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Impact of wheat-legume mix intercrops on wheat epidemics by modelling

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Highlights

- Simulated intercropping decrease disease intensity and improve protectiveness, while simple canopy indicators can predict such effects.
- Pea intercropped with wheat decreased disease intensity compared with faba bean,
- Nitrogen fertilization increased disease intensity.
- This study stressed the critical lack of experimental data on disease in intercropping.

Abstract

1. Context: Intercropping for disease management is a promising strategy for integrated disease management and agroecological transition, although experimental and modelling studies are scarce.
2. Objectives: This study aims to understand and quantify the impact of non-host species choice and nitrogen (N) fertilization on disease epidemics in the context of intercropping.
3. Methods: We collected existing experimental data on LAI based on a literature survey of non-diseased wheat intercropped with different non-host legume species (pea and faba bean) and N fertilization treatments. Based on a foliar epidemic model for intercropping, we simulated epidemics directly on these experimental data of LAI. The model is parameterized for two wheat fungal diseases: Septoria tritici blotch, a rain-borne disease, and wheat leaf rust, an air-borne disease.
4. Results: Our results indicate that intercropping can decrease disease intensity and improve protectiveness for both diseases. Effect depends however on species choice as pea intercropped with wheat leads to lower disease intensity and better intercropping protectiveness compared with faba bean, whereas N fertilization increased disease intensity. We also found that crop indicators describing wheat leaf area index (LAI) can predict disease intensity, whereas indicators describing companion LAI can better predict intercropping protectiveness.
5. Conclusions: Intercropping can significantly reduce fungal epidemics on wheat, and intercropping management practices can be optimized for effective disease management in wheat-legume intercrops. The dilution effect is more related to disease intensity, while the barrier effect is more related to intercropping protectiveness.
6. Implications: These findings pave the way for identifying field indicators to predict epidemics. However, this study also stressed the critical lack of experimental data on disease in intercropping.

Keywords: Septoria tritici blotch, wheat leaf rust, intercropping, crop mixture, fungal epidemic

1. Introduction

Diversification of cropping systems is an important lever to improve the sustainability of disease management (Beillouin et al., 2021; Malézieux et al., 2009; Ratnadass et al., 2012), especially regarding climate change and global biodiversity loss (Carmona et al., 2020; Větrovský et al., 2019), and pesticide use and resistance (Bourguet and Guillemaud, 2016; Brown, 2015; Hawkins et al., 2019). Investigations on cereal mixtures for fungal disease management mainly focused on cultivar mixtures (Finckh et al., 2000; Mundt, 2002; Wolfe, 1985), while research on intercropping remain scare (Beillouin et al., 2021). Studies on cereal-legume intercropping for fungal disease management have reported a significant reduction in disease intensity (Boudreau, 2013; Guo et al., 2020; Luo et al., 2021b, 2022; Schoeny et al., 2010), including with cereals as the host species (Luo et al., 2021b; Zhang et al., 2019). However, these studies focus more on legume diseases than on cereal diseases (Boudreau, 2013; Zhang et al., 2019). Moreover, worldwide, Septoria tritici blotch (STB), caused by *Zymoseptoria tritici*, remains one of the most devastating foliar diseases for wheat (Fones and Gurr, 2015), while wheat leaf rust (WLR), caused by *Puccinia triticina*, causes great annual yield losses too (Huerta-Espino et al., 2011). To our knowledge, no study has explored intercropping for STB and WLR management. Beyond quantifying the effect of intercropping on disease intensity and intercropping protectiveness (i.e., the effectiveness of intercropping to reduce disease intensity) in comparison to sole cropping, knowledge remains scarce on: (i) the underlying mechanisms; (ii) the effects of intercropping management practices such as species choice and fertilization on these mechanisms and intercropping protectiveness; (iii) integrative canopy indicators to better predict and manage epidemics when intercropping is used.

Regarding the underlying mechanisms, epidemics are driven by resource availability and accessibility for pathogens (Borg et al., 2018; Hernández-Ochoa et al., 2022; Levionnois et al., 2023). For wind- and rain-borne foliar diseases, resource availability and accessibility are mainly mediated by the dilution and barrier effects of the crop mixture (Borg et al., 2018; Boudreau, 2013; Levionnois et al., 2023). The dilution effect refers to the substitution of a host by a non-host species, which decreases the overall plant resources available for the pathogen in the cropping system. The barrier effect refers to the substitution or addition of a non-host species that intercepts the spore propagules. However, the dilution and barrier effects on disease intensity and intercropping are not quantitatively known for intercropping. A better knowledge and quantification of both effects for different types of mixtures would help determine the optimal crop mixtures.

Regarding the effects of management practices, the intercropping canopy is driven by host and non-host species choices. Different traits and dynamics (e.g., height, leaf area index, leaf area density, growth onsets and rates) on the one hand, and plant-plant interactions (competition, facilitation, complementary, and compensation; Justes et al., 2021) on the other hand, between host and non-host species, drive various canopy structures and finally epidemics. Most studies investigating cereal-legume intercropping focus on one non-host species at a time, thus limiting the identification of the most effective non-host species for a given pathogen and the related canopy growth characteristics. As another management practice nitrogen (N) fertilization is known to favor epidemics by increasing resource availability for pathogens in sole crops (Précigout et al., 2017). Based on a meta-analysis on intercropping, Zhang et al. (2019) suggested that N fertilization may increase disease intensity depending on the pathosystem but without affecting the intercropping protective effect. However, N fertilization theoretically increases both host and non-host biomass and yield, thus theoretically increasing both resource availability but also the barrier effect. This process also depends on specific plant-plant interactions. For instance, it is well known that cereals benefit more than legumes with N fertilization, which generally lessens the advantage of cereal-legume intercropping (Mahmoud et al., 2022) and theoretically favors epidemics due to the increased resource availability and reduced barrier effect.

In the perspective of disease management in intercropping, dynamically monitoring intercropping and disease development is experimentally demanding and challenging. This is why it is useful to identify the indicators of crop growth and of disease regulation for wheat, the companion crop, or both. These indicators can then be measured more easily and used to characterize the associations and their potential impact on diseases. The complex dynamics of plant growth and epidemics suggest there should be numerous easy-to-measure canopy characteristics that can evaluate disease risk, particularly in intercropping contexts (Luo et al., 2021a, 2021a; Ratnadass et al., 2012; Toffolini et al., 2015). Specifically, it is unknown what should be measured and when. Indeed, intercropping involves complex systems with several species in interaction and different growth dynamics and traits. The identification of these easy-to-measure indicators is, however, a very important issue, as it will enable more studies to be carried out on intercropping for disease management, especially as experiments involving intercropping with disease monitoring are complex and complicated to carry out. It will also enable us to identify mixtures or hosts that are more effective in limiting disease.

To achieve these four goals (i.e., impact of intercropping on disease intensity, intercropping mechanisms, effects of intercropping management practices, and development of

canopy indicators), plant-pathogen modelling is a promising approach (Gigot et al., 2014; Hernández-Ochoa et al., 2022; Levionnois et al., 2023; Mikaberidze et al., 2015; Vidal et al., 2018). Models can explore diverse different virtual associations, in diverse pedoclimatic conditions, and with different management practices, thus permitting to test different indicators. However, modelling such systems is challenging, as experimental data are critically lacking for disease in intercropping systems. These experiments are thus complex and difficult to perform. For instance, the modelling of foliar diseases requires disease and LAI monitoring for different management practices (e.g., species choice, N fertilization, sowing density, spatial arrangement) and pedoclimatic conditions, which is time-consuming.

This is why, to quantify the impact of different intercropping systems on disease epidemics, we developed a methodological modelling strategy with the available data. (1) We collected existing experimental data based on a literature survey of LAI monitoring in wheat intercropped with legumes (Mahmoud et al., 2022). These data incorporate two management practices: different non-host legume species (pea and faba bean) and N fertilization treatments. (2) Based on a previously published model of epidemics in intercropping (Levionnois et al., 2023), we modelled the disease epidemics by injecting the collected LAI data into the model. The study and the model were based on LAI (leaf area index, $m^2\ m^{-2}$) because (i) diseased leaf surface is generally used to study and monitor epidemic foliar diseases (e.g., Kristoffersen et al., 2020; M'Barek et al., 2020), (ii) diseased leaf surface is related to growth and yield losses (Bancal et al., 2007), and (iii) LAI enables to represent effectively both resource availability and spore interception in the model (Levionnois et al., 2023). The model was parameterized for two wheat fungal diseases -STB, a rain-borne disease, and WLR, an air-borne disease- in order to identify how model outputs and intercropping effects can differ according to different disease functional strategy (rain-borne vs. air-borne).

In this study, using the model, we then address the following questions: (1) Can wheat-based intercropping reduce disease intensity? (2) What are the effects of species choice and N fertilization on disease intensity and intercropping protectiveness? (3) What are the leading mechanisms between the dilution and barrier effects in driving disease intensity and intercropping protectiveness? (4) Can simple easy-to-measure indicators predict epidemics in field conditions?

2. Materials and methods

2.1. General methodology

This study was based on data from six field experiments, representing 46 treatments, with wheat intercropped with either pea or faba bean that were either fertilized with nitrogen (N) or not (Bedoussac and Justes, 2010a; Kammoun et al., 2021; Mahmoud et al., 2022), based on the recent literature survey of Mahmoud et al. (2022) of cereal-legume intercrops across Europe that combined various intercropped species and N fertilization levels. The study was also based on a previously released epidemic model of STB and WLR modelling wheat intercropped with legumes (Levionnois et al., 2023). As the study and the model were based on LAI (leaf area index, $m^2\ m^{-2}$), we selected experiments that incorporated monitored LAI data for both wheat and the companion species to supply the model with empiric LAI curves and then to simulate disease development. All LAI data and deviated LAI curves for the model were disease free.

Based on epidemic simulations, we analyzed three disease outputs (disease intensity, disease rate, and intercropping protectiveness; see section *Epidemic model and disease outputs*) by comparing intercropping to the corresponding sole wheat. First, we analyzed the extent to which intercropping can reduce the disease pressure and improve protectiveness for both diseases. Second, to better understand the underlying mechanisms of intercropping and to propose indicators to predict epidemics in field conditions, we analyzed the capacity of easy-to-measure LAI indicators (i.e. maximum LAI, surface under LAI curve, time before maximum LAI) to predict disease outputs. We proposed indicators based on our knowledge of the studied diseases and processes regulating epidemics. Third, we tested the statistical effect of species choice and N fertilization on disease outputs.

2.2. Field experimental data

Based on the recent literature survey of Mahmoud et al. (2022), we gathered data from six factorial experiments conducted in Auzeville, France (43°31′42″N, 1°28′56″E; Table 1). We used the following criteria to include a set of experiments in our database: (1) each treatment is a specific intercrop, with wheat, a given non-cereal species, and a given N application; (2) a given treatment was observed in at least two experiments, defined by a single combination "site x year"; and (3) the two intercropped species in each treatment were monitored for LAI ($m^2\ m^{-2}$) along the cropping season with at least three LAI measurements after sowing. All LAI data here were disease free. A total of six experiments (Bedoussac and Justes, 2010a; Kammoun et al., 2021; Mahmoud et al., 2022) with 46 treatments were retained (Table 1). The initial purpose of this study was to investigate as many as possible management practices (e.g. sowing date, sowing density, etc). However, the necessity to have LAI monitoring for both intercropped

species led to a limited number of treatments where only non-host species choice (pea vs. faba bean) and N fertilization has been properly investigated.

For experiments retained, wheat was only represented by durum wheat (*Triticum durum* L.), with the following cultivars represented: L1823, Acalou, Or Jaune, Nefer, and Sculptur (Mahmoud et al., 2022). Legumes were represented by pea (*Pisum sativum* L.) and faba bean (*Vicia faba* L.), with the following cultivar represented: Aoph10, Geronimo, Isard, and Lucy for pea; Castel, Irena, and Nordiaca for faba bean (Mahmoud et al., 2022). All six experiments were conducted in different years between 2006 to 2013 (Table 1). In each treatment, the two intercropped species were sown at the same time. Treatments varied in spatial arrangements (alternate vs. within row) but with a majority of a within-row pattern (Appendix S1). However, the epidemic model does not consider these patterns but only LAI. Treatments also varied in sowing relative density, but with a majority of substitutive design (i.e. global relative density = 1) and half density relatively to the recommended one for each intercrop (Appendix S1).

In the dataset, 15 out of the 46 treatments were wheat intercropped with pea and 31 were wheat intercropped with faba bean (Appendix S1). Twenty-nine out of the 46 treatments were not N-fertilized (controls) and 17 were N-fertilized, with N-fertilization ranging from 45 to 180 kg N ha^{-1}. The sowing dates of the six experiments ranged from November 8 to December 3. LAI was measured three to five times in the different treatments (Table 1). Additional details of the experimental designs and management practices are reported in Appendix S1 based on the reference publications (Bedoussac and Justes, 2010a; Kammoun et al., 2021; Mahmoud et al., 2022).

2.3. Epidemic model and disease outputs

The model is based on a SEIR (Susceptible, Exposed, Infectious, Removed) model (Li and Muldowney, 1995). The SEIR model is a compartmental model that represent the transition of populations move between different states (or compartments) through differential equations. Specifically, it characterizes four states that govern the development of an epidemic development across populations, generally from susceptible (or healthy) to exposed (or latent), from exposed to infectious, and from infectious to removed. In this study, the SEIR model is adapted to “populations” of crop canopy which is sensitive to a fungal pathogen, expressed in LAI units, in order to simulate fungal epidemic dynamics based on canopy growth. A canopy is modelled with simple growth functions, representing either one or two crops in a within-row mixture. In addition to the crop growth dynamics (LAI curve), the difference between the two crop species is defined by disease susceptibility: a crop susceptible to studied diseases is defined

as wheat, while the non-host is qualitatively and definitely resistant to studied diseases. There is no explicit spatial structure within the canopy. In addition to LAI curves, a set of parameters for each crop describes the relative proportion, growth, phenology, sowing date, and canopy porosity. Interactions between plants (e.g., competition for resources, facilitation) as well as plant resource dynamics are not explicitly and mechanistically taken into account in the model.

The epidemic is modelled in terms of the latent wheat tissue being infected, infectious wheat tissue sporulating, spore flows from spore production to spore dispersal and finally infecting the wheat. Two foliar diseases are modelled, STB and WLR, with two respective sets of pathogen trait parameters describing the infection rate, latent period, spore production rate, and spore mortality rate (Levionnois et al., 2023).

As weather conditions impact epidemics, they are incorporated into the model. For STB, which is a rain-borne disease, rainfall data are used to define spore dispersal events (Levionnois et al., 2023; Robert et al., 2018, 2008). For WLR, weather conditions are implicitly accounted for by an epidemic start parameter, as the more favorable the conditions are for the WLR epidemic in terms of spring mild temperature, the earlier the epidemic starts (Duvivier et al., 2016; Garin et al., 2014). Finally, for both diseases, a parameter for the initial inoculum quantity initializes the epidemic simulation and impacts the epidemics. A complete description of the model and parameters is given in (Levionnois et al., 2023).

The model simulates the latent and then sporulating diseased leaf surface (i.e., latent and infectious LAI) over thermal time (degree day). To quantify disease, we relied on three outputs: disease intensity, disease rate, and intercropping protectiveness. For disease intensity, we relied on AUDPC (area under disease progress curve), measured as the integral of the cumulated wheat LAI that passed through the infectious (or sporulating) state at the end of the season (Madden et al., 2017). AUDPC takes into account both the earliness and severity of disease.

To standardize comparisons of AUDPC, we relied on the disease rate which was measured as relative AUDPC, i.e. the ratio between AUDPC and the 'area under the LAI progress curve' at the end of the cropping season, or the surface under the LAI curve for non-diseases wheat leaf area, as in equation (1).

$$(1)\quad relative\ AUDPC = AUDPC/\sum LAI$$

Intercropping protectiveness (i.e., intercropping effectiveness to reduce disease intensity) was defined as reduction of the AUDPC compared with the sole wheat crop. For a given *in silico* intercropping experiment associated with an AUDPC value, we also simulated an *in silico* experiment by virtually removing the non-host crop (i.e., legume) while keeping the

same wheat LAI and making the two *in silico* experiments comparable, thus leading to a virtual similar sole wheat crop. In other words, the barrier effect provided by the non-host is isolated while the dilution effect is not modified. Then, AUDPC reduction was calculated as in equation (2).

$$(2)\ AUDPC\ reduction = 1 - (AUDPC_{IC}/AUDPC_{SC})$$

where $AUDPC_{IC}$ is AUDPC calculated for a given wheat-legume intercrop and $AUDPC_{SC}$ is AUDPC calculated for the same treatment after virtually removing the legume in the sole wheat.

The key model inputs on which we focused in this study are wheat LAI and companion LAI, weather conditions (rainfall data for STB and epidemic start for WLR), and initial inoculum.

2.4. LAI curve modelling from experimental data for model input

The LAI curves, which provide LAI estimates for each thermal time value (degree days) were made based on the 3-5 measured LAI values per treatment (Table 1) plus an estimated LAI=0 at sowing using a monotonic piecewise cubic spline interpolation (Wolberg and Alfy, 2002). The smooth curve is fitted such as a LAI is estimated every 10 degree-days for simulation purposes. The curves were fitted in Python using the SciPy package (Virtanen et al., 2020) and the PlantGL package (Pradal et al., 2009) from the OpenAlea platform (Pradal et al., 2008).

2.5. Simulation scenarios

To increase the robustness of our study, we ran epidemic simulations for three different weather conditions and three initial inoculum conditions, which both play a crucial role in the resulting epidemics (Estep et al., 2014; Précigout et al., 2023; Robert et al., 2018). We used these simulations to analyze both the effect of species choice and N fertilization on disease intensity and intercropping protectiveness and the capacity of LAI indicators to predict disease intensity and intercropping protectiveness.

For STB, different weather conditions have been related to different rainfall, based on the number of rainfall events during a year, as a rainfall event triggers spore dispersion. Data were based on the daily monitoring performed at the weather station of INRA Grignon (78850 France). We used the year 1997 as an average rainfall year, 2000 as a high rainfall year, and 2007 as a low rainfall year (Garin et al., 2018; Levionnois et al., 2023; Robert et al., 2008). For WLR, the number of days between sowing and the onset of epidemics was used as an integrative parameter for weather conditions, as the more favorable the conditions are in terms of spring mild temperature, the earlier the epidemic starts. We used 800, 900, and 1000 dd after sowing

to simulate favorable, average, and unfavorable conditions, respectively. (Garin et al., 2018; Levionnois et al., 2023)).

For disease initialization, we studied three different values of initial inoculum artificially inserted into the field, expressed as the number of spores, for both diseases: 2e6, 2e5, and 2e4 for STB, and 5e4, 2.5e4, and 1e4 for WLR, which correspond to high, medium, and low initial inoculum, respectively (Robert et al. 2018; Garin et al. 2018). These values were parameterized to mimic epidemic stability throughout successive cropping seasons. More details on how the initial inoculum is incorporated into the equations are given in (Levionnois et al., 2023).

The total number of simulations used for this study is as follows: 2 (sole crop + intercrop) x 2 diseases x 46 field treatments x (3 weather conditions + 3 initial inoculum conditions) = 1104 simulations.

2.6. Predicting simulated disease outputs from LAI indicators

To identify potential crop indicators and to shed light on the mechanisms (i.e., dilution and barrier effects), we used the model to test the capacity of simple LAI indicators to predict the disease outputs. In terms of ecological mechanisms, we know that the LAI of both the host and companion species determines the foliar fungal disease dynamics through resource dilution and resource accessibility effects, respectively (Levionnois et al., 2023). The aim was to move away from dynamic simulations of both host and non-host LAI to simpler single indicators, which required the characterization of LAI growth by measuring key information relating to disease dynamics. We thus extracted different LAI indicators to test which ones were linked to the best prediction. We tested three types of indicators for both wheat and the companion crop: (1) the maximum LAI reached during the cropping season ($LAI_{wheat,max}$ and $LAI_{comp,max}$, respectively); (2) the surface under the LAI curve throughout the cropping season (ΣLAI_{wheat} and ΣLAI_{comp}, respectively); and (3) the date at which the maximum LAI was reached ($tmax(LAI_{wheat})$ and $tmax(LAI_{comp})$, respectively). For ΣLAI_{wheat}, as the level of resource availability at the beginning of the cropping the season is key, we also estimated for wheat the surface under the LAI curve for the 100 first degree-days ($\Sigma LAI_{wheat,(0\text{-}100)}$). For these three types of indicators (maximum LAI, surface under the LAI curve, and timing of maximum LAI), we also examined the difference and the ratio between wheat and the companion crop.

To analyze the disease prediction power of the LAI indicators, we relied on linear or non-linear models (logarithmic and polynomial; $\alpha = 0.05$) depending on best fitting, and compared R^2 between indicators. We also conducted multiple linear models with no interaction based on two explanatory variables: one related to the host and the other to the non-host. Then,

we tested all possible combinations given by the host and non-host LAI indicators. The three best models for each disease output (AUDPC, relative AUDPC, and AUDPC reduction) and for each disease were selected and shown based on the Akaike information criterion with R software and the glmulti package (Calcagno and Mazancourt, 2010). To analyze the effects of weather and initial inoculum conditions on the relationships, we compared the slopes across these conditions.

2.7. Statistical analysis for the effects of species choice and N fertilization

To analyze the potential effects of species choice and N fertilization on the three disease outputs, we adjusted multiple linear mixed-effect models. We analyzed species choice and N fertilization as two fixed effects, with both variables being categorical (faba bean vs. pead intercropped with wheat; no fertilization vs. N fertilization; Table 1). As crop years relate to different pedoclimatic conditions, which are not fully characterized in this dataset, we considered them as a random factor, as in equation (3).

$$(3)\ Y_{ijk} = \mu + S_i + F_j + \varepsilon_{ijk}$$

Where Y_{ijk} is one of the three disease outputs for species i with N-fertilization j in environment k, μ is the overall mean, S_i is the main effect of the i-th species, F_j is the main effect of the j-th N-fertilization level, and ε_{ijk} is the ijk-th residue. To validate the models, we a posteriori analyzed the normality of residuals based on a Shapiro test ($\alpha = 0.05$).

All statistical analyses were performed using R software (R Core Team, 2018). Mixed-effect models were run with the lme function (nlme package) (Pinheiro and Bates, 2006). To analyze P-values ($\alpha = 0.05$), we used type II ANOVA tables (Anova function from the car package), which are more robust for unbalanced designs (Kassambara, 2018).

3. Results

3.1. LAI curves with or with no disease

When intercropping wheat with faba bean or pea with no disease, wheat had a similar range in LAI_{max} (respectively 0.3 to 3.1 $m^2.m^{-2}$ versus 0.4 to 3.3 $m^2.m^{-2}$) (Fig.1A). The range of LAI_{max} for faba bean intercropped with wheat remained the same (0.3 to 3.1 $m^2.m^{-2}$) while for pea grown it was more narrow (0.7 to 1.9 $m^2.m^{-2}$; Fig. 1D). The thermal time at LAI_{max} (tmax(LAI)) ranged from 920 to 1490 dd for wheat and from 1110 to 1640 dd for the companion species (Fig. 1). When intercropping wheat, tmax (LAI_{wheat}) was in the same range for faba bean- and pea intercropped with wheat, ranging from 920 to 1490 dd and from 1100 to 1390 dd,

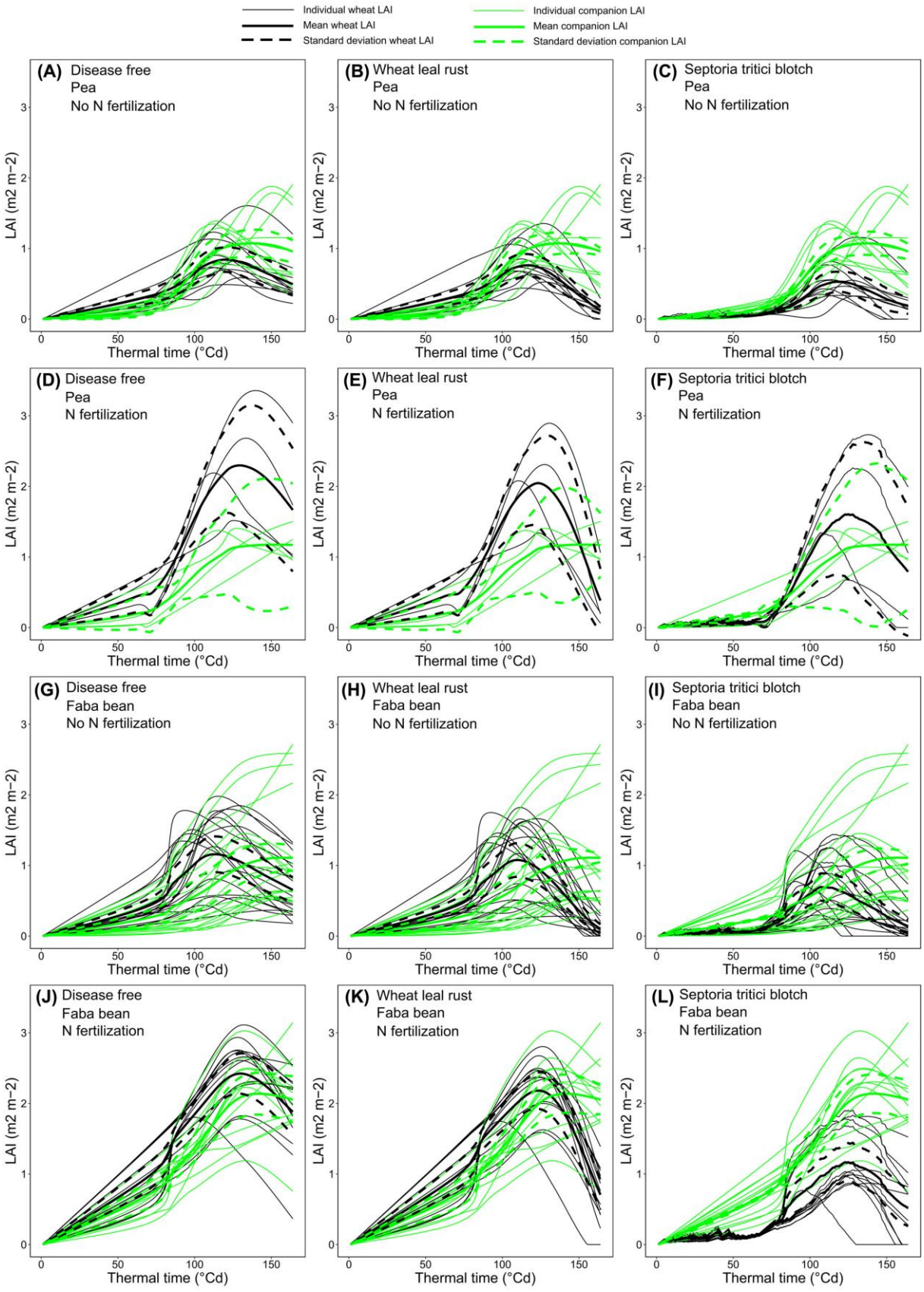


Fig. 1. Wheat and companion leaf area index (LAI) according to the thermal time (°Cd). For simulated diseased curves, only susceptible LAI is plotted (excluding latent and infectious LAI) to better capture the effect of the companion as the latter only acts on spore dispersion in the model. (**A**) Wheat and pea LAI without nitrogen (N) fertilization and disease free. (**B**) Wheat and pea LAI without N fertilization

and with WLR disease. (**C**) Wheat and pea LAI without N fertilization and with STB disease. (**D**) Wheat and pea LAI with N fertilization and disease free. (**E**) Wheat and pea LAI with N fertilization and WLR disease. (**F**) Wheat and pea LAI with N fertilization and STB disease. (**G**) Wheat and faba bean LAI without N fertilization and disease free. (**H**) Wheat and faba bean LAI without N fertilization and WLR disease. (**I**) Wheat and faba bean LAI without N fertilization and STB disease. (**J**) Wheat and faba bean LAI with N fertilization and disease free. (**K**) Wheat and faba bean LAI with N fertilization and WLR disease. (**L**) Wheat and faba bean LAI with N fertilization and STB disease.

respectively, as also for tmax(LAI_{comp}), ranging from 1310 to 1640 dd and from 1110 to 1640 dd, respectively. The surface under the LAI curve throughout the cropping season (ΣLAI) ranged from 32 to 263 for wheat and from 20 to 240 for the companion species. When intercropping wheat, both ΣLAI_{wheat} and ΣLAI_{comp} had larger ranges, with the highest ΣLAI values for faba bean intercropped with wheat (from 32 to 263 and from 20 to 240, respectively) in comparison to pea intercropped with wheat (from 42 to 226 and from 60 to 120, respectively). N fertilization only had a significant effect on wheat LAI indicators (LAI_{max}, tmax(LAI), ΣLAI), with larger LAI and longer LAI growth when N fertilization was applied, while no effect was found for the companion species (Fig. 1; Table S1). Species choice only had a significant effect on the companion LAI indicators (LAI_{max}, tmax(LAI), ΣLAI), while no effect was found for wheat (Fig. 1; Table S1). Specifically, LAI_{max} and ΣLAI were larger for pea intercropped with wheat, while tmax(LAI_{comp}) was larger for faba bean intercropped with wheat.

When WLR or STB diseases were simulated in intercropping (WRL: Fig. 1B, E, H, K; STB: Fig. 1C, F, I, L), they had visible effects on individual and mean LAI curves (Fig. 1), especially for STB (Fig. 1C, F, I, L) and for N fertilization (Fig. 1E, F, K, L). The negative disease effect on wheat LAI was stronger for STB in comparison to WLR because STB epidemic starts at the beginning of the cropping season, while WRL epidemic starts at least 800 dd after (e.g. Fig 1K vs. Fig. 1L).

3.2. Effect of intercropping on disease outputs

Simulated disease outputs covered a wide range and depended on the disease. Simulated AUDPC ranged from 9 to 162 and from 4 to 29 for STB and WLR, respectively (Fig. 2). Lower AUDPC values for WLR were due to the later onset of infection (80 dd after the start of the simulation), while the overall length of the cropping season was the same for both diseases. When intercropping wheat with faba bean, AUDPC ranged from 14 to 162 and from 4 to 29 for STB and WLR, respectively, while with pea it ranged from 9 to 81 and from 4 to 28 for STB and WLR, respectively (Fig. 2).

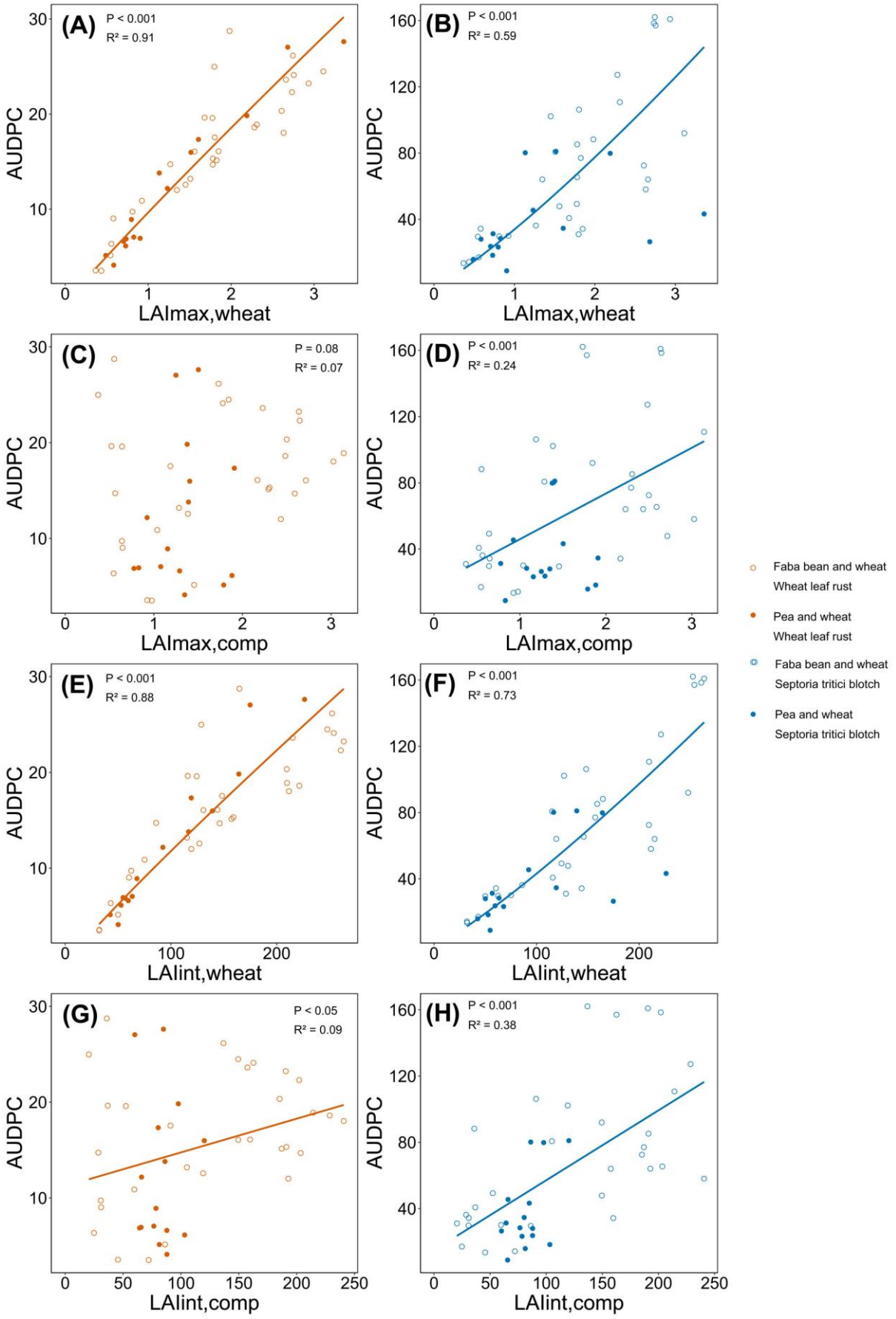

(A)
P < 0.001
R² = 0.91
(B)
P < 0.001
R² = 0.59
(C)
P = 0.08
R² = 0.07
(D)
P < 0.001
R² = 0.24
(E)
P < 0.001
R² = 0.88
(F)
P < 0.001
R² = 0.73
(G)
P < 0.05
R² = 0.09
(H)
P < 0.001
R² = 0.38
AUDPC
LAImax,wheat
LAImax,comp
LAIint,wheat
LAIint,comp
Faba bean and wheat
Wheat leaf rust
Pea and wheat
Wheat leaf rust
Faba bean and wheat
Septoria tritici blotch
Pea and wheat
Septoria tritici blotch

Fig. 2. Area under disease progression curve (AUDPC) according to the wheat and companion leaf area index (LAI) indicators for WLR (orange) and STB (blue). (**A, B**) AUDPC according to the maximum wheat LAI ($LAI_{wheat,max}$). (**C, D**) AUDPC according to the maximum companion LAI ($LAI_{comp,max}$). (**E, F**) AUDPC according to the surface under the wheat LAI curve (ΣLAI_{wheat}). (**G, H)**) AUDPC according to the surface under the companion LAI curve (ΣLAI_{comp}).

Relative AUDPC ranged from 15 to 81% and from 8 to 19% for STB and WLR, respectively (Fig. 3). When intercropping wheat with faba bean, relative AUDPC ranged from 24 to 81% and from 8 to 19% for STB and WLR, respectively, while with pea it ranged from 15 to 69% and from 8 to 15% for STB and WLR, respectively (Fig. 3).

Considering all the treatments, AUDPC reduction in comparison to sole wheat crop ranged from 0.8 to 30% for STB, while for WLR it ranged from 9.4 to 63% (Fig. 4). When intercropping wheat with faba bean, AUDPC reduction ranged from 0.8 to 30% and from 9.4 to 63% for STB and WLR, respectively, while with pea it ranged from 1.4 to 16% and from 26 to 43% for STB and WLR, respectively (Fig. 4).

Overall, simulated AUDPC was higher with favorable weather conditions (rainfall for STB and start of infection for WLR; Fig. 5A,B) and also with favorable initial inoculum (Fig. 6A,B). Simulated AUDPC reduction was higher with unfavorable weather conditions (rainfall for STB and start of infection for WLR; Fig. 5C, D) and also with unfavorable initial inoculum (Fig. 6C, D).

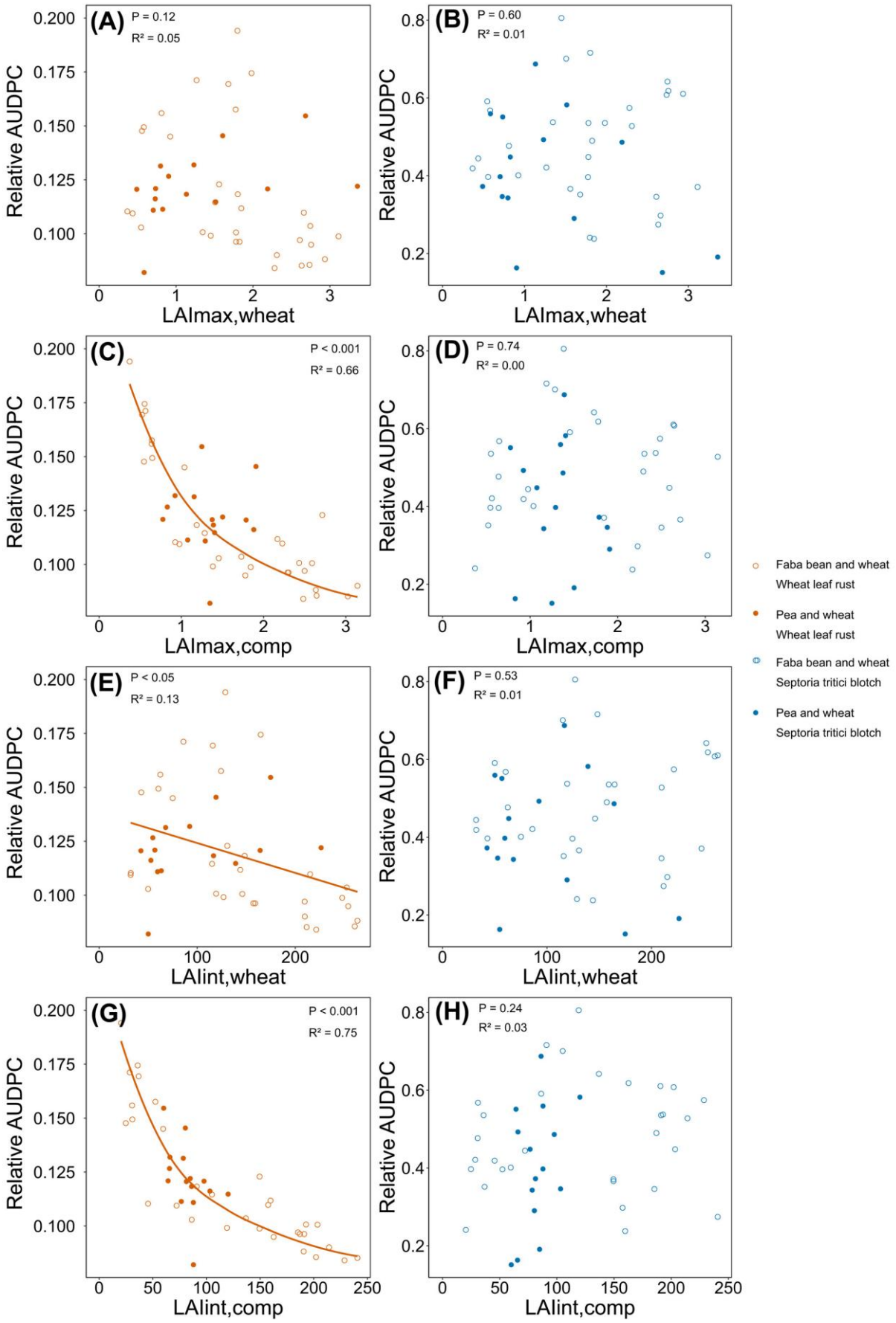

(A)
P = 0.12
R² = 0.05
(B)
P = 0.60
R² = 0.01
(C)
P < 0.001
R² = 0.66
(D)
P = 0.74
R² = 0.00
(E)
P < 0.05
R² = 0.13
(F)
P = 0.53
R² = 0.01
(G)
P < 0.001
R² = 0.75
(H)
P = 0.24
R² = 0.03
Relative AUDPC
LAImax,wheat
LAImax,comp
LAIint,wheat
LAIint,comp
Faba bean and wheat
Wheat leaf rust
Pea and wheat
Wheat leaf rust
Faba bean and wheat
Septoria tritici blotch
Pea and wheat
Septoria tritici blotch

Fig. 3. Relative AUDPC (area under disease progression curve) according to the wheat and companion leaf area index (LAI) indicators for WLR (orange) and STB (blue). (**A, B**) Relative AUDPC according to the maximum wheat LAI ($LAI_{wheat,max}$). (**C, D**) Relative AUDPC according to the maximum companion LAI ($LAI_{comp,max}$). (**E, F**) Relative AUDPC according to the surface under the wheat LAI curve (ΣLAI_{wheat}). (**G, H**) Relative AUDPC according to the surface under the companion LAI curve (ΣLAI_{comp}).

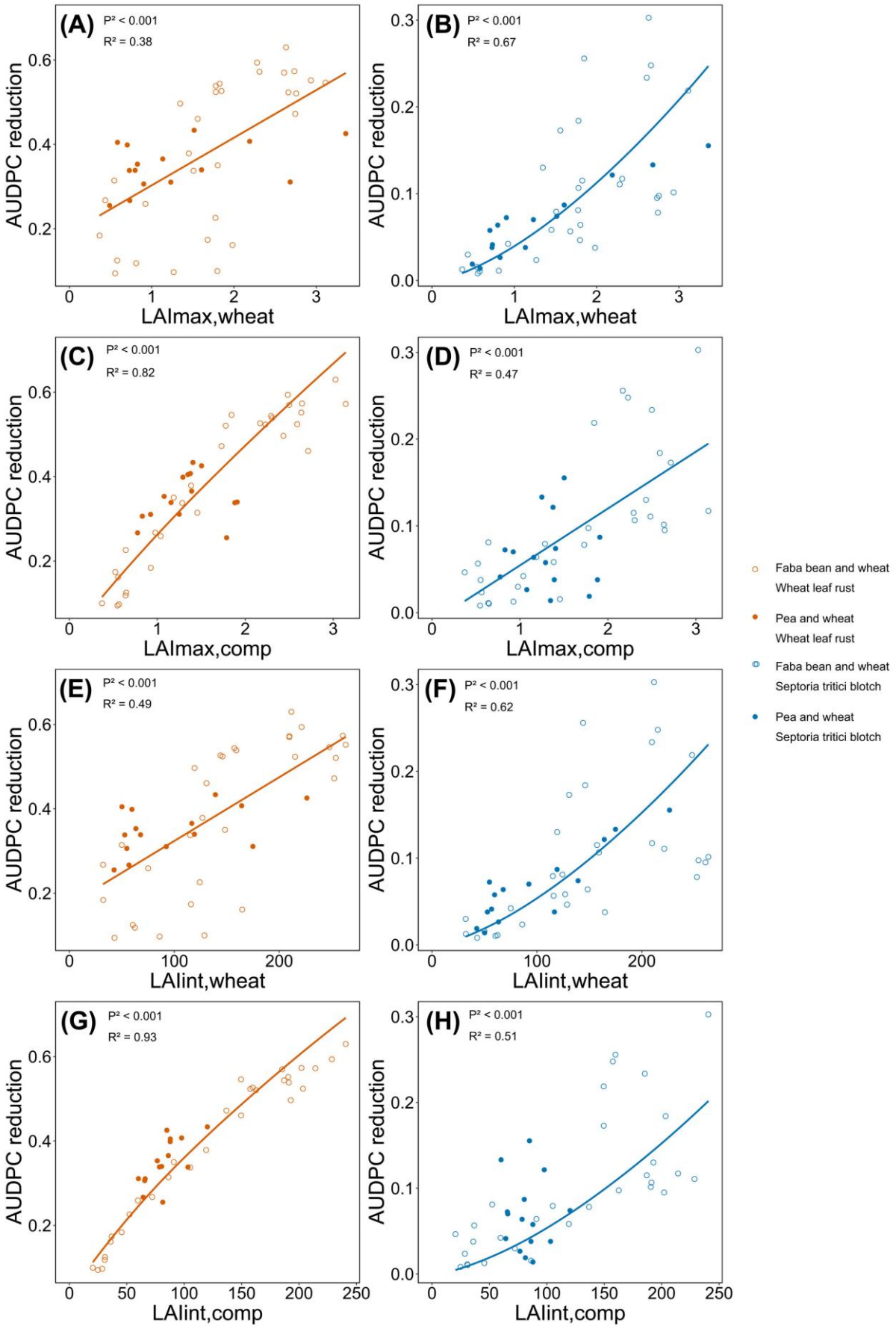

(A)
P² < 0.001
R² = 0.38
(B)
P² < 0.001
R² = 0.67
(C)
P² < 0.001
R² = 0.82
(D)
P² < 0.001
R² = 0.47
(E)
P² < 0.001
R² = 0.49
(F)
P² < 0.001
R² = 0.62
(G)
P² < 0.001
R² = 0.93
(H)
P² < 0.001
R² = 0.51
AUDPC reduction
LAImax,wheat
LAImax,comp
LAIint,wheat
LAIint,comp
Faba bean and wheat
Wheat leaf rust
Pea and wheat
Wheat leaf rust
Faba bean and wheat
Septoria tritici blotch
Pea and wheat
Septoria tritici blotch

Fig. 4. AUDPC (area under disease progression curve) reduction according to the wheat and companion leaf area index (LAI) indicators for WLR (orange) and STB (blue). (**A, B**) AUDPC reduction according to the maximum wheat LAI ($LAI_{wheat,max}$). (**C, D**) AUDPC reduction according to the maximum companion LAI ($LAI_{comp,max}$). (**E, F**) AUDPC reduction according to the surface under the wheat LAI curve(ΣLAI_{wheat}). (**G, H**) AUDPC reduction according to the surface under the companion LAI curve (ΣLAI_{comp}).

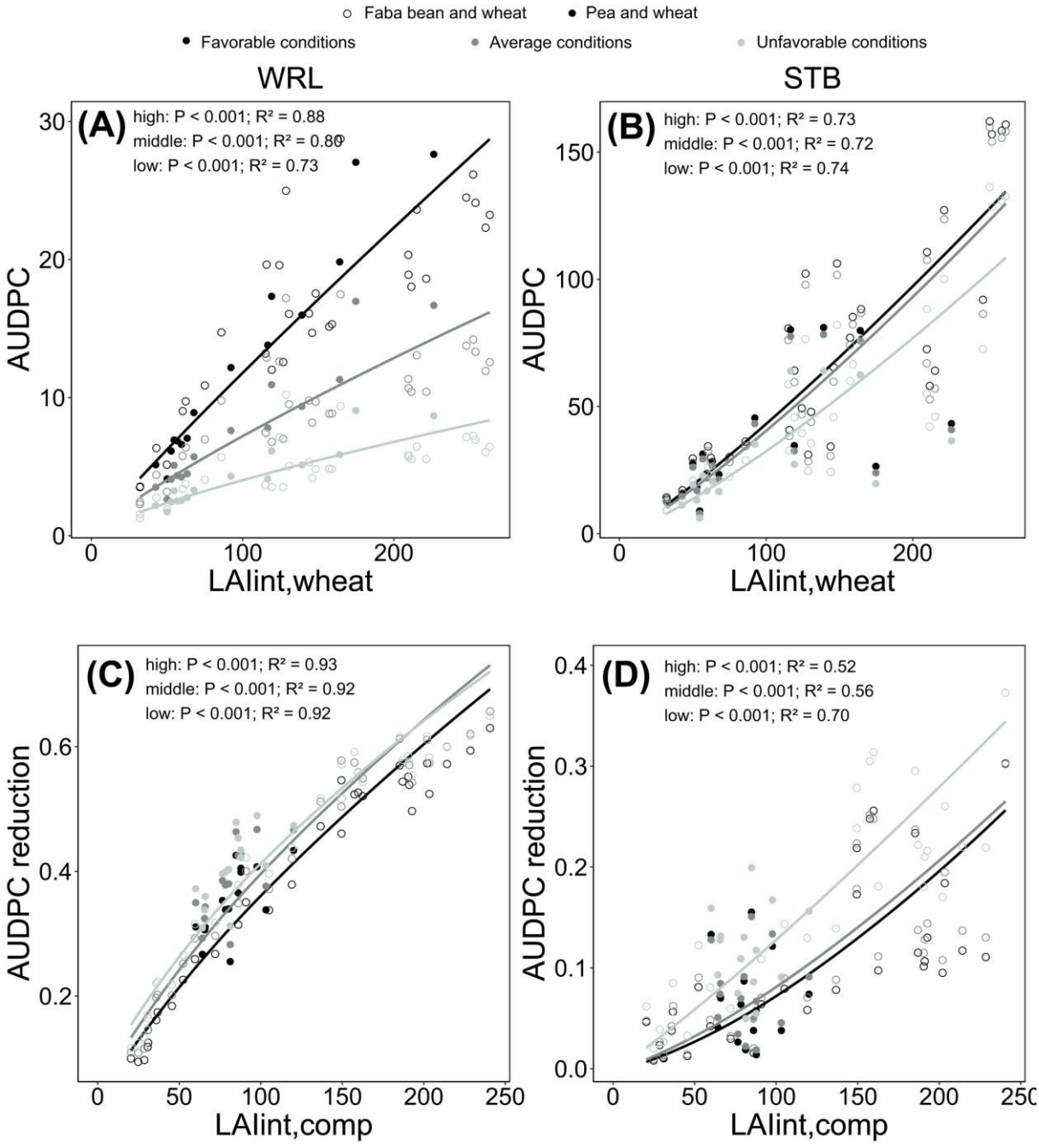


Fig. 5. Area under disease progression curve (AUDPC) and AUDPC reduction according to the wheat and companion leaf area index (LAI) indicators for different weather conditions. (**A**) AUDPC according to the surface under the wheat LAI curve (ΣLAI_{wheat}) for wheat leaf rust (WLR). (**B**) AUDPC according to the surface under the wheat LAI curve (ΣLAI_{wheat}) for Septoria tritici blotch (STB). (**C**) AUDPC reduction according to the surface under the companion LAI curve (ΣLAI_{comp}) for WLR. (**D**) AUDPC reduction according to the surface under the companion LAI curve (ΣLAI_{comp}) for STB. Black: favorable conditions (t_{inf} = 80 dd for WLR; high rainfall in 2000 for STB); gray: average conditions (t_{inf} = 90 dd

for WLR; average rainfall in 1997 for STB); light gray: unfavorable conditions (t_{inf} = 100 dd for WLR; low rainfall in 2007 for STB).

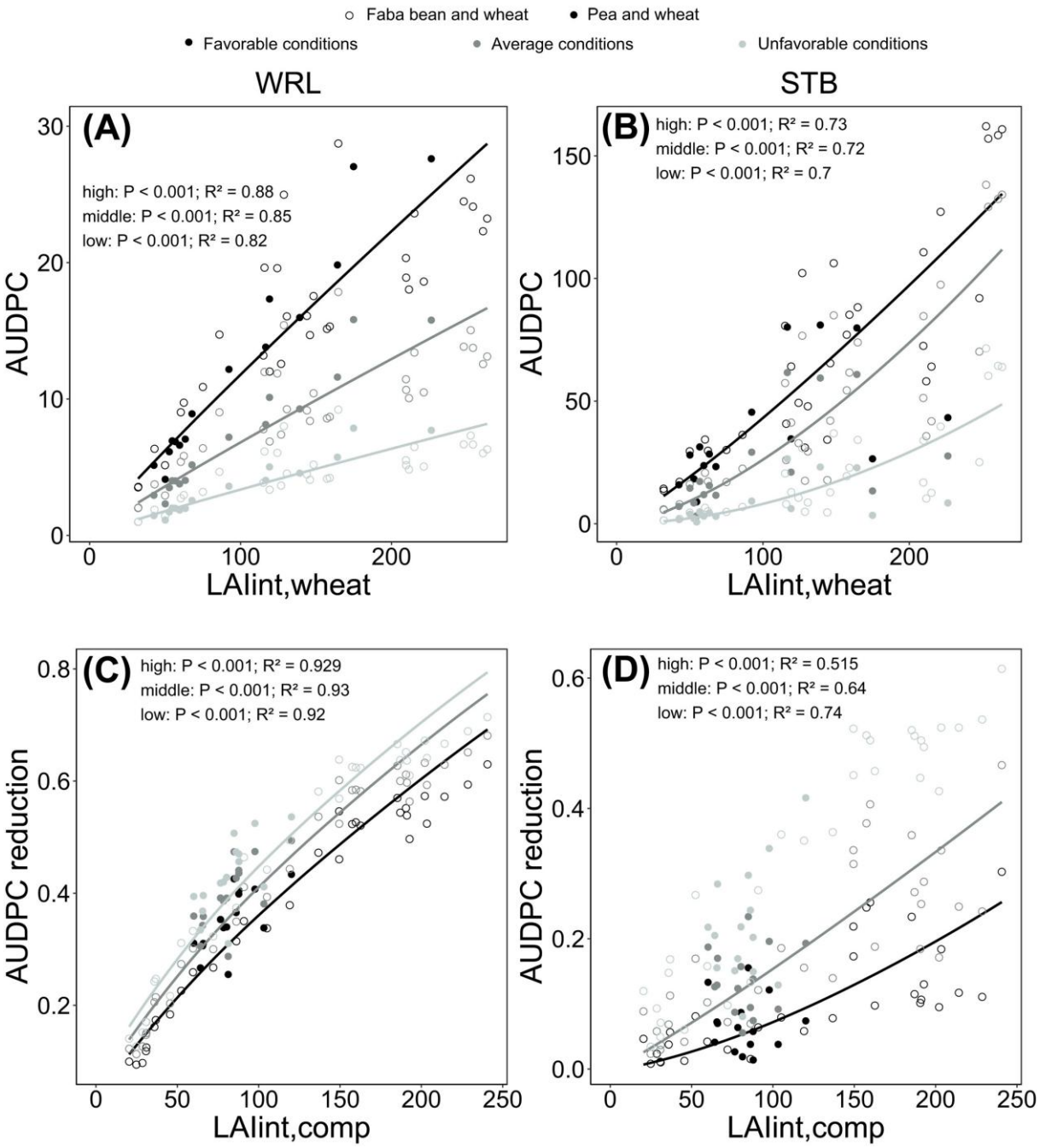


Fig. 6. Area under disease progression curve (AUDPC) and AUDPC reduction according to the wheat and companion leaf area index (LAI) indicators for different initial inoculum. (**A**) AUDPC according to the surface under the wheat LAI curve (ΣLAI_{wheat}) for wheat leaf rust (WLR). (**B**) AUDPC according to the surface under the wheat LAI curve (ΣLAI_{wheat}) for Septoria tritici blotch (STB). (**C**) AUDPC reduction according to the surface under the companion LAI curve (ΣLAI_{comp}) for WLR. (**D**) AUDPC reduction according to the surface under the companion LAI curve (ΣLAI_{comp}) for STB.

3.3. Predicting simulated disease outputs from LAI indicators

AUDPC could be predicted by simple LAI indicators such as LAI_{max} and ΣLAI (or $\Sigma LAI_{wheat,(0-100)}$ in case of STB) of the wheat and companion species and for both diseases (Table 2; Fig. 2). For both diseases, the best disease indicators were those related to wheat, with 85% and 47% of the variance explained by $LAI_{wheat,max}$ for STB and WLR, respectively (Fig. 2A), and with 88% and 73% explained by ΣLAI_{wheat} for STB and WLR, respectively (Fig. 2C). The best indicator depended on the disease (Table 2). For WLR, the best indicator was LAI_{max} (R^2 = 0.91; Fig. 2A), whereas for STB, the best indicators were ΣLAI_{wheat} and $\Sigma LAI_{wheat,(0-100)}$ (R^2 = 0.73 and 0.98, respectively; Fig. 2C ; Table 2). Concerning indicators related to the timing of the maximum, only tmax(LAI_{comp}) weakly predicted AUDPC for WLR (R^2 = 0.10; Fig. 2F).

Relative AUDPC could also be predicted by simple LAI indicators but to a lesser extent than AUDPC (Table 2; Fig. 3). It was noteworthy that almost no indicator predicted relative AUDPC for STB. Only $\Sigma LAI_{wheat,(0-100)}$ and tmax(LAI_{wheat}) predicted relative AUDPC but weakly (R^2 = 0.44 and 0.11, respectively; Table 2). The best indicators related to the companion species for WLR, with 66% of the variance explained by $LAI_{comp,max}$ (Fig. 3B) and with 75% explained by ΣLAI_{comp} (Fig. 3D). Concerning the indicators related to the timing of the maximum, tmax(LAI_{comp}) weakly predicted relative AUDPC for WLR (R^2 = 0.08; Fig. 3F), while tmax(LAI_{wheat}) weakly predicted relative AUDPC for STB (R^2 = 0.11; Fig. 3E).

Reduction in AUDPC in intercrops could also be predicted by simple LAI indicators such as LAI_{max} and ΣLAI of the wheat and companion species, and for both diseases (Table 2; Fig. 4). The best indicators however differed for both diseases. For WLR, the best indicators related to the companion crop, with 82% and 93% of variance explained by $LAI_{comp,max}$ and ΣLAI_{comp}, respectively (Fig. 4B,D). For STB, the best indicators related to both the wheat and companion species, with 67% and 47% of variance explained by $LAI_{wheat,max}$ and $LAI_{comp,max}$, respectively (Fig. 4A,B), and with 62% and 51% of variance explained by ΣLAI_{wheat} and ΣLAI_{comp}, respectively (Fig. 4C,D). For the indicators related to the timing of the maximum, only tmax(LAI_{wheat}) for WLR weakly predicted AUDPC reduction (R^2 = 0.11; Fig. 4E).

Overall, for both diseases, AUDPC was best predicted by wheat LAI indicators, whereas relative AUDPC and AUDPC reduction in intercrops were best predicted by companion LAI indicators (Fig. 2; Fig. 3; Fig. 4; Table 2). Overall , WLR outputs were better predicted than STB outputs, in terms of both percentage of variance explained and number of significant indicators, excepting when $\Sigma LAI_{wheat,(0-100)}$ was introduced and for AUDPC (Table 2; Table S2). Furthermore, tmax(LAI) gave poor predictions, and differences and ratios between the indicators were never as good as the constitutive indicators alone (Table 2).

When implementing multiple models with two LAI curve indicators (host and non-host, respectively), better predictions were found for every disease output and both diseases up to R^2 = 0.92 (Table S2). The value of using the LAI of both crops (wheat and companion) depends very much on the type of output sought and the disease. In particular, R^2 increased from 0.44 with a standalone indicator to 0.53 with two for relative AUDPC of STB, while no increase was observed for AUDPC of both WLR and STB.

The effects of weather conditions on the predictive capacity of LAI indicators depended on the disease and the output (AUDPC or AUDPC reduction) (Fig. 5). Regarding AUDPC best predicted by ΣLAI_{wheat}, weather conditions had a strong effect for WLR, with lower AUDPC for a given ΣLAI_{wheat} value, lower slopes, and lower predictions in less favorable weather conditions (Fig. 5A). The slope was slightly lower for STB and for unfavorable weather conditions, although predictions based on R^2 values did not vary across conditions (Fig. 5B). Regarding AUDPC reduction best predicted by ΣLAI_{comp}, weather conditions had almost no effect for WLR, whereas the slope was higher for STB but the prediction lower in favorable conditions (Fig. 5C,D).

The effects of initial inoculum conditions on the capacity of LAI indicators to predict depended on the disease and the output (AUDPC or AUDPC reduction) (Fig. 6). Regarding AUDPC best predicted by ΣLAI_{wheat}, initial inoculum conditions had a strong effect for both diseases, with lower AUDPC for a given ΣLAI_{wheat} value, lower slopes, and lower predictions in less favorable weather conditions (Fig. 6A,B). Regarding AUDPC reduction best predicted by $\Sigma LAI_{comp,}$ weather conditions had almost no effect for WLR (Fig. 6C). For STB, initial inoculum conditions had a strong effect with higher AUDPC reduction, higher slope, and better predictions in less favorable initial inoculum conditions (Fig. 6D).

3.4. Significant effects of species choice and N fertilization on simulated diseases

Effects of species choice and N fertilization depend on both the disease output (AUDPC, relative AUDPC, and AUDPC reduction) and the disease (Table 3). N fertilization significantly ($P < 0.001$) increased the AUDPC for both diseases, while species choice did not affect the AUDPC for either disease ($P > 0.05$; Table 3). Overall, these results remained consistent for different weather (Table S3) and initial inoculum (Table S4) conditions. However, some interactions exist between species choice and weather conditions, as species choice had a significant effect on AUDPC for STB only under unfavorable weather conditions ($P < 0.01$), with higher AUDPC when intercropping wheat with faba bean (Table S3). Also, species choice had a significant effect on AUDPC for STB under average and unfavorable initial inoculum

conditions ($P < 0.05$), with higher AUDPC when intercropping wheat with faba bean (Table S4).

Regarding relative AUDPC, significant effects of species choice were only found for WLR ($P < 0.001$) such that relative AUDPC was higher for faba bean intercropped with wheat (Table 3). N fertilization had no effect on relative AUDPC for WLR ($P > 0.05$). Species choice and N fertilization had no effect for STB ($P > 0.05$). These results were consistently the same for different weather conditions (Table S3). However, these results changed slightly with the different initial inoculum conditions such that N fertilization had a significant effect on relative AUDPC under average and favorable initial inoculum conditions for STB ($P < 0.05$ and 0.01, respectively; Table S4), with higher relative AUDPC when N fertilization is applied.

Concerning AUDPC reduction in intercrops, significant effects were only found for WLR from both species choice ($P < 0.001$) and N fertilization ($P < 0.05$) such that AUDPC reduction was higher for pea intercropped with wheat and with N fertilization (Table 3). Conversely, there was no effect of species choice and N fertilization on AUDPC reduction for STB ($P > 0.05$). However, these results slightly changed with the different weather and initial inoculum conditions (Table S3; Table S4). Considering the weather conditions, N fertilization had no effect on AUDPC reduction under average and unfavorable weather conditions for WLR ($P > 0.05$), and species choice had a significant effect on AUDPC reduction under unfavorable weather conditions for STB ($P < 0.05$) such that AUDPC reduction was higher for pea intercropped with wheat (Table S3). Considering the initial inoculum conditions, N fertilization had no effect on AUDPC reduction under unfavorable initial inoculum conditions for WLR ($P > 0.05$), and species choice had a significant effect on AUDPC reduction under unfavorable initial inoculum conditions for STB ($P < 0.05$) such that AUDPC reduction was higher for pea intercropped with wheat (Table S4).

4. Discussion

Our results confirm that species choice and N fertilization influence simulated disease intensity and intercropping protectiveness compared with sole wheat. Specifically, N fertilization increased disease intensity without impacting intercropping protectiveness. For WLR, when intercropped with faba bean, disease rate increased and protectiveness decreased in comparison to pea. Moreover, we found that wheat host LAI indicators were highly related to disease intensity, while non-host LAI indicators were best related to intercropping protectiveness. This could be interpreted as, the dilution effect is more related to disease intensity, while the barrier effect is more related to intercropping protectiveness. This paves the way for identifying field

indicators to predict diseases for integrated pest management. Finally, this study encourages further research on intercropping for disease management and points to the critical lack of experimental data, which hinders the identification and optimization of intercropping management practices for disease management.

4.1. Effects of intercropping on simulated disease

The epidemic model applied to experimental monitored LAI data showed that overall, intercropping decreased the simulated disease intensity in comparison to a theoretical sole crop, reducing disease by up to 63% and 30% for WLR and STB, respectively. These results are consistent with two reviews analyzing the effect of cereal-legume intercropping systems with a focus on both cereal and legume pathogens (Boudreau, 2013; Zhang et al., 2019), with an average 45% decrease in disease incidence observed in Zhang et al. (2019). These authors also investigated yellow rust (*Puccinia striiformis*), and species close to *P. triticina*, and found an average 28% reduction in disease incidence. Comparisons with our results are nevertheless limited, as we used different disease measurements, as yellow rust and WLR (investigated here) are different diseases. Moreover, the disease reductions for WLR reported here are probably poorly estimated, as the *in silico* experiments were run for a relatively short cropping season (~1640 dd). Our modelling results for disease reduction with intercropping support crop diversification as an important lever for sustainable disease and pest management (Beillouin et al., 2021; Boudreau, 2013; Précigout et al., 2023; Ratnadass et al., 2012).

4.2. Underlying mechanisms of intercropping protectiveness

Regarding wind- and rain-borne diseases, several putative mechanisms are considered for disease reduction using intercropping (Borg et al., 2018; Boudreau, 2013; Zhang et al., 2019): (1) the dilution effect to decrease the resources available for the pathogen and/or the rate of spore deposition; (2) the barrier effect with the non-host crop that intercepts spores on the trajectory between two host crops; (3) alterations in microclimate conditions; (4) changes in host physiology and resistance; and (5) direct pathogen inhibition (i.e., allelochemicals). Based on their meta-analysis, Zhang et al. (2019) concluded that the dilution and barrier effects are probably the leading mechanisms. Accordingly, Schoeny et al. (2010) captured the effect of microclimate but concluded that the dilution and barrier effects are more important drivers. Finally, this is consistent with other studies that explain most of the disease intensity and/or intercropping protectiveness with only dilution and/or barrier effects (Levionnois et al., 2023; Skelsey et al., 2005).

Our study is noteworthy from this perspective, as it continually connects disease intensity, disease rate, and intercropping protectiveness with host and non-host LAI indicators. We found that host maximum host LAI and the surface under the LAI curve for host generally best predicted disease intensity, while non-host LAI generally best predicted disease rate and intercropping protectiveness. In other words, the dilution effect (that can be approximated by host LAI) is more related to disease intensity, while the barrier effect (that can be approximated by non-host LAI) is more related to disease rate and intercropping protectiveness. This is consistent with absolute disease intensity being a direct function of resource availability by the host LAI, whereas intercropping protectiveness is a direct function of the quantity of non-host LAI. However, this is not contradictory to the fact that both non-host and host LAI indicators predict disease intensity and intercropping protectiveness, as they are partly inversely related. The fact that the surface under the LAI curve is usually a better predictor than maximum LAI is in agreement with the polycyclic diseases studied here, which depend on the temporal distribution of LAI (Robert et al., 2018, 2008).

Overall, we found better predictions for WLR compared with STB, except for the surface under the LAI curve for the 100 first degree-day ($\Sigma LAI_{wheat,(0\text{-}100)}$), which best predicted AUDPC for STB, especially in comparison to the same indicator but for the whole season (ΣLAI_{wheat}). There are several possible explanations here. The start of the epidemic during the cropping season is later for WLR than for STB (800 dd vs. 0 dd in the model), such as the WLR epidemic starts when the host LAI is well-developed (even close to LAI_{max}). Therefore, the WLR starts when plenty of resource is directly available for the pathogen, which may explain the closer relationship between host LAI and AUDPC for WLR. Conversely, the STB epidemic starts at the same time of the development of both host and non-host species. Therefore, the STB epidemic is more limited by resource availability, and above all, is more exposed to interactions and feedbacks between the pathogen and the host (i.e. negative impacts on host growth), and between the pathogen and the barrier, leading to a less direct relationship between host LAI and AUDPC for STB. Finally, the fact that $\Sigma LAI_{wheat,(0\text{-}100)}$ best predicted AUDPC for STB, strengthens the idea that epidemics are sensitive to resources directly available for the pathogen, especially in initial conditions of polycyclic diseases (Robert et al., 2018, 2008). The better predictions of disease outputs from LAI indicators for WLR indicates that the degree of synchronization between the epidemic start and the host and non-host development in driving epidemics and intercropping protectiveness is paramount (Levionnois et al., 2023; Robert et al., 2018).

Moreover, regarding temporality, pea-based intercropping promotes higher protectiveness because of its higher and earlier growth in comparison to faba bean, thus promoting the synchronization between the epidemic and the barrier. Moreover, temporal indicators measured as the date at which the maximum LAI was reached can predict disease outputs, but with weak predictions. Specifically, for STB, the later the date of the maximum wheat LAI, the lower the disease rate and the higher the intercropping protectiveness. Furthermore, for WLR only, the later the date of the maximum companion LAI, the higher the disease intensity and disease rate and the lower the intercropping protectiveness. These results are also in agreement with the idea that the epidemic will be minimized, and intercropping protectiveness will be promoted with the late growth of the resource combined with the early onset of the barrier.

Finally, we observed a weak effect of different weather conditions or initial inoculum on the goodness of prediction of LAI indicators for disease intensity and intercropping protectiveness. This suggests that the underlying mechanisms simulated by our model are relatively independent of the weather conditions or initial inoculum. However, disease intensity remains positively related to more favorable conditions, which is in agreement with previous studies (Levionnois et al., 2023; Précigout et al., 2023; Robert et al., 2018).

4.3. Effects of intercropping management practices on simulated disease

Nitrogen fertilization and species choice (pea vs. faba bean) had different effects depending on the disease or output (disease intensity vs. disease rate vs. intercropping protectiveness). For N fertilization, our results consistently highlight the higher disease intensity for both diseases with little or no effect on the disease rate or intercropping protectiveness. This result is consistent with experimental studies investigating N fertilization with wheat or legume diseases (Luo et al., 2022, 2021b). This is also partially consistent with the meta-analysis of Zhang et al. (2019), which found an effect of N fertilization on disease intensity for one of the six investigated diseases (wheat powdery mildew) but no effect on intercropping protectiveness as in our study. Nevertheless, half of the diseases investigated by Zhang et al. (2019) are legume-specific. Accordingly, another experimental study focusing on legume-specific diseases found no effect of N fertilization on disease intensity and intercropping protectiveness (Guo et al., 2020). Combined with our results, this literature survey suggests that N fertilization differentially impacts disease intensity between cereal and legume pathogens, with a trend toward higher disease intensity with N fertilization but mainly for cereal diseases. This is consistent with the known phenomenon of higher cereal competitiveness in cereal-legume intercropping when N

fertilization is applied (Duchene et al., 2017; Mahmoud et al., 2022). However, these findings call for caution, as N fertilization may offset the negative impact on disease intensity by increasing yield (Luo et al., 2022, 2021b).

Our results indicate the higher disease rate and lower intercropping protectiveness with faba bean -compared to pea- intercropped with wheat for WLR but no effect for STB. In other words, in the agricultural conditions explored here, pea intercropped with wheat is more effective for management of wind-borne diseases such as WLR. This result is noteworthy, as it supports the fact that species choice can be a lever for intercropping-based disease management. This result was surprising, since faba bean is generally larger and with larger leaves than pea (Guinet et al., 2018), suggesting that it should act as a more effective barrier and thus increase intercropping protectiveness. This discrepancy may be related to the difference in LAI dynamics at the start of the WLR epidemics. Indeed, in our dataset, pea generally achieved high growth rates earlier than faba bean. Pea reached its maximum LAI around 1400 dd, while faba bean generally continued to grow slowly, with some treatments not reaching their maximum until ~2000 dd for the longest experimental monitoring (Fig. 1). Therefore, high and early growth appears to be an important criterion when choosing the companion species for WLR.

The different companion LAI dynamics may explain why we did not observe an effect of species choice for STB in terms of both disease intensity and intercropping protectiveness. Indeed, contrary to WLR, the STB epidemic starts at the beginning of the cropping season (800 dd and 0 dd, for WLR and STB respectively). However, pea and faba bean have both low growth rates at the start of the cropping season (between 0 and ~800 dd) in comparison to wheat (Bedoussac and Justes, 2010b). The WLR epidemic then starts when the barrier is already in place, but this is not the case for STB. This is consistent with the meta-analysis of Zhang et al. (2019), which found higher protectiveness during the early season due to lower epidemic pressure.

4.4. Canopy indicators for integrated disease management

As discussed above, our model allowed to explore the capacity of a wide range of LAI indicators to predict disease intensity, disease rate, and intercropping protectiveness, whereas investigating numerous indicators would be difficult in field conditions. Our model also indicates that these predictions are relatively independent of the environmental conditions (weather and initial inoculum), thus pointing to their robustness. Finally, we found that multiple models based on several LAI indicators provided the best predictions, suggesting that several indicators could be used for *in situ* forecasting. However, the capacity of these indicators to

make such predictions must now be tested in field conditions. This would pave the way for easy-to-measure canopy indicators based on plant traits that can be used as diagnostic criteria (Ratnadass et al., 2012). These indicators would be valuable tools for integrated disease management to adapt strategies and tactics at both the intra- and intercropping season levels in the context of intercropping.

4.5. Model limitations and perspectives

The model used in this study has several limitations that deserve to be improved to better tackle the questions asked here. To our knowledge, it is the first model incorporating both intercropping and epidemic. Indeed, existing models simulate either intercropping only (Gaudio et al., 2019), either crop epidemic only, offering no base of comparison. At least two issues limit the development of such models. First, they are intrinsically more complex as they incorporate several physiological and ecological processes: the physiological crop functioning, the plant-plant interaction regarding intercropping, the plant-pathogen interaction regarding epidemic, and feedbacks. Then, the issue is to not dramatically increase the number of parameters (Wallach et al., 2025). Yet, only few crop models or individual-based models are able to simulate annual intercropping (Gaudio et al., 2019), which are already complex models. Regarding epidemic model, some mechanistic models exist, focusing on physiology (Willocquet et al., 2025), dispersion (Gigot et al., 2014; Vidal et al., 2017), or both (Robert et al., 2008), but are already quiet complex. Adding a supplementary module to these existing models is then challenging. Consequently, there is an important issue to identify the appropriate conceptual and mathematical framework for modelling diseases in intercropping. The second issues relates to the critical lack of empirical data of diseases in intercropping, which limits further model calibration and validation.

Our model also suffers from a weak mechanistic basis, then there are several improvements which can be relatively easily considered. For instance, the model currently takes into account two climatic variables: temperature (as the date of different biological events measured in thermal time) and rainfall. This is a limitation as it is well-known that fungal epidemics are driven by interactions between microclimatic variables (e.g. radiance, moisture, canopy temperature, wind) and epidemic processes (e.g. spore production and dispersion, infection rate, latency)(Boudreau, 2013; Calonnec et al., 2013; Caubel et al., 2012). Then, the impacts of these climatic variables on disease simulations could be explored. Especially, intercropping with different species could shape different canopy structures and microclimates that could finally be the source of specific effects of intercropping on epidemics (Boudreau,

2013; Schoeny et al., 2010; Vidal et al., 2017). This is an interesting avenue deserving further work. Data on these meteorological aspects would therefore be invaluable as a complement to LAI and disease data in appropriate field trials.

Finally, the results presented here should be taken with caution due to the weak statistical power of the collected dataset, especially regarding pea intercropped with wheat (Fig. 1). To our knowledge, studies that target cereal diseases and directly compare different non-host species are scarce. Kinane and Lyngkjaer (2002) investigated both pea and faba bean intercropped with wheat, respectively, but initially failed to obtain sufficiently high disease intensity to measure the effect of intercropping in comparison to sole crop. Most studies targeting cereal diseases have investigated faba bean intercropped with wheat (Luo et al., 2022, 2021b; Zhang et al., 2019). This lack of data calls for further studies comparing different intercropped companion species that reflect the different LAI dynamics in mixtures with the aim to improve disease management. Other intercropping management practices such as fertilization, sowing dates, rotation, and tillage should be studied given their impact on LAI dynamics and mixture development (Colbach et al., 2021; Hernández-Ochoa et al., 2022). These data are also critical to better validating intercropping models such as the one used in this study.

5. Conclusion

This study supports that (i) N fertilization favors wheat diseases, while companion species choice potentially impacts disease intensity, (ii) the dilution and barrier effects may be the leading mechanisms driving disease intensity and intercropping protectiveness, and (i) canopy indicators can be used in field conditions to predict disease outputs and optimize disease management. Overall, these results suggest that intercropping management practices (N fertilization and species choice in this case) can be optimized for effective disease management in wheat-legume intercrops. These results also suggest that the target for driving the dilution and barrier effects – mediated by intercropping management practices – are the spatial distribution of host and non-host species (here measured by LAI) and their (de)synchronization with the pathogen taking into account the life cycle of the pathogens (epidemic onset, sporulation period, etc.). Therefore, beyond the need to promote research on intercropping from a disease management perspective, in our view, future studies should emphasize the following three aspects: (1) incorporating intercropping management practices (species and cultivar choice, N fertilization, differential sowing date, spatial arrangement, sowing density, etc.); (2) characterizing the underlying mechanisms that better target and optimize disease-minimizing

practices; and (3) integrating monitoring LAI and epidemic data, which favors the understanding of mechanisms and the proposing of crop indicators. The proposed canopy indicators (e.g., surface under the LAI curve) should be tested in field conditions regarding their capacity to predict disease outputs. Finally, model development taking into account microclimatic variables and other management practices, parameterization, and evaluation are all critically lacking and should be better targeted to understand and optimize intercropping from a disease management perspective.

CRediT authorship contribution statement

Sébastien Levionnois: Writing – original draft, Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software**. Noémie Gaudio:** Writing – review and editing, Data curation, Methodology, Resources, Supervision**. Rémi Mahmoud:** Writing – review and editing, Data curation, Formal analysis, Methodology, Resources**. Christophe Pradal:** Writing – review and editing, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Validation**. Corinne Robert:** Writing – review and editing, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation**.**

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Conflicts of interest

We have no conflict of interest to declare.

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TABLES

Table 1. Description of the six experiments of wheat-legume mixtures used in this study.

Site	Plot	Year	Sowing date	Legume	N fertilization treatments	Number of treatments*
Auzeville	Cochard	2010	11/20/2009	Faba bean	Yes	16
Auzeville	PP	2011	12/03/2010	Faba bean	Yes	3
Auzeville	SGs	2007	11/09/2006	Pea	Yes	3
Auzeville	TE	2006	11/08/2005	Pea	Yes	1
Auzeville	TO	2013	11/20/2012	Pea	Yes	8
Auzeville	ZN	2012	11/14/2011	Faba bean/Pea	No	15

*Including controls

Table 2. Linear mixed-effect models between Area under disease progression curve (AUDPC), relative AUDPC, and AUDPC reduction and agricultural practices, with experiment/year set as the random effect.

Disease	Response variable	Explanatory variables	P	Effect
Wheat leaf rust	AUDPC	Species	0.10	
		N fertilization	**< 0.001**	no fertilization < fertilization
	Relative AUDPC	Species	**< 0.001**	pea < faba bean
		N fertilization	0.37	
	AUDPC reduction	Species	**< 0.001**	faba bean < pea
		N fertilization	**< 0.05**	no fertilization < fertilization
Septoria tritici blotch	AUDPC	Species	0.19	
		N fertilization	**< 0.001**	no fertilization < fertilization
	Relative AUDPC	Species	0.64	
		N fertilization	0.36	
	AUDPC reduction	Species	0.50	
		N fertilization	0.82	

Bold values refer to significant correlations ($P < 0.05$). The effect column indicates in which groups (no fertilization vs. fertilization; pea vs. faba bean intercropped with wheat) the response variable is superior or inferior.

Table 3. Relationships between Area under disease curve (AUDPC), relative AUDPC, AUDPC reduction, and leaf area index (LAI) indicators

Disease	**LAI-curve descriptors**	**P**	**R^2**	**P**	**R^2**	**P**	**R^2**
		AUDPC		Relative *AUDPC*		*AUDPC* reduction	
WRL	$LAI_{wheat,max}$	**< 0.001**	**0.91**	0.12	0.05	**< 0.001**	**0.38**
	$LAI_{comp,max}$	0.08	0.07	**< 0.001**	**0.66**	**< 0.001**	**0.82**
	$LAI_{wheat,max}$ - $LAI_{comp,max}$	**< 0.001**	**0.60**	**< 0.01**	**0.22**	0.16	0.05
	$LAI_{wheat,max}$ / $LAI_{comp,max}$	**< 0.001**	**0.53**	**< 0.001**	**0.47**	**< 0.01**	**0.15**
	Σ LAI_{wheat}	**< 0.001**	**0.88**	**< 0.05**	**0.13**	**< 0.001**	**0.49**
	Σ LAI_{wheat}(0-100)	**< 0.001**	**0.38**	**< 0.001**	**0.25**	**< 0.001**	**0.33**
	Σ LAI_{comp}	**< 0.05**	**0.09**	**< 0.001**	**0.75**	**< 0.001**	**0.93**
	Σ LAI_{wheat} - Σ LAI_{comp}	**< 0.001**	**0.62**	**< 0.01**	**0.20**	0.23	0.03
	Σ LAI_{wheat} / Σ LAI_{comp}	**< 0.001**	**0.44**	**< 0.001**	**0.58**	**< 0.001**	**0.23**
	Σ LAI_{wheat} / (Σ LAI_{wheat} + Σ LAI_{comp})	**< 0.001**	**0.58**	**< 0.001**	**0.32**	0.13	0.05
	tmax(LAI_{wheat})	0.08	0.07	0.10	0.06	**< 0.05**	**0.11**
	tmax (LAI_{comp})	**< 0.05**	**0.10**	**< 0.05**	**0.08**	0.41	0.02
	tmax (LAI_{wheat}) - tmax (LAI_{comp})	0.45	0.01	**< 0.01**	**0.17**	**< 0.05**	**0.10**
STB	$LAI_{wheat,max}$	**< 0.001**	**0.59**	0.60	0.01	**< 0.001**	**0.67**
	$LAI_{comp,max}$	**< 0.001**	**0.24**	0.74	0.00	**< 0.001**	**0.47**
	$LAI_{wheat,max}$ - $LAI_{comp,max}$	0.09	0.06	0.39	0.02	0.60	0.01
	$LAI_{wheat,max}$ / $LAI_{comp,max}$	0.58	0.01	0.16	0.04	0.084	0.00
	Σ LAI_{wheat}	**< 0.001**	**0.73**	0.53	0.01	**< 0.001**	**0.62**
	Σ LAI_{wheat}(0-100)	**< 0.001**	**0.98**	**< 0.001**	**0.44**	0.29	0.02
	Σ LAI_{comp}	**< 0.001**	**0.38**	0.24	0.03	**< 0.001**	**0.51**
	Σ LAI_{wheat} - Σ LAI_{comp}	**< 0.01**	**0.13**	0.60	0.01	0.76	0.00
	Σ LAI_{wheat} / Σ LAI_{comp}	0.91	0.00	0.15	0.05	0.42	0.01
	Σ LAI_{wheat} / (Σ LAI_{wheat} + Σ LAI_{comp})	0.08	0.07	0.44	0.01	0.47	0.01
	tmax (LAI_{wheat})	0.52	0.01	**< 0.05**	**0.11**	0.05	0.08
	tmax (LAI_{comp})	0.81	0.00	0.06	0.08	0.46	0.01
	tmax (LAI_{wheat}) - tmax (LAI_{comp})	0.84	0.00	0.83	0.00	0.60	0.01

Bold values refer to significant correlations ($P < 0.05$).

SUPPLEMENTARY INFORMATION

Appendix S1. A spreadsheet file describing details for experiments and treatments used in this study: cultivars, nitrogen fertilization, spatial arrangement, relative density, sowing density, soil texture, annual rainfall, mean annual temperature.

Table S1. Statistical linear mixed-effect models to test correlations between leaf area index (LAI) indicators and agricultural practices, with experiment/year set as the random effect.

Response variable	Explanatory variables	P	Effect
$LAI_{wheat,max}$	Species	0.31	
	N fertilization	**< 0.001**	no fertilization < fertilization
$LAI_{comp,max}$	Species	**< 0.01**	faba bean < pea
	N fertilization	0.49	
ΣLAI_{wheat}	Species	< 0.25	
	N fertilization	**< 0.001**	no fertilization < fertilization
ΣLAI_{comp}	Species	**< 0.001**	faba bean < pea
	N fertilization	0.39	
$tmax(LAI_{wheat})$	Species	0.69	
	N fertilization	**< 0.01**	no fertilization < fertilization
$tmax(LAI_{comp})$	Species	**< 0.001**	pea < faba bean
	N fertilization	0.14	

Bold values refer to significant correlations ($P < 0.05$). The effect column indicates in which groups (no fertilization vs. fertilization; pea vs. faba bean intercropped with wheat) the response variable is superior or inferior.

Table S2. Statistical multiple models with two leaf area index (LAI) indicators (host and non-host) to test correlations between LAI indicators and simulation model outputs (Area under disease progression curve or AUDPC, relative AUDPC, AUDPC reduction). For each output, the three best statistical models are presented based on the Akaike information criterion.

Disease	**Output**	**LAI-curve descriptors**	**P**	**R^2**	**Standalone best-descriptor**	**R^2**
WLR	*AUDPC*	$LAI_{wheat,max}$ + Σ LAI_{comp}	**< 0.001**	**0.92**	$LAI_{wheat,max}$	**0.91**
		Σ LAI_{wheat} + Σ LAI_{comp}	**< 0.001**	**0.91**		
		$LAI_{wheat,max}$ + $LAI_{comp,max}$	**< 0.001**	**0.91**		
	Relative *AUDPC*	$LAI_{wheat,max}$ + Σ LAI_{comp}	**< 0.001**	**0.71**	Σ LAI_{comp}	**0.75**
		Σ LAI_{wheat} + Σ LAI_{comp}	**< 0.001**	**0.69**		
		Σ LAI_{comp}	**< 0.001**	**0.64**		
	AUDPC reduction	$LAI_{wheat,max}$ + Σ LAI_{comp}	**< 0.001**	**0.91**	Σ LAI_{comp}	**0.93**
		tmax(LAI_{wheat}) + Σ LAI_{comp}	**< 0.001**	**0.90**		
		Σ LAI_{wheat} + Σ LAI_{comp}	**< 0.001**	**0.90**		
STB	*AUDPC*	Σ LAI_{wheat}(0-100)	**< 0.001**	**0.98**	Σ LAI_{wheat}(0-100)	**0.98**
		Σ LAI_{wheat}(0-100) + tmax(LAI_{comp})	**< 0.001**	**0.98**		
		Σ LAI_{wheat}(0-100) + Σ LAI_{comp}	**< 0.001**	**0.98**		
	Relative *AUDPC*	Σ LAI_{wheat}(0-100) + $LAI_{comp,max}$	**< 0.001**	**0.53**	Σ LAI_{wheat}(0-100)	**0.44**
		Σ LAI_{wheat}(0-100) + tmax(LAI_{comp})	**< 0.01**	**0.52**		
		Σ LAI_{wheat}(0-100) + Σ LAI_{comp}	**< 0.05**	**0.52**		
	AUDPC reduction	$LAI_{wheat,max}$ + $LAI_{comp,max}$	**< 0.001**	**0.63**	$LAI_{wheat,max}$	**0.67**
		$LAI_{wheat,max}$ + Σ LAI_{comp}	**< 0.001**	**0.62**		
		Σ LAI_{wheat} + $LAI_{comp,max}$	**< 0.001**	**0.56**		

Bold values refer to significant relationships ($P < 0.05$).

Table S3. Statistical linear mixed-effect models to test the effect of agricultural practices on simulation model outputs (Area under disease progression curve or AUDPC, relative AUDPC, and AUDPC reduction), with experiment/year set as the random effect, and for three different weather conditions.

Disease	Response variable	Explanatory variables	Favorable	Average	Unfavorable
Wheat leaf rust	AUDPC	Species	0.10	0.08	0.07
		N fertilization	**< 0.001**	**< 0.001**	**< 0.01**
	Relative AUDPC	Species	**< 0.001**	**< 0.001**	**< 0.01**
		N fertilization	0.37	0.18	0.10
	AUDPC reduction	Species	**< 0.001**	**< 0.001**	**< 0.001**
		N fertilization	**< 0.05**	0.06	0.11
Septoria tritici blotch	AUDPC	Species	0.19	0.13	**< 0.01**
		N fertilization	**< 0.001**	**< 0.001**	**< 0.001**
	Relative AUDPC	Species	0.64	0.62	0.49
		N fertilization	0.36	0.26	0.14
	AUDPC reduction	Species	0.50	0.35	**< 0.05**
		N fertilization	0.82	0.73	0.75

Bold values refer to significant correlations ($P < 0.05$). The effect column indicates in which groups (no fertilization vs. fertilization; pea vs. faba bean intercropped with wheat) the response variable is superior or inferior.

Table S4. Statistical linear mixed-effect models to test the effect of agricultural practices on simulation model outputs (Area under disease progression curve or AUDPC, relative AUDPC, and AUDPC reduction), with experiment/year set as the random effect, and for three different initial inoculum.

Disease	Response variable	Explanatory variables	Favorable	Average	Unfavorable
Wheat leaf rust	AUDPC	Species	0.10	0.09	0.08
		N fertilization	**< 0.001**	**< 0.001**	**< 0.001**
	Relative AUDPC	Species	**< 0.001**	**< 0.001**	**< 0.001**
		N fertilization	0.37	0.43	0.44
	AUDPC reduction	Species	**< 0.001**	**< 0.001**	**< 0.001**
		N fertilization	**< 0.05**	**< 0.05**	0.06
Septoria tritici blotch	AUDPC	Species	0.19	**< 0.05**	**< 0.05**
		N fertilization	**< 0.001**	**< 0.001**	**< 0.001**
	Relative AUDPC	Species	0.64	0.59	0.50
		N fertilization	0.36	**< 0.05**	**< 0.01**
	AUDPC reduction	Species	0.50	0.18	**< 0.05**
		N fertilization	0.82	0.67	0.16

Bold values refer to significant correlations ($P < 0.05$). The effect column indicates in which groups (no fertilization vs. fertilization; pea vs. faba bean intercropped with wheat) the response variable is superior or inferior.