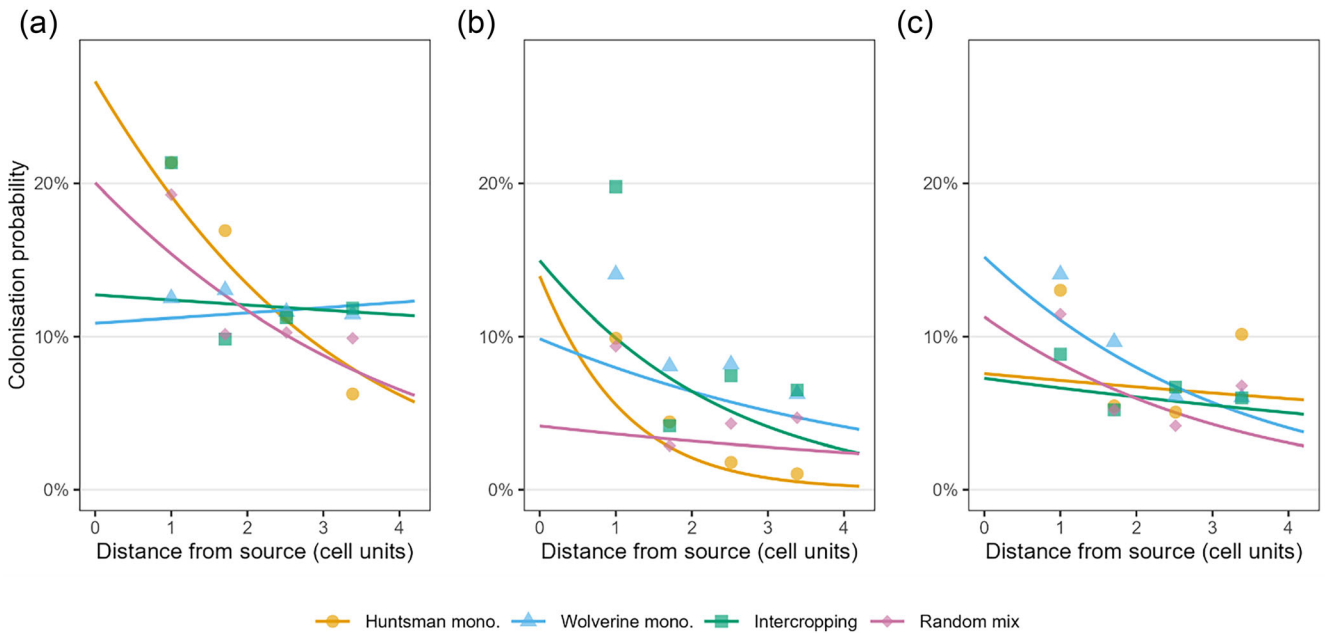

FIGURE 2 Distance-decay of adult colonisation probability from the source plant. Lines show population-level predictions from binomial GLMMs fitted to plant-level presence/absence data with treatment, distance from source and treatment × distance as fixed effects, day as an additive fixed effect, and block and tray as random effects. Predictions are averaged across census days. Points show observed proportions of plants colonised within concentric distance rings (0–1, 1–2, 2–3 and >3 cell units from the source), collapsed across days 1–7. One cell unit = 4.5 cm. A significant treatment × distance interaction ($p < 0.05$, Wald test) indicates that the spatial gradient of colonisation differs among planting treatments. (a) *Sitobion avenae* (non-viruliferous), (b) *Rhopalosiphum padi* (non-viruliferous), and (c) *R. padi* (BYDV-PAV viruliferous).

reduction on Huntsman relative to Wolverine. The random mix (3.0%) was intermediate and did not differ significantly from either monoculture ($p > 0.005$, Wald test). For viruliferous *R. padi*, colonisation did not differ among treatments ($\chi^2_3 = 2.45$, $p = 0.48$, Wald test; Figure 1c), with marginal means ranging from 5.4% in the random mix to 7.3% in Wolverine monocultures.

3.3 | Spatial gradient of colonisation

Plant-level colonisation probability declined with distance from the source plant in all experiments, but the rate of decline was treatment-dependent. For *S. avenae*, the treatment × distance interaction was significant ($\chi^2_3 = 16.39$, $p < 0.001$, Wald test; Figure 2a). On Huntsman monocultures, colonisation declined by approximately 35% per unit distance from the source ($\beta = -0.43 \pm 0.09$), whereas on Wolverine ($\beta = 0.03 \pm 0.10$) and in the intercropping treatment ($\beta = -0.03 \pm 0.09$), colonisation probability was spatially uniform. The Huntsman slope differed significantly from Wolverine ($p < 0.001$, Wald test) and intercropping ($p = 0.003$, Wald test), but not from the random mix ($\beta = -0.32 \pm 0.10$;$p = 0.430$, Wald test). The same interaction was significant for BYDV-negative *R. padi* ($\chi^2_3 = 15.01$, $p = 0.002$, Wald test; Figure 2b). The Huntsman monoculture showed a steep distance-decay ($\beta = -1.01 \pm 0.20$), corresponding to a 64% decline in colonisation probability per unit distance; aphids were overwhelmingly concentrated on and immediately around the source plant. By contrast, the decline per unit distance was only 21% on Wolverine ($\beta = -0.23 \pm 0.11$), 38% in the intercropping treatment ($\beta = -0.47 \pm 0.12$), and 13% in the random mix ($\beta = -0.14 \pm 0.15$), representing 4.4-fold, 2.2-fold and 7.2-fold shallower gradients, respectively. Slope contrasts confirmed that Huntsman differed from Wolverine ($p < 0.001$, Wald test), intercropping ($p = 0.019$, Wald test) and the random mix ($p < 0.001$, Wald test). For viruliferous *R. padi*, the treatment × distance interaction was not significant ($\chi^2_3 = 5.09$, $p = 0.17$, Wald test; Figure 2c). Distance-decay slopes were shallow across all treatments, ranging from -0.07 ± 0.12 on Huntsman to -0.36 ± 0.12 on Wolverine, corresponding to declines of 7–30% per unit distance. The day × distance interaction was not significant in any experiment (all $p > 0.49$, Wald tests), indicating that spatial gradients were stable over the assessment period.

3.4 | Cultivar preference within random mixtures

Sitobion avenae preferentially colonised Huntsman over Wolverine plants within the random mix treatment ($\chi^2_1 = 8.04$, $p = 0.005$, Wald test; Figure 3a). Huntsman plants were 55% more likely to be colonised than Wolverine overall (OR = 1.55, $p = 0.007$, Wald test), with estimated marginal colonisation probabilities of 12.5 ± 1.7% and 8.5 ± 1.3%, respectively. This preference strengthened over time: by day 5, estimated colonisation probabilities were 15.3 ± 2.9% on Huntsman and 8.1 ± 2.1% on Wolverine, with the odds of colonising Huntsman 2.1x those for Wolverine ($p = 0.024$, Wald test). By day 7, estimated colonisation probabilities were 15.2 ± 2.9% and 8.6

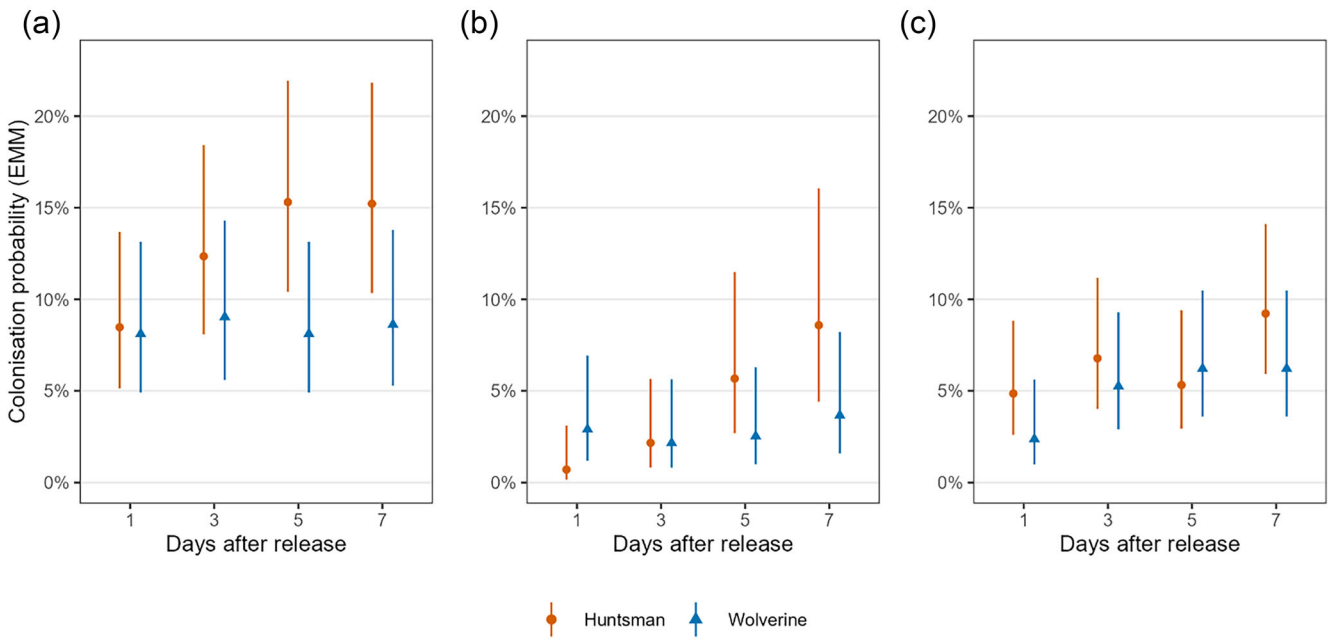

FIGURE 3 Cultivar preference of adult aphids within the randomised mixture treatment. Points show estimated marginal mean colonisation probability (±95% asymptotic confidence intervals) for plants of each cultivar at each census day, derived from binomial GLMMs fitted to plant-level presence/absence data with cultivar, day and cultivar × day as fixed effects, distance from source and source plant cultivar identity as covariates, and block and tray as random effects. Analysis was restricted to the random mix treatment to avoid the cultivar–position confound present in the intercropping arrangement. (a) *Sitobion avenae* (non-viruliferous), (b) *Rhopalosiphum padi* (non-viruliferous), and (c) *R. padi* (BYDV-PAV viruliferous).

± 2.1%, respectively, with the odds of colonising Huntsman 1.9× those for Wolverine ($p = 0.039$, Wald test). A consistent pattern was observed in the intercropping treatment ($\chi^2_1 = 11.07$, $p < 0.001$, Wald test), although the confounding of cultivar with row position limits interpretation. Source plant cultivar did not influence colonisation ($p = 0.79$, Wald test). For BYDV-negative *R. padi*, the cultivar × day interaction was significant ($\chi^2_3 = 7.99$, $p = 0.046$, Wald test; Figure 3b), reflecting an emerging preference for Huntsman over time. At day 1, there was no clear preference. By day 7, Huntsman plants were 2.5× more likely to be colonised than Wolverine, with estimated colonisation probabilities of 8.6 ± 2.9% and 3.7 ± 1.5%, respectively ($p = 0.026$, Wald test). The marginal cultivar effect averaged across all days was not significant (OR = 1.08, $p = 0.79$), indicating that the preference was time-dependent. In the intercropping treatment, cultivar identity had no effect ($p = 0.36$, Wald test), but source plant cultivar was highly significant ($\chi^2_1 = 14.11$, $p < 0.001$, Wald test). Aphids released on Wolverine were 3.3× more likely to colonise surrounding plants, a 230% increase in colonisation probability relative to those released on Huntsman. Viruliferous *R. padi* showed no cultivar preference in random mixtures (variety: $\chi^2_1 = 1.69$, $p = 0.19$, Wald test; variety × day: $\chi^2_3 = 1.94$, $p = 0.59$, Wald test; Figure 3c). Estimated marginal colonisation probabilities averaged across days were 6.4 ± 0.9% on Huntsman and 4.7 ± 0.8% on Wolverine. At day 7, the corresponding estimates were 9.2 ± 2.1% and 6.2 ± 1.7%. In the intercropping treatment, however, Huntsman was preferentially colonised ($\chi^2_1 = 9.89$, $p = 0.002$, Wald test), and source cultivar was again significant ($\chi^2_1 = 4.31$, $p = 0.038$, Wald test).

3.5 | Nymph production on non-source plants and plant-level density

Total nymph counts increased over the seven-day assessment period in all experiments (all $p < 0.001$, Wald tests; Figure 4). For *S. avenae*, nymph production did not differ among treatments ($\chi^2_3 = 1.55$, $p = 0.67$, Wald test), with estimated means at day 7 ranging from 32.1 ± 4.9 nymphs per tray in the random mix to 39.5 ± 5.9 in the intercropping treatment, a difference of <25%. BYDV-negative *R. padi* showed a significant treatment effect ($\chi^2_3 = 8.90$, $p = 0.031$, Wald test; Figure 4b), with a marginally non-significant treatment × day interaction ($\chi^2_9 = 16.86$, $p = 0.051$, Wald test). Nymph production on Huntsman monocultures was markedly lower than on all other treatments: by day 5, estimated nymph counts on Huntsman were 1.28 ± 0.58 per tray, 87% lower than on Wolverine (9.92 ± 3.96; ratio = 0.13, $p = 0.001$, Wald test) and 83% lower than in the intercropping treatment (7.64 ± 3.08; ratio = 0.17, $p = 0.004$, Wald test). Plant-level density summaries identified the basis of this treatment effect (Table S1). For BYDV-negative *R. padi*, the lower nymph production recorded on non-source plants in Huntsman monocultures reflected restricted spread across the tray rather than reduced nymph density on occupied plants. By day 5, Huntsman monocultures contained 0.75 ± 0.22 nymph-bearing non-source plants per tray, compared with 3.83 ± 0.81 in Wolverine monocultures. By day 7, the corresponding values were 3.33 ± 1.02 and 7.92 ± 1.33 nymph-bearing non-source plants per tray. However, nymph density on nymph-bearing non-source plants was similar between Huntsman and Wolverine monocultures at day 5 (5.29 ± 1.49 vs. 4.36

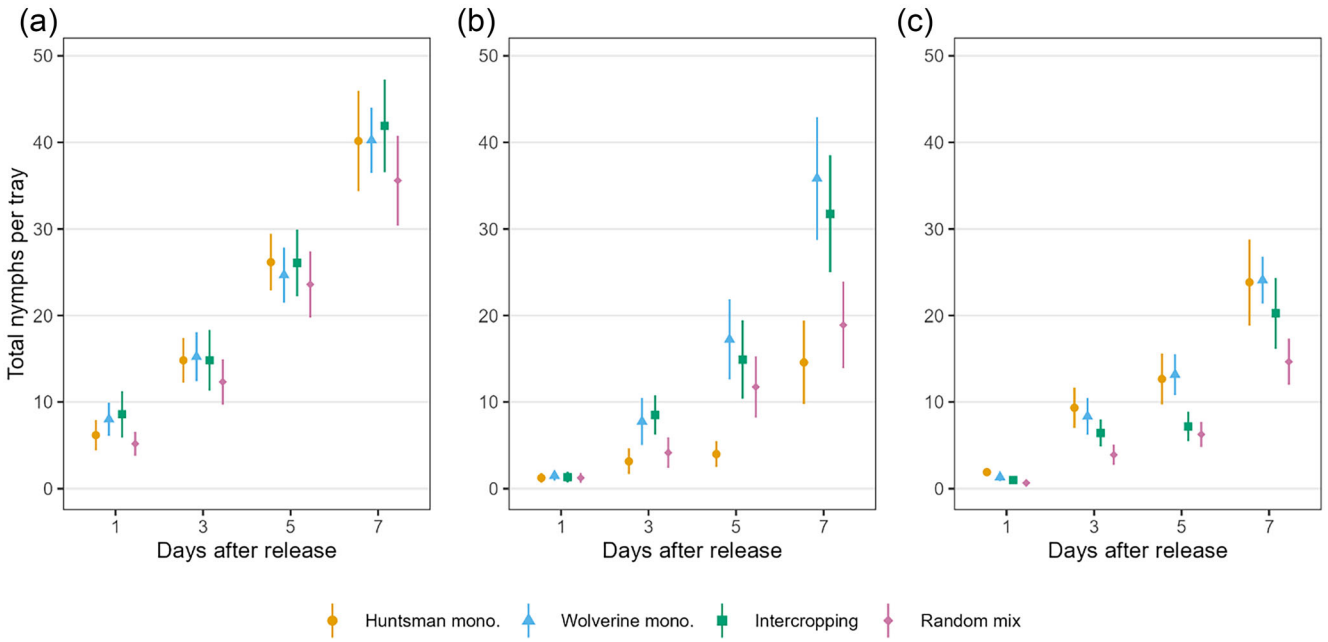

FIGURE 4 Effect of planting treatment on nymph production on non-source plants over time. Points show treatment means and vertical bars show ±1 SE of total nymph counts on the 34 non-source plants in each tray at each census day ($n = 12$ trays per treatment per time point). Nymph counts were analysed using negative binomial GLMMs (NB2 parameterisation) with treatment, day and treatment × day as fixed effects and block and tray as random effects. Where DHARMa diagnostics indicated significant zero-inflation, a zero-inflated negative binomial model was fitted for comparison. (a) *Sitobion avenae* (non-viruliferous), (b) *Rhopalosiphum padi* (non-viruliferous), and (c) *R. padi* (BYDV-PAV viruliferous).

± 0.45 nymphs per plant) and day 7 (4.46 ± 1.32 vs. 4.37 ± 0.41 nymphs per plant). A focused offset model identified no effect of cultivar on nymph density on nymph-bearing non-source plants ($\chi^2_1 = 0.06$, $p = 0.808$, Wald test). Source-plant counts showed a complementary pattern. Huntsman source plants retained more adults than Wolverine source plants at day 5 (7.50 ± 0.56 vs. 4.08 ± 0.89 adults per plant) and day 7 (6.58 ± 0.63 vs. 2.00 ± 0.87 adults per plant). Source-plant nymph counts were also higher on Huntsman than Wolverine, with a significant cultivar × day interaction ($\chi^2_1 = 6.31$, $p = 0.012$, Wald test). Source-plant nymph counts were 47.1 ± 3.64 on Huntsman and 33.9 ± 2.77 on Wolverine at day 5, increasing to 70.3 ± 5.16 and 40.9 ± 3.24, respectively, by day 7. Whole-tray nymph abundance including the source plant was therefore similar between Huntsman and Wolverine monocultures at day 5 (51.75 ± 2.71 vs. 53.17 ± 4.38 nymphs per tray) and day 7 (85.83 ± 4.74 vs. 79.17 ± 5.93 nymphs per tray). Viruliferous *R. padi* showed no clear treatment effect on nymph production on non-source plants ($\chi^2_3 = 6.31$, $p = 0.098$, Wald test; Figure 4c), and there was no treatment × day interaction ($\chi^2_9 = 6.54$, $p = 0.684$, Wald test). Nymph production increased strongly over time ($\chi^2_3 = 384.82$, $p < 0.001$, Wald test). By day 7, estimated nymph counts ranged from 11.54 ± 2.95 in the random mix to 22.68 ± 5.58 in Wolverine monocultures, but the Huntsman–Wolverine comparison was not significant (ratio = 0.76, $p = 0.427$, Wald test).

3.6 | Source plant cultivar identity

In mixture treatments, the cultivar onto which aphids were released influenced subsequent dispersal of *R. padi* but not *S. avenae*. For *S. avenae*, source cultivar did not affect colonisation ($\chi^2_1 = 0.58$, $p = 0.445$, Wald test), with estimated colonisation probabilities of 10.9 ± 0.9% from Huntsman source plants and 12.0 ± 1.2% from Wolverine source plants. For both *R. padi* experiments, aphids released onto Wolverine colonised surrounding plants at significantly higher rates than those released onto Huntsman. In the BYDV-negative experiment, colonisation was 7.7 ± 1.4% from Wolverine source plants compared with 2.6 ± 0.6% from Huntsman source plants ($\chi^2_1 = 15.82$, $p < 0.001$, Wald test). In the BYDV-positive experiment, colonisation was 7.5 ± 0.8% from Wolverine source plants compared with 4.4 ± 0.6% from Huntsman source plants ($\chi^2_1 = 10.50$, $p = 0.001$, Wald test). When included as a factor in the dispersal extent models, source cultivar improved model fit for both *R. padi* experiments, and the treatment effect was no longer significant after this adjustment ($p = 0.26$ and $p = 0.19$, Wald tests). This indicates that cultivar suitability at the point of release, rather than the surrounding planting configuration, was the primary driver of *R. padi* dispersal in mixture treatments.

4 | DISCUSSION

This study identified that the dispersal responses of cereal aphids to wheat cultivar and planting configuration are driven by three interacting factors: (1) aphid species, (2) host plant cultivar and (3) BYDV infection status of the vector. Critically, the cultivar-specific effects observed for non-viruliferous *R. padi* were absent in viruliferous individuals while *S. avenae* showed minimal sensitivity to cultivar or configuration across all experiments. Together, these findings challenge

the assumption that cultivar mixture benefits generalise across vector species and infection states, with important implications for BYDV management.

S. avenae colonised non-source plants at comparable rates across all treatments, suggesting that walking dispersal in this species is relatively indiscriminate with respect to cultivar arrangement. By contrast, non-viruliferous *R. padi* showed a 67–69% reduction in colonisation on Maris Huntsman monocultures relative to RGT Wolverine, increasing to 82% by day 5. This species-specific divergence is consistent with the known differences in host utilisation between these taxa outlined in the Introduction, whereby broad cultivar acceptance in *S. avenae* contrasts with the stronger cultivar-specific responses of *R. padi* (Gianoli, 2000; Hesler et al., 1999; Leather & Dixon, 1984; Watt, 1979). The contrasting dispersal phenotypes observed here demonstrate that the efficacy of cultivar-based management will depend not only on the resistance profile of the cultivars deployed but also on the target vector species. The absence of a treatment effect on *S. avenae* nymph production indicates that cultivar identity exerts minimal bottom-up control over *S. avenae* population growth under these experimental conditions, and that management of this species requires alternative approaches. On Maris Huntsman monocultures, non-viruliferous *R. padi* exhibited a sharp spatial gradient in colonisation, declining by 64% per unit distance from the source plant by day 5. We interpret this pattern as evidence of rapid arrestment on a preferred host: aphids that encounter Maris Huntsman accept the plant readily and cease exploratory movement, resulting in high colonisation density near the release point and progressively fewer individuals reaching distant positions. This is supported by the mixture experiments, in which *R. padi* preferentially colonised Maris Huntsman over Wolverine, with the preference emerging progressively over the seven-day assessment period. The direction of this preference, towards the 1970s cultivar, suggests that Maris Huntsman functions as the more acceptable host and that the steep distance-decay in monoculture reflects strong host acceptance rather than deterrence. On Wolverine monocultures, by contrast, colonisation was spatially uniform, indicating that aphids moved freely across multiple plant positions without arresting. The distinction between arrestment on a preferred host and antixenotic deterrence by a resistant host is mechanistically important as both produce a steep spatial gradient in colonisation, but they imply opposite host–vector relationships and lead to fundamentally different predictions for mixture performance.

Despite the strong evidence for host preference, Maris Huntsman monocultures supported fewer nymphs than the other treatments on non-source plants by day 5. At the tray level, this could be interpreted in two ways. First, it could represent a spatial-demographic effect in which adults arrest near the source plant, concentrating reproduction on very few plants and reducing the number of nymphs recorded on surrounding non-source plants. Alternatively, preference and performance could be partially decoupled, with *R. padi* accepting Maris Huntsman readily for settling and probing but experiencing reduced reproductive output owing to differences in phloem composition, sieve element accessibility or secondary metabolite profiles (Prado & Tjallingii, 2007; Züst & Agrawal, 2016). Such mismatches between preference and performance are well documented in aphid–plant systems (Gripenberg et al., 2010), although previous work with these cultivars suggests that this is unlikely to be the primary explanation here (Leandro et al., 2025).

The plant-level density analysis supports the spatial-demographic explanation rather than a preference–performance mismatch. In BYDV-negative *R. padi*, lower nymph production on non-source plants in Huntsman monocultures reflected reduced spread across the tray and concentration of aphids on the source plant. Nymph density on nymph-bearing non-source plants was not lower on Huntsman than on Wolverine, and whole-tray nymph abundance including the source plant was comparable between the two monocultures. Thus, the reduced non-source nymph counts on Huntsman do not indicate that Maris Huntsman is a poorer reproductive host. Instead, they show that adults remained on or near the preferred source plant, fewer surrounding plants were colonised, and reproduction was spatially concentrated at the release point. This distinction is important because Maris Huntsman lacks BYDV resistance genes and has been historically associated with high aphid infestations (Lowe, 1982), but this does not mean that aphid population growth should be distributed uniformly across all plant positions in a dispersal arena. We cannot exclude subtle cultivar effects on per-capita fecundity because adults were not individually confined and nymphs could not be assigned to individual mothers, but the available plant-level data provide no evidence that Maris Huntsman reduces nymph density on occupied plants.

The mixture treatments disrupted this spatial concentration effect. In randomised mixtures, neither *S. avenae* nor non-viruliferous *R. padi* showed the steep distance-dependent colonisation decline characteristic of Maris Huntsman monocultures; instead, colonisation was spatially uniform in a pattern resembling Wolverine monocultures. We propose that Wolverine plants within the mixture function as "stepping stones" that disrupt the arrestment process: aphids that walk to a Wolverine plant fail to arrest, continue moving and thereby reach positions that would have been less frequently colonised in a pure Maris Huntsman stand. This aligns with the framework of Hambäck et al. (2014), who proposed that diluting one genotype with another can negate the benefits of the dominant cultivar by creating corridors for pest movement, although in our system the mechanism is the interruption of arrestment on a preferred host rather than the dilution of a resistant one. The source plant identity effect reinforced this interpretation: aphids released on Wolverine colonised surrounding plants at 178% higher rates than those released on Maris Huntsman, indicating that *R. padi* actively emigrates from Wolverine. This is consistent with Wolverine being a less preferred host and potentially with *Bdv2*-mediated resistance conferring secondary effects on the vector itself, even in the absence of virus (Aradottir & Crespo-Herrera, 2021; Leandro et al., 2025).

Together, these results indicate that the Maris Huntsman–Wolverine mixture did not function as a system of associational resistance. For non-viruliferous *R. padi*, the mixture created associational susceptibility relative to the low-dispersal Maris Huntsman monoculture because the inclusion of Wolverine as an emigration source,

combined with Maris Huntsman as a preferred settling destination, increased overall dispersal and colonisation. For *S. avenae*, cultivar arrangement produced no detectable suppression, indicating that mixture effects did not generalise across vector species. This adds to growing evidence that the pest-suppressive potential of cultivar mixtures depends critically on the specific functional traits of the component cultivars and their interactions, rather than being a universal property of diversity (Barot et al., 2017; Mansion-Vaquié et al., 2019; Mansion-Vaquié et al., 2020; Tooker & Frank, 2012). Moreover, for specialist phloem-feeders dispersing by walking within established stands, the relevant scale of host-finding is the individual plant rather than the field, and physical proximity of suitable and unsuitable hosts becomes the critical determinant of dispersal outcome. When the preferred host is interspersed with a less preferred cultivar, the mixture does not reduce host-finding efficiency but instead disrupts the arrestment process that would otherwise concentrate aphids on the nearest acceptable plant.

BYDV-PAV-viruliferous aphids colonised non-source plants at uniformly high rates regardless of cultivar arrangement, showed no distance-dependent decline in colonisation and exhibited no cultivar preference within mixtures. This contrasts sharply with the cultivar-specific responses of non-viruliferous *R. padi* and is consistent with the prediction of the Vector Manipulation Hypothesis that virus infection should promote a dispersal phenotype favouring inoculation of new hosts (Ingwell et al., 2012; Mauck et al., 2018). Critically, the uniform, distance-independent dispersal observed here extends existing evidence from binary-choice assays (Ingwell et al., 2012) to a spatially explicit, multi-plant arena, demonstrating that BYDV-PAV infection promotes a restless, exploratory phenotype in which aphids move extensively without settling, regardless of cultivar. In the context of our arrestment interpretation, BYDV infection appears to abolish the host-acceptance response that normally causes *R. padi* to arrest on Maris Huntsman. This is consistent with the finding that viruliferous aphids carrying turnip yellows virus exhibited enhanced locomotor activity and that post-acquisition effects on vector behaviour exceeded plant-mediated pre-acquisition effects (Chesnais et al., 2020). These results suggest that virus manipulation of vector dispersal operates at a level that overrides cultivar-specific host-acceptance cues.

The loss of cultivar effects under viruliferous conditions has direct implications for BYDV management. If the restless dispersal phenotype of viruliferous *R. padi* prevents arrestment on any cultivar and promotes movement to uninfected plants irrespective of host identity, then cultivar mixtures incorporating BYDV-resistant and susceptible genotypes may be less effective at constraining secondary virus spread than predicted from aphid performance data alone. In a mixture context, the enhanced dispersal of viruliferous vectors could increase inoculation events on susceptible neighbours, potentially offsetting the benefit of reduced virus replication in resistant plants. This scenario aligns with McElhany et al. (1995), who found that the epidemiological outcome of cultivar deployment depends critically on whether vectors discriminate between host genotypes after virus acquisition. The mechanisms underlying the cultivar effects on non-viruliferous *R. padi* dispersal remain to be elucidated but may involve volatile-mediated plant–plant interactions. The absence of a mixture benefit for aphid suppression in our system, and the facilitation of dispersal through mixtures, suggests that the Maris Huntsman–Wolverine combination does not produce the favourable allelobiotic interactions reported for certain barley cultivar pairings (Dahlin et al., 2018; Ninkovic et al., 2002). Moreover, if the cultivar effects on non-viruliferous *R. padi* are primarily driven by contact-mediated host acceptance rather than volatile-mediated orientation, VOC-based mixture effects may be of secondary importance. The viruliferous result suggests that any host-acceptance response, whether volatile- or contact-mediated, is rendered functionally irrelevant once virus-induced behavioural modification occurs. Future work should characterise the VOC profiles of these cultivars and test whether alternative pairings produce synergistic resistance responses that prove more robust to viruliferous-vector override.

Several methodological considerations qualify these findings. First, our experimental system measured ambulatory dispersal within seed trays, representing only one component of within-crop movement; alate dispersal over longer distances may be subject to different selective pressures and cultivar cues (Powell et al., 2006; Webster, 2012). Second, the use of seedling-stage wheat means that cultivar effects may differ at later growth stages when plant architecture, phloem composition and volatile emission profiles change substantially (Pettersson et al., 1994). To address this, field-scale studies across the growing season will be needed to determine whether the patterns observed here scale to agronomic conditions. Third, the absence of natural enemies precludes assessment of top-down effects that may differ between monocultures and mixtures and that could interact with the bottom-up cultivar effects documented here (Cook-Patton et al., 2011; Markovic et al., 2025). Our results demonstrate that the dispersal responses of cereal aphids to wheat cultivar and planting configuration are species-specific, cultivar-dependent and fundamentally altered by BYDV infection status. The rapid arrestment of non-viruliferous *R. padi* on Maris Huntsman monocultures was the single most effective configuration for limiting dispersal, but this advantage was systematically eliminated both by the inclusion of Wolverine as a mixture component and by BYDV-PAV infection of the vector. The finding that viruliferous *R. padi* disperse uniformly regardless of cultivar arrangement challenges the assumption that cultivar mixtures will provide consistent protection against virus spread. These findings underscore the need for vector species- and virus status-specific approaches to the deployment of cultivar mixtures for BYDV management and suggest that the interaction between cultivar-mediated host acceptance and virus-mediated behavioural manipulation is a critical but underexplored determinant of mixture efficacy.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in dispersal responses of cereal aphids at https://doi.org/10.6084/m9.figshare.31872928.

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