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Differential Varietal Responses in Faba Bean Concerning Pea Aphid and *Pea Necrotic Yellow Dwarf Virus* (PNYDV) When Intercropped With Oat

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ABSTRACT

The pest status of pea aphid (*Acyrthosiphum pisum* H.) in faba bean (*Vicia faba* L.) cultivation has gained importance because it transmits *Pea necrotic yellow dwarf virus* (PNYDV), a novel nanovirus in Europe. This study evaluated two faba bean varieties, 'Fuego' and 'GL Sunrise', grown under sole crop (SC) and intercrop (IC) conditions with oat (*Avena sativa* L.) to assess their response to biotic stress by vector infestation and PNYDV infection. In a 2-year field experiment (2021–2022), an additive, alternate row design with infector rows in each plot receiving regular releases of viruliferous *A. pisum* was used. 'GL Sunrise' consistently had lower aphid infestations than 'Fuego' in both cropping systems. Furthermore, intercropping with oat reduced vector movement due to the row barrier effect. In 2021, PNYDV was absent, so aphid pressure mainly resulted in nutrient depletion, with minor effects on nitrogen fixation and yield. Land equivalent ratios (LER) were slightly below 1.0. In 2022, PNYDV infection compounded by heat and drought led to a significant reduction in symbiotic N-fixation and yield of *V. faba* in SC systems. In IC systems, the oat component benefited from the reduced competitiveness of both stressed *V. faba* varieties, and this additional oat yield resulted in LER values above 1.0. The IC system thus ensured a lower spread of aphids and PNYDV and greater yield stability. Due to the only moderate agronomic performance of GL Sunrise under Central German growing conditions, a further screening for stress-tolerant faba bean genotypes is recommended.

1 | Introduction

Leguminous crops are becoming increasingly important as plants that contribute to the supply of protein from local production. In Germany, faba bean is used to feed livestock (Geisler 1991) and is one of the most important sources of biological nitrogen fixation, forming associations with bacteria, increasing nitrogen reserves in the soil for subsequent crops (Corre-Hellou et al. 2011; Jensen 1996; Jensen et al. 2010). The faba bean cultivation area has increased approximately fourfold over the past 10 years, reaching 61700 ha in 2024 (Statistisches Bundesamt 2025). However, leguminous crops are exposed to biotic and abiotic stressors that cause strong yield fluctuations.

Aphids are particularly important stressors, causing both direct feeding damage to plants and indirect damage through the transmission of viral diseases. Over 30 different viral diseases can be transmitted by *Acyrthosiphum pisum* H (Dubnik 1991), which is probably a major vector of *pea necrotic yellow dwarf virus* (PNYDV) according to Ziebell (2017). A decade ago, this new virus spread epidemically in Central Europe, particularly in Germany and Austria, causing significant losses to legumes, especially faba beans and peas (Gaafar et al. 2016). PNYDV is not a seed-borne virus and initial infestations in spring-sown faba bean are usually established by alighting viruliferous winged spring migrants entering from perennial legumes (Ziebell 2016) during their spring flight (Moericke 1954). Such primarily

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infected plants become stunted and chlorotic and later turn black, resulting in plant death. Developing aphid progeny then spread towards neighbouring plants in the perimeter, where the infected plants appear later as yellowish foci, scattered within the unaffected main field (Saucke, Uteau, et al. 2019).

PNYDV often occurs alongside other viruses, particularly *pea enation mosaic virus* (PEMV) (Saucke, Seeger, et al. 2019), *bean leafroll virus* (BLRV) (Krüssel and Zahn 2018; Kumari and Makkouk 2007), potyvirus, and recently *alfalfa mosaic virus* (Bröker et al. 2026). The severity and timing of viral infections significantly impact yield, with earlier infections leading to greater losses (Krüssel and Zahn 2018; Seeger et al. 2022; Van Emden and Harrington 2017). Abiotic factors, particularly temperature, also influence both directly and indirectly the severity of virus infections. Due to climate change, particularly after warm winters, an earlier flight of vectors becomes more frequent (Habekuß et al. 2009; Harrington et al. 2007), resulting in early viral infections and substantial crop losses (Krüssel and Zahn 2018; Ziebell 2017).

Recently, intercropping (bi-cropping) systems, particularly combining grain legume with cereals, have been increasingly adopted (Gronle et al. 2015). These systems offer multiple agronomic advantages, such as 'overyielding', which is commonly quantified using the land equivalent ratio (LER) (Jensen et al. 2015; Klimek-Kopyra et al. 2015). The LER measures land-use efficiency in intercropping compared to sole cropping: a value >1 indicates that intercropping produces a higher total yield and is more resource-efficient, whereas a value <1 indicates that sole cropping is more productive. Because of these benefits, intercropping has recently been promoted by government initiatives (DAFA 2024). Projects such as 'IntercropVALUES' (https://intercropvalues.eu) and 'VORWERTS' (https://vorwerts-projekt.de) address technical challenges during both harvest and post-harvest processing also, highlighting the considerable regional organic value chains and ecological potential of cereal–legume intercrops in northern Hesse. Thus, growing faba bean simultaneously with oats in the same field contributes to improved weed control (Auferkamp 2018) and crop stabilization (Dhima et al. 2014). In faba bean (*Vicia faba* L.), nitrogen acquisition—referred to here as the 'N-economy'—includes both symbiotic atmospheric nitrogen fixation and soil nitrogen uptake (Sinclair and Vadez 2002; Unkovich et al. 2008). Evaluating the N-economy allows assessment of how biotic stressors, such as aphid vectors and *Pea necrotic yellow dwarf virus* (PNYDV), affect nitrogen use efficiency, crop performance and productivity. This concept is particularly relevant in sole and intercrop systems, where varietal differences and interspecific interactions can influence overall nitrogen dynamics and yield outcomes. In terms of crop protection, functional crop diversification is expected to affect colonization by aphids which is traditionally discussed in the context of resource- and/or natural enemies hypothesis (Risch 1983). However, little is known about IC in plant–PNYDV–vector relationships probably reducing PNYDV-infections (Fischl et al. 2020; Grausgruber-Gröger and Moyses 2021). Furthermore, the selection of faba bean cultivars was based on their contrasting responses to *Pea necrotic yellow dwarf virus*. The cultivar 'Fuego', which is commonly grown in northern Hesse, is known to be susceptible to PNYDV, whereas 'GL Sunrise' has shown comparatively lower virus symptom expression in field trials, likely due to reduced secondary plant-to-plant spread (Seeger et al. 2022). This contrast makes the two cultivars particularly suitable for evaluating varietal differences in virus dynamics and crop performance under both sole cropping and intercropping conditions. Although the underlying mechanisms are not yet fully understood, we initiated small-scale field experiments in 2021 and 2022, designed as a combined intercropping/infector plant approach with oats to investigate the role of biotic stress within the faba bean/pea aphid/PNYDV-pathosystem employing these two particular varieties.

The aims of this research were therefore:

i. to assess spatial vector and PNYDV spread in infector plots in both varieties grown in sole crop (SC) and intercrop (IC) variants
ii. to investigate vector and PNYDV impact on varietal differences in N-economy, the agronomic performance in SC and IC treatments and resulting productivity indicated by Land Equivalent Ratio (LER) parameters and
iii. to evaluate whether and to what extent an intercropping approach can modify the epidemiological status of PNYDV infection in faba bean, thereby reducing disease incidence and improving yield stability under field conditions.

2 | Material and Methods

2.1 | Experimental Site and Design

The small-scale field experiments were conducted in two consecutive years in 2021 and 2022 spring-growing seasons at the organically managed experimental farm of the University of Kassel in Neu-Eichenberg, Germany (9°54′ E, 51°22′ N). Regarding crop rotation, the previous crops were maize (*Zea mays* L.) and winter wheat (*Triticum aestivum* L.) for trials 2021 and 2022, respectively. The topsoil of the experimental field was a Haplic Luvisol with a proportion of 0.834 silt, 0.133 clay and 0.033 sand and an altitude of 220–250 m above sea level. The annual mean temperature of the years 2001–2023 was 9.6°C, the mean annual precipitation 654 mm. Before the start of the trial, the soil was prepared by disk harrowing and mechanical weeding, following standard agronomic practices commonly used by faba bean growers in the region and consistent with the management applied at the experimental farm of the University of Kassel in Neu-Eichenberg. No mineral fertilizer inputs or insecticides were applied in both years. After sowing, weeds were controlled mechanically according to organic agricultural practice, using a cultivator star tiller (Table S1).

In both years 6 m × 6 m treatment plots were arranged in a 3-factorial randomized complete block design (RCBD) with four replications, separated by 3 m wide bare soil walkways (Figure 1). The experiment followed a 2 × 2 × 2 factorial design (cropping system × faba bean variety × aphid treatment), resulting in eight treatment combinations, plus an additional sole oat control, giving a total of nine treatments and 36 plots. Treatment factors were

- factor 1: cropping system in two factor levels, (1a) sole cropping (SC) and (2b) intercropping (IC);

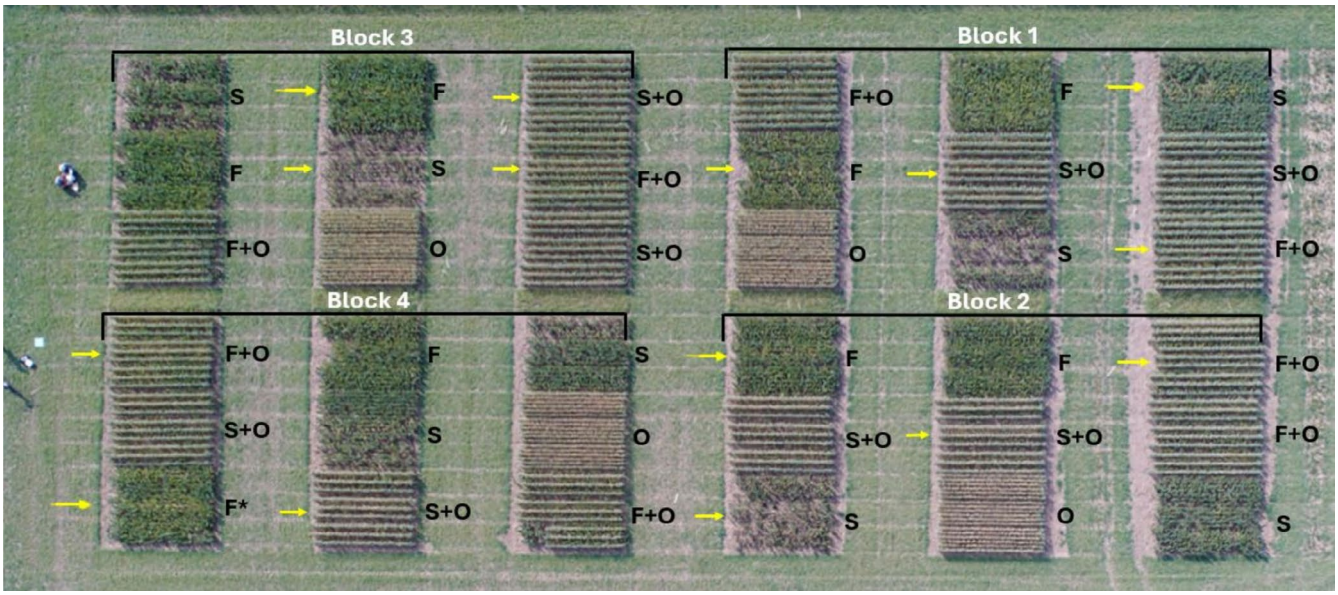


FIGURE 1 | Experimental field design 2022 (36 plots in 4 blocks); crop components in sole crop (SC) and Intercrop (IC) system: faba bean variety. F, 'Fuego'; O, oat; S, 'GL Sunrise'; yellow arrows indicate infector rows with repeated viruliferous aphid releases. F*: This individual plot indicates the positions where the samples were taken (see Figure 2); Neu-Eichenberg, Datum 30.06.2022. [Colour figure can be viewed at wileyonlinelibrary.com]

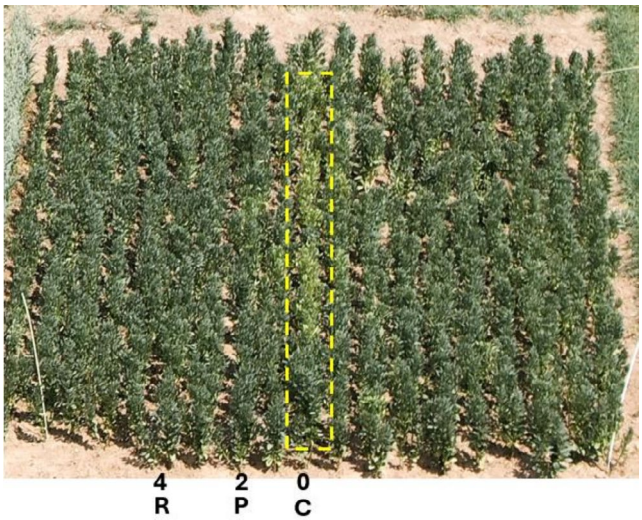


FIGURE 2 | Positions of the samples for aphid census in treatment 'Fuego' sole crop; C, core aphid release row = 0 row and every second row apart from release row; P, perimeter = row 2; R, reference = row 4. The yellow arrow indicates the release of viral aphids in the middle row (F* plot, see Figure 1), Neu-Eichenberg Datum 30.06.2022. [Colour figure can be viewed at wileyonlinelibrary.com]

- factor 2: faba bean variety, (2a) cv. 'GL Sunrise' and (2b) cv. 'Fuego', selected based on their contrasting susceptibility to PNYDV infection;
- factor 3: infector row treatments in two factor levels: (3a) with viruliferous aphid releases, (3b) without release (naturally infested control plots).

In addition, a sole oat (*Avena sativa* cv. 'Max') treatment was included as a non-factorial control.

The substitutive intercropping design employed alternating rows of faba bean and oat (variety 'Max'). In both years, each plot consisted of 18 rows, each 6 m long (Table S1). In the intercropping (IC) treatment, plots were arranged as alternating rows of faba bean and oat, comprising nine rows of each species per plot. Seed rates sown at 01.04.2021 and 23.03.2022, respectively, were for faba bean 45 kernels m^{-2} in SC and IC and for oat 300 m^{-2} in SC and 50% reduced oat density in the IC plots.

2.2 | Production of PNYDV Viruliferous Aphid

For establishing infector plants within the field experiments, all aphid- and plant materials were previously propagated in a climate chamber maintained at 20°C, 18-h photoperiod and 70% ± 10% relative humidity in the research greenhouse at the University Kassel, Campus site Witzenhausen (https://www.uni-kassel.de/fb11agrar/en/fachgebiete-einrichtungen/gewaechshaeuser).

In the first step, faba bean seedlings were grown from seeds 'Fuego' as single plants in 0.35 L plastic pots (0.07 × 0.07 × 0.08 m) in commercial zero soil (Fruhstorfer potting soil LD 80; Heinrichs Agrar GbR, Germany), augmented with 1 g sieved arable soil obtained from the experimental farm at Neu-Eichenberg to provide rhizobia for natural nodulation. In a second step, stock cultures of two *A. pisum* strains, a green and a red-coloured form, were started from a single virgo and were maintained parthenogenetically on the faba bean seedlings ('Fuego') in the same greenhouse and climatic regime in insect cages (aerarium size L: 0.60 × 0.60 × 0.90 m; Aerarium Nets GmbH, Bern, Switzerland). In the first year 2021, the green *A. pisum* form was used. However, distinguishing experimentally released individuals from resident field populations of the same colour morph proved difficult under field conditions. This strain was procured as wingless virginoparous females from stock cultures maintained at the Federal Research Centre for Cultivated Plants,

JKI-Braunschweig, Germany (JKI-BS), since 2005, originating from a faba bean site located at the experimental farm, Neu-Eichenberg, University Kassel. In the second year (2022), a red field-collected biotype of *A. pisum* was therefore used to enable clear visual discrimination between released and naturally occurring aphids. Wingless virginoparous females were collected from faba bean (*Vicia faba* L.) at the same experimental site in April 2022. The red biotype served as a marker to distinguish released red *A. pisum* from resident green forms. Confirmed non-viruliferous aphids were transferred for propagation on PNYDV-infected faba bean plants as primary donors, obtained from JKI-Braunschweig. All aphid strains were first confirmed to be non-viruliferous (PEMV and PNYDV-negative) and infector plant material was confirmed to be PNYDV positive using DAS-ELISA (double-antibody sandwich enzyme-linked immunosorbent assay) with polyclonal antibodies (coating antibodies and conjugate) raised against PNYDV as described previously by Fletcher et al. (2016). Aphids were allowed to feed for 5 days on the infector plants for PNYDV acquisition and viruliferous aphids were transferred to healthy faba bean seedlings for additional 5 days. These PNYDV inoculated seedlings were cultivated further for at least 20 days (Gaafar 2019) and served now as donor plants for mass propagating viruliferous PNYDV-aphid material to be field released later into the field experiments. At the day of release, aphids were gently removed from the plants. Harvested aphid fresh mass was determined with an analytical precision scale (Sartorius, QUINTIX224-1S), resembling about 1 g for approximately 950 aphids. For each release date (Table S2) harvested fresh masses were divided into 16 equal lots. After transfer to the field in a cooling container (8°C), they were distributed evenly on top of the central row plants within the respective 16 release plots (Table S2). To minimize potential confounding effects due to aphid movement between plots, sufficiently large plot sizes were used and non-release control plots were included in the experimental design. Moreover, infestations were dominated by wingless (apterous) aphids, which typically exhibit limited dispersal and remain on their host plants. The development of winged (alate) morphs, which enable longer-distance dispersal, generally occurs only under conditions of high population density or resource limitation, neither of which were observed during the course of this study.

2.3 | Post Release Aphid Census

Visual census of resident aphids either as naturally occurring aphids as well as remaining aphids after release was performed by shaking off the upper 20 cm main shoots into an empty tray (yellow pan trap, Syngenta Agro GmbH, L 0.33 × W 0.26 × D 0.07 m) at 13.07.2021 and 25.07.2022. Sampling comprised entire faba bean rows in three plot positions—the row of release = central row with direct vector exposure (= core) (Table S1), two rows apart from central row (= perimeter) and four rows apart from central row (= reference), see Figure 2. In the plots where virus-infected aphids were not released, a single sample was taken from the centre of the plot. The aphid densities per individual plant of the respective plot positions were calculated by dividing the number of aphid individuals by the number of individual plants in the respective row.

2.4 | PNYDV Incidence

In order to check for the infection status and secondary PNYDV spread within the rows of the respective release plots, for each replicate pooled *V. faba* leaf samples were taken from three randomly selected individual plants with representative growth within each of the above-mentioned three plot positions: core, perimeter and reference (Table S1) at 12.08.2021 (BBCH 86) and 18.07.2022 (BBCH 82). These 64 samples with nine leaves each were frozen individually in extraction bags (BIOREBA AG, Switzerland) and kept at −20°C for later analysis at JKI-BS. Samples were tested by DAS-ELISA for the presence of PNYDV and PEMV as described by Gaafar et al. (2017) and Grigoras et al. (2010).

2.5 | Above-Ground Biomass and N_2 Fixation

From each plot, the biomass above ground was harvested from a 0.4 m^2 section at 12.07.2021 (field bean BBCH 76 and oat BBCH 70) and at 14.07.2022 (field bean BBCH 80 and oat BBCH 79) (Table S1). The main shoot length and shoot numbers were recorded, and samples were dried at 60°C to determine dry weight and total N content in the biomass with a mass spectrometer and a thermal conductivity detector in an organic elemental analyser (vario MAX CHN; www.elementar.com/de/).

The amount of symbiotically fixed nitrogen in faba bean dry matter (%Ndfa) was calculated using the $\delta^{15}N$ method (Shearer and Kohl 1986). Oat obtained from the oat SC plots served as the reference crop. Analyses of $^{15}N/^{14}N$ ratio and $\delta^{15}N$ used an isotope ratio mass spectrometer (Finnigan MAT 251 or ThermoQuest Finnigan DELTAplus) at the Centre for Stable Isotope Research and Analysis, University of Göttingen, using an elemental analyser NA1110 (CE-Instruments, Rodano, Milano, Italy) and a mass spectrometer Delta XP (Thermo Electron, Bremen Germany) with a Conflo III interface (Werner et al. 1999). Finally, % Ndfa was calculated according to Büchi et al. (2015) with a p value of −0.08, which was determined for 'Fuego'.

2.6 | Yield Assessments

Both crop components were harvested manually as mature plants (0.25 m^2 cuts above-ground per plot) between BBCH 90 and BBCH 92 for yield assessment (Table S1). For faba bean, the number of pods per plant were recorded. The harvested kernels were dried at 60°C, and the thousand kernel weight (TKW) and the kernel dry weight were recorded. Gravimetric yield parameters were extrapolated to tonne per hectare with a standardized moisture of 14%. The bean and oat samples were ground with a cutting mill (Retsch, SM 300; www.retsch.de/de) and raw protein content of faba bean and oat was based on total nitrogen content, employing a standard crude protein factor 6.25 (VDLUFA 1997). For oat the number of kernels per plant, TKW and raw protein were assessed accordingly.

2.7 | Land Equivalent Ratio (LER)

In order to evaluate biotic stress responses of both faba bean varieties in SC and IC situations, we calculated the land equivalent

ratio (LER) separately for core, perimeter and reference position according to Mead and Willey (1980) and Simmonds and Vandermeer (1989) as follows:

$$\text{LER} = \frac{\text{Yield oats (Intercrop)}}{\text{Yield oats (Solecrop)}} + \frac{\text{Yield beans (Intercrop)}}{\text{Yield beans (Solecrop)}}$$

2.8 | Climatic Data

The 2021 growing season (March–August) received ~425 mm of rainfall (+13% vs. 1990–2020 average of ~375 mm), with peaks in June (105 mm) and August (120 mm) (Figure S1). In contrast, the 2022 growing season was severely dry (~195 mm, −48%), despite a wet April (55 mm). From May to mid-August, rainfall was consistently low, with extreme heat in July (max 39°C) and the following drought in August (15 mm) causing significant crop stress until harvest (Figure S1).

2.9 | Statistical Analysis

Analysis of variance (ANOVA) for a factorial randomized block design conducted over 2 years was performed using linear models (LM) for continuous data, such as nitrogen content, yield, thousand kernel weight (TKW) and protein yield. Additionally, aphid numbers per plant were analysed using a generalized linear model (GLM) to investigate the relationships between variables. The response variable was modelled using a quasipoisson distribution to account for overdispersed count data of aphids. Normality of residuals was assessed with histograms and Shapiro–Wilk normality test. Homogeneity of variance was tested by Levene's test for model residuals and visual methods.

Post hoc comparisons of means was performed with using the packages 'emmeans' (version = '1.4.8'), Tukey HSD tests and Student's *t*-test for paired comparisons, with a significance threshold of $p \leq 0.05$ (Lenth et al. 2019). The analysis was conducted in R (version R-4.1.1) using the stats package. Graphs of climatic data and linear regression analyses were constructed using Microsoft Excel (version 2019).

Mean aphid numbers per plant and mean nitrogen contents were expressed as percentage of change in all treatments relative to control plot, using the following formula:

$$\text{Percent change} = \frac{X2 - X1}{X1} \times 100$$

here $X2$ denotes mean value of treatments and $X1$ denotes mean control plot value. Qualitative changes as increases are indicated by (↑), decreases by (↓).

3 | Results

3.1 | Aphid Infestation and Aphid Spread

Total aphid infestation within the release rows (core) was consistently higher than in naturally infested control plots in both years (Table 1). In 2021 aphid counts were highest in core rows, exceeding natural control plot infestation in IC- and SC-treatments by 394% and 217% in 'GL Sunrise' and 300% and 125% in 'Fuego', respectively. A steep decline from core towards perimeter- and reference rows occurred, the reference rows being almost equal to naturally infested control plots (non-significant). This pattern of highest densities in core and descending infestation towards adjacent rows applied also to 2022 but at a higher overall natural infestation level in all treatments. Furthermore, in 2022 the relative increase/decrease ratio for the aphid total in the reference rows was slightly increased in SC (+4% in 'GL Sunrise' and 9% in 'Fuego') and significantly higher in IC treatments with +155% and +127%, respectively. Red and green aphid counts in 2022 were higher within release rows than in reference rows and control plots, applying to all SC and IC treatments and both years (Table 1). Vetch aphid *Megoura viciae* was not encountered in 2021 and contributed just marginally to the total of all aphid species in 2022.

At variety level, 'Fuego' showed consistently higher aphid counts than 'GL Sunrise', which is reflected in the relative varietal ratios. They tended to be above 1.0 in both cropping systems in 2021 and 2022 and were significant in the cross-year evaluation for IC with a single exception for the reference rows, in which 'Fuego' was less infested than 'GL Sunrise' (Table 2).

3.2 | PNYDV and PEMV Incidence

The serological analysis of all leaf samples in 2021 revealed that there was no PNYDV infection at any of the sampling positions. However, sporadic natural PEMV infections were detected in both varieties and in several sampling positions, without a clear special pattern in SC and IC treatments, including the naturally infested control plots. The overall infection status resulted in 0% PNYDV and about 9% PEMV-positive leaf samples (64 samples, 9 PEMV-positive) (Table 3). In 2022, the distribution of infections reversed: all PNYDV-positive detections in SC occurred in core rows for 'GL Sunrise' and half in 'Fuego', while in IC treatment, all leaf samples tested positive for PNYDV except for one 'GL Sunrise' sample from the perimeter. Unlike in 2021, no PEMV infections were detected in 2022 (Table 3), although most plants displayed symptoms of yellowing, particularly in 'GL Sunrise'. Given the absence of PEMV in serological assays, these yellowing symptoms are unlikely to be virus-induced and were more likely associated with abiotic factors such as heat stress, accelerated senescence or nutrient limitations (e.g., nitrogen), particularly under organic cultivation conditions.

3.3 | N-Economy and Symbiotic N_2 Fixation

In 2021, aphid release in 'Fuego' SC treatments revealed a non-significant decrease in the absolute amounts of symbiotic fixed N in core row- and control treatments (e.g., 213 kg N ha^{-1} in core and 248 kg N ha^{-1} in control plot) fluctuating between 13% and 22% reduction (Figure 3). The data provided are based on the complete data set from all sampling positions with airborn and soil-N amounts and its relative in- und decreases in percent according to treatment (Table S4a,b). The same applied to 'GL Sunrise' SC treatments at an overall lower N-fixation level (e.g., 125 kg N ha^{-1} in core and 157 kg N ha^{-1} in control

TABLE 1 | Mean aphid numbers per plant of the green and the red *Acyrthosiphum pisum* form, *Megoura viciae* and the total of all aphid individuals observed in the aphid census 2021 and 2022 in sole crop (SC) and inter crop (IC) treatments.

Treatment		2021				2022				
		A. pisum (green)	*A. pisum* (red)	Total	In-/decrease	*A. pisum* (green)	*A. pisum* (red)	*Megoura viciae*	Total	In-/decrease
Fuego										
SC	Core	0.92 c[1]	0.33 ab	1.26 b	↑[3] 125%	1.27 a	1.27 c	0.00 a	2.54 abc	↑ 97%
	Perimeter	0.48 abc	0.03 a	0.51 ab	↓ 9%	1.11 a	0.99 bc	0.02 ab	2.12 ab	↑ 64%
	Reference	0.40 abc	0.03 a	0.43 ab	↓ 23%	1.07 a	0.32 ab	0.01 ab	1.41 a	↑ 9%
	Control plot	0.53 abc	0.03 a	0.56 ab		1.04 a	0.17 a	0.08 a	1.29 a	
IC	Core	0.81 bc	0.48 b	1.28 b	↑ 300%	0.91 a	3.57 e	0.14 ab	4.62 d	↑ 175%
	Perimeter	0.47 abc	0.19 ab	0.66 ab	↑ 106%	1.49 a	2.63 de	0.1 ab	4.22 cd	↑ 151%
	Reference	0.24 a	0.04 a	0.29 a	↓ 9%	1.43 a	1.96 cd	0.42 b	3.81 bcd	↑ 127%
	Control plot	0.27 ab	0.05 a	0.32 a		1.00 a	0.31 ab	0.38 ab	1.68 a	
GL sunrise										
SC	Core	0.91[2] b	0.55 c	1.46 b	↑ 217%	0.78 abc	0.62 a	0.01 ab	1.41 a	↑ 74%
	Perimeter	0.42 ab	0.05 a	0.47 a	↑ 2%	0.68 ab	0.43 a	0.01 ab	1.12 a	↑ 38%
	Reference	0.33 ab	0.03 a	0.36 a	↓ 22%	0.62 ab	0.22 a	0.00	0.84 a	↑ 4%
	Control plot	0.43 ab	0.03 a	0.46 a		0.70 ab	0.08 a	0.03 a	0.81 a	
IC	Core	0.50 ab	0.39 bc	0.89 ab	↑ 394%	0.47 a	3.44 b	0.09 ab	4.01 b	↑ 146%
	Perimeter	0.19 a	0.04 a	0.23 a	↑ 28%	1.22 bc	2.48 b	0.14 ab	3.84 b	↑ 136%
	Reference	0.13 a	0.04 a	0.17 a	↓ 6%	1.64 c	2.12 b	0.41 b	4.16 b	↑ 155%
	Control plot	0.16 a	0.02 ab	0.18 a		0.81 abc	0.57 a	0.26 ab	1.63 a	

Note: Mean values within columns followed by different letters indicate significant differences; emmeans, $p < 0.05$.
[1]Within variety 'Fuego' SC, IC treatments.
[2]Within variety 'GL Sunrise' SC, IC treatments.
[3]↑: increase, ↓: decrease; the increase/decrease ratio represents the relative aphid (*A. pisum*) density in a given plot compared to the corresponding control plot (ratio = treatment/control). Values > 1 indicate an increase, whereas values < 1 indicate a decrease. This ratio is used as a qualitative proxy to illustrate relative differences in aphid abundance among plot positions.

plot). The reduction in nitrogen fixation compared to the control plots (157 kg N ha^{-1}) shows only minor differences across the core (125 kg N ha^{-1}; 20% ↓), perimeter (151 kg N ha^{-1}; 4% ↓) and reference (191 kg N ha^{-1}; 22% ↑) positions (Table S4b).

In 2022 as well, 'Fuego' SC treatments yielded more atmospheric N than 'GL Sunrise' in all sampling positions. Mean symbiotic N-fixation *in core rows* was now significantly reduced when compared with control plots in both varieties, namely in 'Fuego' controls with 185 kg down to 94 kg air-born N ha^{-1} (Figure 3) resembling 49% mean reduction and 'GL Sunrise' controls with 86 kg down to 39 kg air-born N ha^{-1} and 55% reduction (Table S4a,b). The relative N derived from atmosphere (%Ndfa) consistently dominated soil N-consumption contributing more than a half to the accumulated N total in all SC treatments and sampling positions in both years and both varieties (range 57%–75% over all SC-treatments). The N-totals revealed a similar and significant reduction response towards viruliferous aphid release. In 'Fuego' 247 kg accumulated N in controls dropped down to 44% in core rows and in 'GL Sunrise' from 127 kg down to 46%, respectively (Table S4a,b). In the IC system in general, all absolute N acquisition parameters

TABLE 2 | Relative varietal aphid infestation level in variety 'Fuego' versus 'GL Sunrise' as the coefficient of aphid infestation in 'Fuego' divided by 'GL Sunrise' in both years and cross-year evaluation within release and control plots without aphid release in SC and IC treatments.

Variants		'Fuego'/'GL Sunrise'					
		2021		2022		Cross year 2021/2022	
Cultivation system	Sampling position	Rel. infestation	p[1]	Rel. infestation	p	Rel. infestation	p
SC	Core	0.86	0.74	1.80	0.29	1.32	0.61
	Perimeter	1.09	0.49	1.89	0.17	**1.65**	**0.003**
	Reference	1.19	0.65	1.68	0.65	1.53	0.86
	Control plot	1.22	0.56	1.59	0.65	1.46	0.20
IC	Core	1.44	0.28	1.15	0.07	**1.20**	**0.001**
	Perimeter	2.87	0.77	1.10	0.25	**1.20**	**0.005**
	Reference	1.71	0.81	0.92	0.16	**0.95**	**0.001**
	Control plot	**1.78**	**0.003**	**1.03**	**0.03**	**1.11**	**0.001**

Note: Bold type indicates significant varietal differences with $p < 0.05$.
[1]p value < 0.05 (Student's t-test).

TABLE 3 | Land equivalent ratios (LERs) as partial LERs of grain yield in *V. faba* (bean) and oat components and resulting LER totals in 2021 and 2022.

		2021			2022		
Variety	Position	LER *V. faba*	LER oat	LER total	LER *V. faba*	LER oat	LER total
'Fuego'	Core	0.37 a AB	0.48 ab AB	0.85 a A	0.16 a A	1.03 a A	1.19 a A
	Perimeter	0.37 a AB	0.52 b BC	0.89 a A	0.22 a A	0.99 a A	1.21 a A
	Reference	0.45 a AB	0.50 b ABC	0.95 a A	0.19 a A	1.02 a A	1.21 a A
	Control plot	0.55 a B	0.37 a A	0.92 a A	0.23 a A	0.82 a A	1.05 a A
'GL Sunrise'	Core	0.33 a A	0.60 a BC	0.93 a A	0.18 a A	1.00 a A	1.18 a A
	Perimeter	0.38 a AB	0.60 a BC	0.98 a A	0.2 a A	0.96 a A	1.16 a A
	Reference	0.40 a AB	0.62 a BC	1.02 a A	0.14 a A	1.08 a A	1.23 a A
	Control plot	0.32 a A	0.64 a C	0.96 a A	0.18 a A	0.96 a A	1.14 a A

Note: Different lower case letters indicate significant differences within 'Fuego' and 'GL Sunrise' treatments. Upper case letters within columns indicate significant differences between 'Fuego' and 'GL Sunrise' variants (Tukey, $p < 0.05$).

showed consistently lower values than in SC in both years. In IC treatments 2021 absolute symbiotic N fixed in kg ha^{-1} in 'Fuego' was higher than in 'GL Sunrise' spanning 47 kg to 64 kg N ha^{-1} and 27 kg to 35 kg N ha^{-1}, respectively. Within IC treatments, the overall fixation level did not show significant differences within sampling positions and no clear reduction pattern in comparison to the control plots. Fixation levels remained relatively stable in 'GL Sunrise' and increased by 9%–18% in 'Fuego' (Table S4a,b).

In IC treatments 2022 as well, absolute N-fixation in 'Fuego' was higher than in 'GL Sunrise' although %Ndfa spanned a similar range with 85–91 %Ndfa in 'Fuego' and 84%–91% in 'GL Sunrise'. The oat component 2021 in 'Fuego' plots contributed 34–39 kg and in 2022 about 51–69 kg N ha^{-1} to the N-total but in 'GL Sunrise' plots oat contributed 35–47 kg in 2021 and in 2022 about 55–64 kg N ha^{-1} to the N-total, respectively. Neither for soil N uptake in component crops, nor for the resulting mean N yield total significant differences between sampling position as

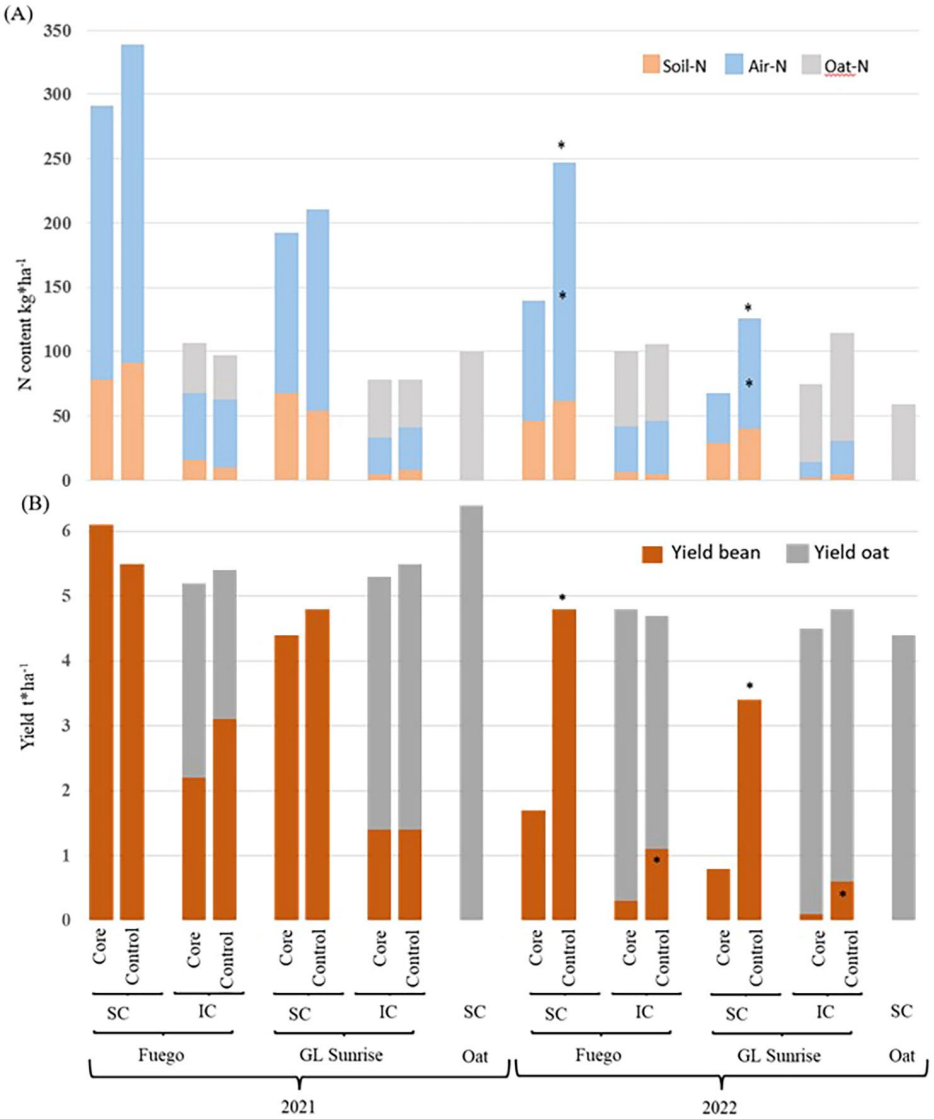


FIGURE 3 | (A) Accumulated nitrogen derived from the atmosphere in the above-ground biomass of faba bean (air-N) and oat and/or the soil compartment (soil-N) as absolute kg N ha^{-1} within position core and corresponding control plots in SC and IC treatments including either the *V. faba* variety 'Fuego' or 'GL Sunrise'. (B) Resulting yield performance according to biotic stress by viruliferous aphid release in sampling position core and control plots in both varieties. Asterisks indicate significant differences for component yields and yield totals at 5% level using emmeans between varieties per location, treatment and year. The complete data set for all sampling positions is given for (A) in Table S4a,b and for (B) in Table S5 (Neu-Eichenberg at BBCH 762021 & 2022 at BBCH 80). [Colour figure can be viewed at wileyonlinelibrary.com]

well as corresponding IC-control plot were observed (Figure 3; Table S4a,b).

3.4 | Yield Parameters

In both faba bean varieties and in both years, SC yield parameters (number of pods per main shoot, kernel weight and yield) were higher in SC than in IC and 'Fuego' kernel yield was consistently higher compared to 'GL Sunrise' (for complete data sets see Table S5). In particular, SC-infector plots in 2021 showed in both varieties and in all sampling positions similar kernel yields as the corresponding control plots with no significant differences. However, SC treatments revealed consistently higher pod numbers per main shoot, grain yield and crude protein yield than corresponding IC treatments. In the latter, the oat component performed significantly weaker when intercropped in 'Fuego' control plots without aphid release and this tendency occurred also in IC 'GL Sunrise' to a lesser, non-significant extent. Oat TKW and crude protein yield were almost unaffected by any treatment in both varieties, except the lowered crude protein yield in IC 'Fuego' control plots.

In 2022 the described SC/IC differences were similar but much more pronounced and significant in 'Fuego' which reached a SC grain yield of just 1.7 t in the core compared to 4.8 t ha^{-1} in the control plot and 0.3 t and 1.1 t ha^{-1} in the IC treatment, respectively (Figure 3; Table S5). In 'GL Sunrise' yields were much lower in general and yield parameters declined less sharply from control plots over reference, perimeter down to the core sampling position. In both varieties, particularly faba bean crude

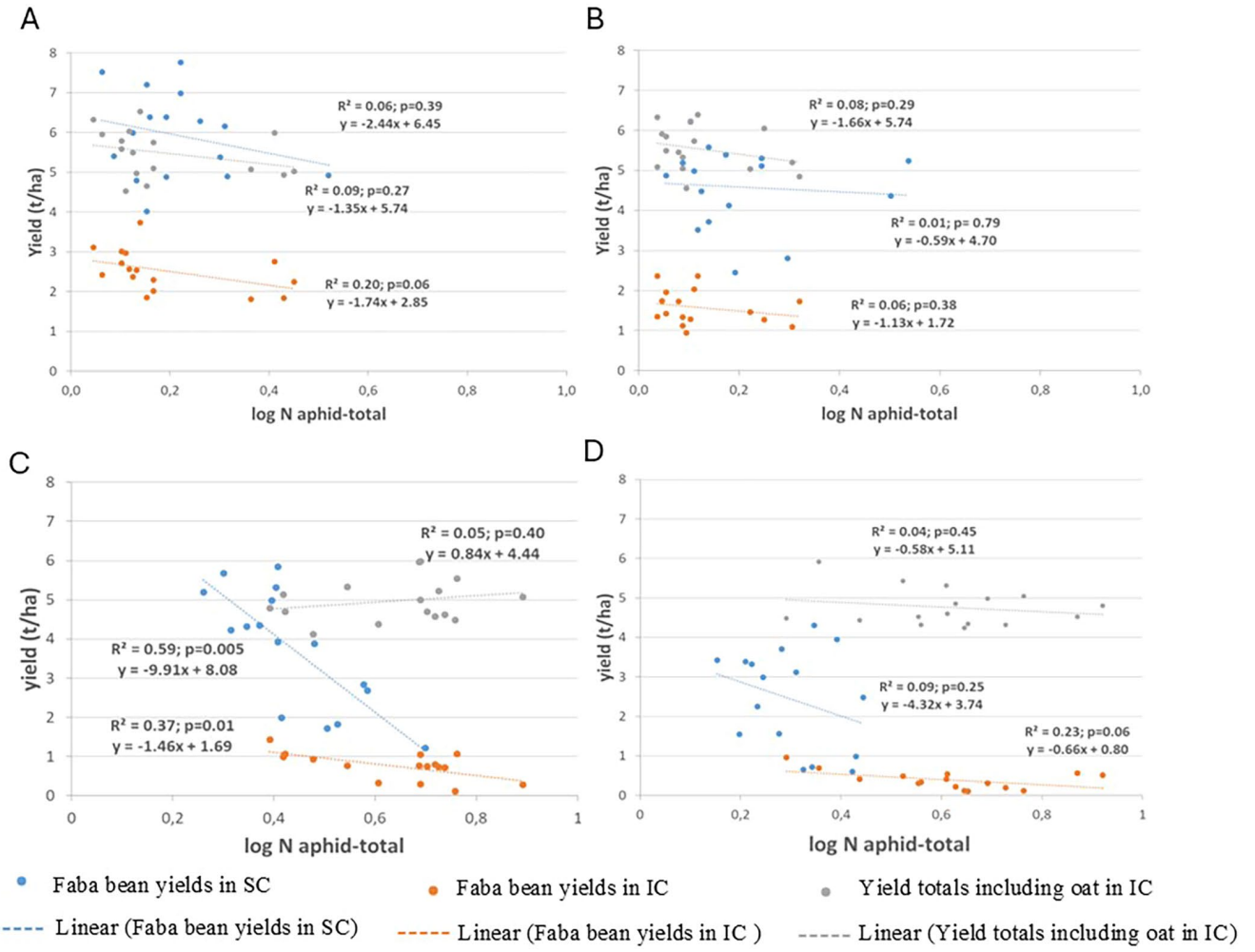


FIGURE 4 | Regressions between logarithmized aphid-total densities per plant, faba bean grain yield and yield total including oat in SC and IC variants for 'Fuego' (A) and 'GL Sunrise' (B) in 2021 and 'Fuego' (C) and 'GL Sunrise' (D) in 2022. [Colour figure can be viewed at wileyonlinelibrary.com]

protein IC yields were significantly reduced, whereas oat in SC and IC treatments showed consistently marginal responses to viruliferous aphid release concerning grain, crude protein and TKW (non-significant) (Table S5).

3.5 | Land Equivalent Ratio

The partial faba bean LERs in 2021 did not show significant differences within treatments, ranging from 0.37 to 0.55 in 'Fuego' and 0.31 to 0.4 in 'GL Sunrise'. Oat partial LERS in 'Fuego' treatments were lowest in the control plot without aphid release and in 'GL Sunrise' non-significantly higher in aphid release plots, resulting in LER totals being predominantly below 1.0 (Table 3). In 2022, however, partial faba bean LERs were consistently lower spanning 0.16–0.23 in 'Fuego' and 0.14–0.2 in 'GL Sunrise'. In contrast to 2021, partial oat LERs approached almost 1.0 (0.82–1.08 in 'Fuego', 0.96–1.08 in 'GL Sunrise') and LER totals exceeded 1.0 consistently (range 1.05–1.23). The differences between variety and respective sampling position were non-significant (Table 3).

In 2021, faba bean grain yields in both varieties and yield totals including the oat component responded to rising aphid densities with slightly, but non-significantly decreasing slopes in SC and IC (Figure 4). In 2022, 'Fuego' encountered first of all higher aphid infestation levels than 'GL Sunrise'. Secondly, its partial grain yields responded strongly in SC and IC treatments, descending significantly from about 5.9 t ha^{-1} down to lowest 1.1 t ha^{-1} at highest aphid density (see also Table 1). Notably, both 2021 and 2022, the total yield, including the oat component, for both varieties was not significantly influenced by aphid density, with regression p values of 0.29 for 'GL Sunrise' in 2021 and 0.45 for 'GL Sunrise' in 2022 (Figure 4).

4 | Discussion

This study investigated biotic stress responses in faba bean, employing a combined infector plant/intercropping approach with oat. The two experimental years differed substantially in both biotic and abiotic stress conditions, which strongly influenced crop performance and vector–virus dynamics. While

intercropping did not improve the performance of faba bean as an individual crop component in terms of partial yield, pod number or nitrogen acquisition, the overall system performance was stabilized through the complementary contribution of the oat component, as reflected by the land equivalent ratio (LER) and total productivity (Figure 4). Thus, the advantage of the intercropping system is best interpreted at the whole-system level rather than as enhanced resilience of faba bean alone.

4.1 | Aphid Establishment and Dispersal Within Infector Plots

At first glance, the vector establishment rates in infector plots appear to be relatively poor, considering that about 4500–5600 individuals in total per row had been released in each year (Table S2). But in general, *A. pisum* is known to be an inconspicuous colonizer in faba bean at field conditions, not forming such dense colonies such as, for example, the black bean aphid *Aphis fabae* (Kraft and Pfleger 2001). Potential limiting factors for higher infestation rates can be seen firstly in 'reduced fitness effects', associated with the entire handling process from mass propagation in the greenhouse, aphid harvesting, weighing, assembly and transfer of crowded aphid cohorts to their final destination. Secondly, being placed on terminal shoots, apterous individuals will likely require more time for orientation and adaptation to the field environment than resident individuals. Those individuals which failed to instantly settle in the upper canopy may have fallen to the ground, putting them at higher risk for predation and add to natural mortality by biotic and abiotic factors. In view of the above-mentioned factors, it can be assumed that the overall loss rates were high and therefore restricting subsequent mass propagation in both varieties.

Concerning the spatial vector spread, the majority of infectious aphids and their progeny stayed within core rows in more than threefold higher densities than in adjacent perimeter and reference rows in both varieties and both years (Table 1). This poor 'spill over-effect' from core to perimeter rows is underpinned by the spatial distribution of the red-coloured *A. pisum* biotype in 2022. We utilized the red biotype as a kind of marker to distinguish between released red and resident green *A. pisum* forms, the latter being predominant in naturally infested control plots throughout the entire vegetation period in both years (Table 1, 2022). Overall, aphid distribution patterns suggest that spatial position within the plot had a stronger effect on vector abundance than cropping treatment alone. Aphid densities were consistently highest in core rows, exceeding natural control plot infestations, whereas differences between IC and SC at the whole-plot level were less consistent across years. This sharp drop from core to much lower infested reference rows was exaggerated in IC situations with alternating faba bean and oat rows (Table 1). In intercropped plots, the wingless aphids generated after initial infestation often encounter dense oat rows when attempting to move to neighbouring faba bean rows. These non-host rows act as a barrier, causing aphids to return to their original host plant rather than crossing the oat row. This combined effect is referred to as a 'barrier/mirror mechanism', hypothesized to limit row-to-row dispersal within intercropped treatments for both faba bean varieties (Hooks and Fereres 2006; Waweru et al. 2021).

4.2 | Varietal Effects on Vector Performance

At varietal level, 'Fuego' supported much higher aphid densities than 'GL Sunrise' in SC and MC as indicated by the aphid infestation ratios exceeding 1.0 in the cross-year evaluation (Table 2). This varietal difference was consistent in all sampling positions of infector plots as well as for the naturally infested control plots (Table 2). This is in line with our previous empirical field investigations (Seeger et al. 2018). However, because in the greenhouse reproduction parameters were similar in both varieties for *A. pisum* and further species of the aphid–vector complex (Berawe et al. 2024), post-release numeric vector propagation is probably not the main cause for lower aphid counts in 'GL Sunrise'. Currently, the responsible mechanisms are suspected in the early colonization phase, being associated with either optical (Cartier and Auclair 1964; Döring and Chittka 2007; Döring and Kirchner 2022; Dubnik 1991; Moericke 1955), haptic leaf surface (White and Eigenbrode 2000), and/or gustatory varietal traits, dealing rather with vector settling and/or movement on the plant surface till host acceptance (Berawe et al. 2024).

4.3 | PNYDV Establishment and Focal Growth

The results for both the artificial establishment of PNYDV and natural occurrence of PEMV were very contrasting in the first and second year. In 2021, PNYDV was completely absent in diagnostic leaf samples obtained from release and control plots, although PNYDV propagation and release procedure of virulent *A. pisum* followed the same protocols of Seeger et al. (2022) and same diagnostics of Gaafar et al. (2017) and Grigoras et al. (2010). Thus, the yield impact of biotic stress in 2021 was mainly attributed to direct nutrient drain and thus the numeric aphid incidence (Figure 3) accompanied by visually mild and late occurring PEMV symptoms ranging from 5% to 33% PEMV-positive plants with serologically confirmed PEMV (Table S3). None of the treatments showed a clear spatial PEMV pattern between sampling position or SC, MC treatments, indicating external natural PEMV entry into experimental plots (Table S3). Although serological virus diagnostics aimed to just qualitatively confirm plotwise PNYDV infection status rather than to envisage a quantitative survey, we just can state that varietal PEMV incidence differed and occurred mainly in 'Fuego' (Table S3). In any case, this pattern again confirms specific varietal traits in 'GL Sunrise', attenuating vector-mediated entry of various plant viruses, as reported previously also for PNYDV, PEMV, BLRV and TuYV (*turnip yellows virus*) in comparison to 'Fuego' at field condition (Saucke, Seeger, et al. 2019; Seeger et al. 2018). Such data addressing up to date varietal virus susceptibility in faba bean are supplementing previous screenings (Abraham et al. 2000; Makkouk et al. 2002) and could encourage an analogous varietal evaluation concerning PNYDV as recently performed in field pea (*Pisum sativum*) (Tan et al. 2022).

The absence of PNYDV incidence in 2021 indicates very low natural virus pressure, supported by the lack of typical symptoms (Saucke, Uteau, et al. 2019). Despite releasing a high number of

viruliferous aphids, no transmission occurred, likely due to insufficient virus acquisition or loss of genome segments during propagation or in an early growth stage of the infector plant. PNYDV's multipartite genome requires all eight segments for successful infection, making propagation challenging. Future studies should use multiple donor-plant batches and continuous serological monitoring to avoid or at least to reduce the risk of insufficient virus transmission.

No natural infection background for PNYDV nor PEMV was encountered in 2022. Thus, PNYDV incidence originated from inoculations and was solely restricted to core rows, with no signs for carry over to the next perimeter rows in SC and MC treatments, confirmed by visually and serological means (Table S3). This is also in line with the above-mentioned lacking 'spill over' for released vector aphids (see above). Therefore, the suspected barrier/mirror effect assigned to non-persistently viral diseases vectored by winged migrants at field edges (Fereres 2000; Fereres and Moreno 2009; Hooks and Fereres 2006) applies also to secondary PNYDV spread from plant to plant within crop stands, transmitted persistently by aptere *A. pisum*. At present, it can be expected that the alternate row design will limit also natural epidemic vector-/PNYDV spread and focal growth in IC treatments, but due to the lack of natural PNYDV pressure, this will need further investigation in years with higher natural PNYDV abundance.

4.4 | N-Economy

Taking the non-release SC control plots as a baseline for faba bean N-status, varietal traits in 'Fuego' led to a consistently better N-performance. For example, in 2021, 'Fuego' accumulated 339 kg versus 211 kg N ha^{-1} in 'GL Sunrise' (Table S4a,b). The higher N-status in 'Fuego' was due to a significantly higher symbiotic N-fixation (248 kg 'Fuego' versus 157 kg N ha^{-1} in 'GL Sunrise'), at conditions of moderate natural infestation background of the vector and virus complex with PNYDV as well as PEMV. Even if experimentally enhanced in infector plots in 2021, vector pressure was just weakly affecting N-fixation and N-totals in both faba bean varieties. These moderate but non-significant reductions were probably due to (i) solely nutrient drain by resident vectors coupled with a lower damage potential of *A. pisum*-infestation at field condition and (ii) the absence of PNYDV pressure and lacking weather extremes like draught (Figure 1) in that particular year. In contrast, in 2022, faba bean SC-infector plots faced the combined interaction of vector- and PNYDV-incidence, resulting in a significantly reduced N-status in both varieties, which is in line with investigations by Seeger et al. (2022) stating no principal difference in terms of PNYDV-sensitivity in between these particular varieties.

In IC-control plots 2021, forming the baseline for the non-release situation, the mutual competition between faba bean and oat lowered N-acquisition in both crop components, finally resulting in N-totals of 98 kg versus 78 kg N ha^{-1}, respectively (Table S4a,b). This difference is biologically relevant because nitrogen acquisition directly determines vegetative growth, pod formation and final yield, and even moderate shifts in N uptake may substantially alter interspecific competition and resource allocation in intercropping systems. Here, interspecific competitive relationships between faba bean and oat were marginally affected by additional biotic stress because vector pressure was exclusively related to nutrient drain by direct suction damage as PNYDV-infections had failed in this particular year.

In Season 2022 overall air-N, soil-N and resulting N-totals in SC and IC treatments were substantially lower than in the previous season. Although infector plots were exposed to both pest aphid- and PNYDV-incidence, overall crop performance was dominated by the superior effects of adverse abiotic climatic conditions, characterized by extended heat and drought in 2022 (see also yield data below). In comparison to the previous year, this went to the expense of N acquisition in faba bean, particularly in 'GL Sunrise' and conversely to the advantage of the oat component (IC-'Fuego' oat ranging from 34 kg to 39 kg N ha^{-1} in 2021 and 51 kg to 69 kg N ha^{-1} in 2022, 'GL Sunrise' ranging from 35 kg to 47 kg N ha^{-1} and 55 kg to 64 kg N ha^{-1}, respectively) (Table S4a,b). On the one hand, this confirms the high competitive potential of oat in grain legume MC-combinations in general (Dhima et al. 2014; Rauber et al. 2000), as it contributed an almost constant share to the total N sum in all variants. On the other, oat did not fully compensate for weak N-uptake by stressed faba bean, particularly in 'GL Sunrise' plots (Table S4a,b). Therefore, concerning the N-economy, climatic stress dominated the relatively weaker biotic stress effects in IC treatments and differences were mainly attributed to distinct varietal traits where 'Fuego' performed better than 'GL Sunrise'.

Drought stress significantly affects the growth and nitrogen acquisition of faba bean. Water limitation reduces both the number and functionality of root nodules, leading to decreased symbiotic nitrogen fixation. In addition, drought lowers the activity of key nitrogen-metabolizing enzymes in the nodules and negatively impacts soil microbial communities, including nitrogen-fixing rhizobia. These combined effects disrupt the soil nitrogen cycle, reducing the availability of nitrogen to the plant and ultimately limiting growth, pod development, and yield under water-limited conditions (Fundazioa 2005; Sinclair and Vadez 2002).

Finally, although weak and not always significant, these cropping system responses are in line with established complementary N-resource use mechanisms within mixed and intercropping systems (Jensen et al. 2020; Liebman and Mohler 2001; Rodriguez et al. 2020).

4.5 | Yield

Experimentally enhanced vector pressure within SC-infector plots in 2021 did not exert significant reduction in yield parameters in both varieties, when compared with the corresponding non-release control plots, with the exception of a higher TKW in core of 'Fuego'. In general, faba bean yields in 'Fuego' were consistently higher than in 'GL Sunrise' in both years, which follows the same pattern as mentioned for N-economy (see above). This trend is consistent with regional variety trials conducted in Hesse, where 'Fuego' has been reported to achieve higher yield levels than 'GL Sunrise' under comparable field conditions (LSV 2019). Significant differences between core, perimeter and

reference sampling positions were missing in both varieties in 2021, which can be attributed to four influencing factors: (a) unfavourable climatic conditions for faba bean growth in terms of precipitation and temperature regime (Figure S1), (b) the moderate species-specific damage potential of *A. pisum*, being coupled with (c) the absence of PNYDV-infections in aphid release plots and in the same time (d) low yield impact of abundant natural PEMV-incidence within the entire field experiment (Table S3). In contrast, in 2022 faba bean faced (a) adverse climatic conditions in terms of heat and draught, (b) direct *A. pisum* damage in interaction with (c) PNYDV-incidence and (d) lacking natural PEMV background. This particular constellation of stress factors in IC treatments resulted in significant yield losses in faba bean but not in the oat component (Table S5).

During the late phase of the 2022 growing season, GL Sunrise exhibited an abrupt and premature senescence following the heatwave period. Parallel investigations of the root rhizosphere and pathogen community by Šišić et al. (2023) revealed clear varietal differences. Specifically, elevated abundances of putative root pathogens, including *Fusarium oxysporum* and *F. avenaceum*, were detected in 'GL Sunrise', whereas these pathogens were absent or occurred only at low levels in the visually less affected 'Fuego' plots. These findings indicate a higher susceptibility of 'GL Sunrise' to heat-associated root fungal diseases and are consistent with established principles of cereal–legume intercropping, where varietal stress tolerance strongly influences system performance (Agegnehu et al. 2006; Helenius and Ronni 1989; Jensen et al. 2010; Rodriguez et al. 2020).

Correlating all aphid census data and yield responses into linear regressions (Figure 3), distinct varietal yield differences and year effects occurred. Whereas in 2021 rising aphid densities impacted faba bean partial yield in SC and IC just with a weak tendency with similar yield totals, in 2022 yield decline in 'Fuego' responded more sharply to combined vector and PNYDV pressure than 'GL Sunrise'. Thus, the relative yield performances of both varieties responded similarly to viruliferous vector load, but at distinct absolute yield levels. These findings emphasize that partial indicators such as faba bean yield, pod number or N acquisition alone do not fully capture the agronomic value of the intercropping system. Although faba bean performance was reduced in IC compared with SC, the oat component compensated for these losses, resulting in improved land-use efficiency under stress conditions, particularly in 2022.

Finally, both varieties showed similar patterns for crop component LERS, for example, partial LER of 0.55 for 'Fuego' in 2021 was coupled with dropping partial oat LERs down to 0.37, while conversely, consistently low partial LERS of faba bean below 0.23 in the climatically difficult year 2022 were compensated by higher partial yields approaching or exceeding 1.0 for oats (Table 3). Therefore, contrasted environmental stress causing differing LERS illustrates the plasticity of interspecific competition and/or complementary resource use (Willey 1990). Because LERS reflect relative yield composition and do not judge absolute yields, the absence of a yield advantage under the favourable climatic conditions of 2021 indicates that both crops mainly acted as dominant species and therefore competed for the same resources (Hauggaard-Nielsen et al. 2006; Wit and Van Den Bergh 1965). In 2022, complementary resource use by stressed faba bean and oats became more apparent. Oats expelled high plasticity converting most available soil-N into yield, whereas faba bean relied mostly on symbiotic N-acquisition (Table S4a,b). As a result, both varieties achieved similar IC-yield levels at enhanced biotic/abiotic stress conditions in the particular year (Figure 4C,D).

The contrasting yield responses observed in 2021 and 2022 demonstrate that the effects of aphid pressure, virus incidence, and intercropping performance were highly season-dependent. In particular, the absence of PNYDV infection in 2021 restricted a comprehensive assessment of yield responses to vector-borne viral stress under favourable climatic conditions, thereby limiting the extrapolation of the results across seasons.

5 | Conclusions

Our results show that faba bean exposure to contrast biotic/abiotic stress constellations responded with substantial yield decline of the faba bean component in both varieties, particularly when grown in IC treatments with oats as a strong competitor. The encountered yield-stabilizing effects in IC treatments were mostly attributed to the plasticity in oat yield. Its complementary resource use almost compensated for faba bean yield decline with an adjusted yield contribution according to the respective stress level in the legume crop component.

Overall, given the fluctuating epidemic potential of PNYDV and increasing uncertainties regarding climatic extremes in the future, faba bean cultivation will benefit from both the development of PNYDV-resistant varieties with improved agronomic traits and their incorporation into more resilient intercropping systems. However, given the pronounced year-to-year variability observed in this study, these conclusions should be interpreted within its season-specific context and need further validation through multi-year field experiments.

Author Contributions

Ahmed Berawe: conceptualization, methodology, formal analysis, data curation, funding acquisition, writing – original draft. **Heiko Ziebell:** validation, investigation, resources, writing – review and editing. **Judith Nora Seeger:** conceptualization, visualization. **Helmut Saucke:** conceptualization, methodology, investigation, validation, visualization, supervision, resources, project administration, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in DaKS|Research data repository https://doi.org/10.48662/daks-513.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Monthly total rainfall (mm) and mean

air temperature (°C) during the 2021, 2022 and 30-year long-term mean growing seasons. Weather data were obtained from the weather station located in the research station in Neu-Eichenberg. **Table S1:** Details of the field experiments at Neu-Eichenberg in 2021 and 2022. **Table S2:** Dates and numbers of viruliferous *A. pisum* released into the *V. faba* infector rows of the field experiment Neu-Eichenberg 2021 and 2021. **Table S3:** Detection of positive PNYDV and PEMV samples in 2021 and 2022. **Table S4:** (a, b) Accumulated nitrogen in the above-ground biomass of faba bean and oat derived from the atmosphere (air-N) and/or the soil compartment (soil-N) as absolute kg N ha^{-1} and as % nitrogen derived from atmosphere (% Ndfa) within core-, perimeter- and reference rows in plots with viruliferus aphid release and corresponding control plots in SC and IC treatments including either the *V. faba* variety 'Fuego' or 'GL Sunrise' (Neu-Eichenberg at BBCH 762021 and 2022 at BBCH 80). **Table S5:** Yield parameters according to biotic stress by viruliferous aphid release in sampling position core, perimeter, reference and control plot in the two *V. faba* varieties 'Fuego' and 'GL Sunrise' in sole crop (SC) and mixed (IC) treatments with oat in 2021 and 2022.