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Disease regulation in intercropping systems depends on spatial arrangement – A modelling study

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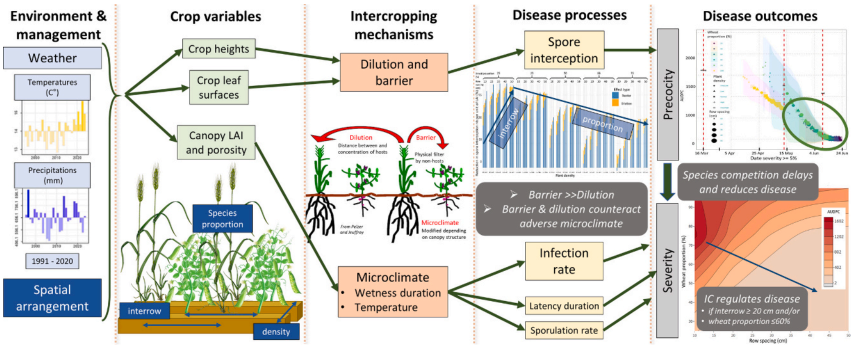
HIGHLIGHTS

- Coupled models highlight complex mechanisms of disease regulation in intercrops.
- Intercropping significantly delays the disease onset compared to sole cropping.
- The main benefit in disease control when intercropping is its barrier effect.
- Increasing the distance between rows was the most influential agronomic lever.
- Intercropping's unfavourable microclimate is offset by barrier and dilution effects.

GRAPHICAL ABSTRACT



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ABSTRACT

Context: Cultural diversification is presented as an effective method to increase the resilience of agrosystems in the face of climate change and the need to reduce reliance on artificial inputs. In particular, there is a growing interest in understanding how diversified cultures can help in reducing pesticide use.

Objective: In the case of intercropping, specific mechanisms have been identified which impact disease development: dilution and barrier effects as well as changes in microclimate in the canopy, but they are hardly characterised.

Methods: We propose a process-based modelling approach to study a virtual wheat/pea intercrop submitted to a brown rust epidemic, coupling two previously validated models. We thus deciphered in silico the effect of dilution, barrier and microclimate mechanisms and their sensitivity to changes in spatial arrangement of the field.

Results and conclusions: We found that in 93% of cases, intercropping reduced disease, by up to half with 60% wheat. Moreover, intercropping had overall beneficial effects in terms of disease control by protecting the photosynthetic capacity of wheat for 37 days longer on average. Furthermore, barrier and dilution effects counteracted the adverse microclimate throughout the crop cycle.

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Significance: Given the complex interactions between spatial arrangement and interannual variability, we argue that modelling is a valuable tool to run multiple simulations, identify scenarios most conducive to effective disease protection, and provide a reflexion on further research directions.

1. Introduction

The current global context puts increasing pressure on agricultural systems to deliver more with less. Between climate change, the loss of arable land, and rising demands for more environmental protection, the maintenance of production levels is becoming a substantive and pressing challenge (Baffes and Etienne, 2024). In particular, effects on crop growth and disease epidemics are already being felt leading to decreased levels of production, and the reliance of agriculture on techniques inherited from the 20th century is increasingly less effective (Intergovernmental Panel On Climate Change IPCC, 2023). Disease resistance and the need for limiting environmental pollution reduce the availability of phytochemical solutions for crop protection. The solutions therefore need to be found elsewhere and one of the avenues explored by researchers and farmers is agroecology.

Agroecology proposes to apply ecological processes to cropping systems as a strategy to improve crop production via ecosystem services such as protection against diseases (Deguine et al., 2023; Vialatte et al., 2021). Natural ecosystems are typically more resilient to disease outbreaks and the central role of biodiversity in this mechanism is well-established (Cappelli, Domeignoz-Horta, Loaiza, and Laine, 2022). Hence, the diversification of cropping systems is of strategic interest to tackle climatic and environmental issues currently identified. Academic research increasingly invests in the quantification of the efficiency of diversified systems, in terms of the regulation of pests and diseases, as well as the provision of other ecosystem services (Beillouin, Ben-Ari, Malézieux, Seufert, and Makowski, 2021; Tamburini et al., 2020). The latest IPCC report (2023) also mentions the utility of agroecological approaches for the sustainability of eco and agrosystems in the face of climate change.

As a way to introduce greater diversity into agricultural systems, InterCropping (IC) is defined as a system in which at least two different crop species are grown in the same field at the same time (Bedoussac et al., 2015; Bommarco, 2024; Willey, 1979). Since fungal pathogens are highly specialised in their host preferences, their regulation thanks to plant diversity is indeed an essential agroecological approach. Therefore, crop diversification, by introducing contrasted host and non-host species, is a pillar of the mechanisms involved in crop resilience. Its ability to regulate pests and diseases, and thus reduce pesticides use, is well identified experimentally and theoretically (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024; Beillouin, Ben-Ari, Malézieux, Seufert, and Makowski, 2021; Bommarco, 2024; Borg et al., 2018; Hatt and Döring, 2023).

Three main mechanisms have been recognised as having a major influence on disease outcomes (Boudreau, 2013; Gigot, de Vallavieille-Pope, Huber, and Saint-Jean, 2014; Vialatte et al., 2025):

- First a dilution effect with a smaller concentration of host plant and availability of organs susceptible to the pathogen,
- Then a barrier effect with an alteration in spore interception thanks to a physical obstacle to spore dispersal and deposition,
- And finally, a change in canopy microclimate with an impact mainly on other disease processes such as infection, latency and sporulation.

Dilution and barrier effects often work hand in hand in diversified systems by reducing the amount of inoculum reaching the susceptible crop, as evidenced by spore trap experiments (see for example Gao et al., 2021 or Gómez-Rodríguez, Zavaleta-Mejía, González-Hernández, Livera-Muñoz, and Cárdenas-Soriano, 2003). The scale of this effect, however, is highly dependent on the experimental set up (design, types of crops, types of diseases, etc), with reduction going from 30 to over 80% (for example Schoeny, Jumel, Rouault, et al., 2010). Microclimate on the other hand provides more or less suitable environments for spores to germinate and produce secondary inoculum. Different set ups will produce canopies with reduced or increased humid conditions (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024), making it arduous to predict outcomes, especially when considering the dilution and barrier effects at the same time. Hence, the full understanding and the field application of IC remain major challenges, because multiple components, as well as their interactions are at play, including potential instability of these interactions across years and field designs (Boudreau, 2013; Vialatte et al., 2025).

Previous empirical work has mostly focused on cultivar mixtures and fewer works are available on crop mixes (Finckh et al., 2000; Sapoukhina, Paillard, Dedryver, and de Vallavieille-Pope, 2013). In addition, effects of IC are difficult to separate and quantify experimentally (Boudreau, 2013), especially because their hierarchy is highly dependent on environmental conditions and field design, making it impossible to experimentally implement many combinations in the field (Borg et al., 2018; Mamine and Farès, 2020; Zustovi et al., 2024).

Models can help in designing spatial arrangements of fields which are likely to favour biological mechanisms involved in disease regulation. In particular, they may reproduce the dilution, barrier and microclimate effects while considering the interactions between the components of the complex system (pedo-climatic context, host plant, pathogen, crop management) for the whole crop cycle. Although there are a number of agronomic levers available when designing a field, the following have been identified as relevant because of their potential for practical implementation: plant density, the distance between plants and the relative proportions of the intercropped species (Baccar et al., 2011; Borg et al., 2018; Gardarin et al., 2022; Homulle et al., 2025).

Since the foundation works by Boote, Jones, Mishoe, and Berger (1983), previous modelling studies have focused on understanding each fine process involved in disease regulation, i.e. canopy architecture and spore dispersal (Vidal, Gigot, de Vallavieille-Pope, Huber, and Saint-Jean, 2018) but these process-centred approaches offer limited insights at the field spatial and temporal scales. Spatially distributed models have so far explored the dynamic of pests and pathogen populations within a field or a landscape (Blumenthal and Jordan, 2001; Collard, Tixier, Carval, Lavigne, and Delattre, 2018; Hambäck, Inouye, Andersson, and Underwood, 2014) but have not usually considered growth dynamics of host and non-host plants, all needed to understand the system as a whole (Bondad, Harrison, Whish, Sprague, and Barry, 2023; Calonnec et al., 2012). To meet this challenge, a mechanistic crop modelling approach provides both a conceptual framework for combining plant and pathogen processes, and a quantitative prediction of disease regulation outcomes (Bregaglio et al., 2021; Calonnec et al., 2012; Colbach, 2010; Dionisi, Aubertot, and Sester, 2023). Examples of modelling studies involving this approach include a wheat and tan spot pathosystem with DSSAT (Ferreira et al., 2021), a wheat foliar diseases system (Audsley, Milne, and Paveley, 2005) and a stripe rust and wheat system with APSIM (Whish, Herrmann, White, Moore, and Kriticos, 2015). Although they described damaging effects of diseases, all these works involve sole crops and not intercrops.

Using a previously validated coupling of a mechanistic crop model with an aerial fungal disease model, we propose to apply it to a novel intercrop situation with an in silico experiment to study the effect of variations in plant density, distance between plants and species proportions on disease outcomes and regulation mechanisms. To the best of our knowledge, there has never been any works on coupled crop and disease models in the context of intercropping (Adam et al., unpublished, under revision). By coupling the two validated models and applying it to a common intercrop situation, we can conduct a multi-factorial exploration and mechanistic attribution of disease regulation processes.

To implement this virtual experiment, we chose a case study from Southern France using wheat and pea to examine a wheat brown rust epidemic. Wheat is one of the most grown cereal species globally (Baffes and Etienne, 2024), including in France (Laurent, Ullmann, and Castel, 2023; Aubry et al., 2026), and pea is the most commonly associated plant with wheat in field experiments (Zustovi et al., 2024). Brown rust is also a global challenge for wheat growing (Chai, Senay, Horvath, and Pardey, 2022), and as a disease thriving in warmer conditions, it could become even more of a problem with a changing climate (Caubel et al., 2017).

In this article, we aim to address the following issues regarding intercrops:

- how does spatial arrangement impact disease regulation when modifying the following parameters: density, distance between rows and species proportion?
- how much do the mechanisms of dilution, barrier and microclimate influence the regulation of pathogens and what is the impact of field design?

Given the complexity of the wheat-pea-brown rust system and the above questions, we conducted a virtual experiment using two validated coupled models to explore the impact of various intercrop situations on disease regulation from a theoretical perspective.

We thus used a modelling approach to i) study the effects of IC and spatial arrangement on disease progression and outcomes, and ii) quantify the impacts of the mechanisms involved in disease regulation specific to IC: dilution and barrier (spore dynamics), as well as microclimate changes (infection via wetness duration and temperature).

2. Materials and methods

Two coupled models were used to represent the entire pathosystem:

- STICS-IC (Vezy et al., 2023), a new version of the soil-crop model STICS which simulates intercrop systems as a whole (crops, pedoclimatic context and farming practices);
- MILA (Caubel et al., 2014, 2017), an epidemiological model which simulates the different processes in the life cycle of a fungal pathogen.

The advantages of these two models are two-fold:

- they have been validated on experimental data, on wheat/pea intercrops for STICS-IC and on SC wheat with brown rust for MILA.
- input files for calibrated disease, soil and plant parameters were readily available from previously published works.

We designed an in silico experiment consisting of a wheat/pea system with a brown rust (BR) disease. We describe below the models used as well as the characteristics of the experimental design and the results analysis.

2.1. Modelling framework

The model STICS-IC (Vezy et al., 2023) is a research branch version of the standard crop model STICS (Beaudoin et al., 2023), a process-oriented and mechanistic model used by a wide community of researchers, students and agronomists (Hoogenboom, 2025). It simulates annual and perennial crops as well as bi-specific intercrops taking into account the weather, soil properties and farming practices, including field design. STICS computes daily state variables related to the carbon, nitrogen and water cycles of the agrosystem. It takes into account many physiological processes defining crop development through specific responses to temperature and photoperiod, as well as growth processes like radiation interception, resource competition, canopy 2D geometry and biomass allocation. Water, nitrogen and thermal stresses are considered as limiting factors reducing crop growth and yield formation. Phenology, which refers to the plant development, governs the crop cycle time period. Crop growth is driven by energy interception and results in plant carbon accumulation. Depending on plant type, crop development is driven either by i) a thermal index (degree-days), ii) a photo-thermal index which also takes photoperiod into account or iii) a vernalo-photo-thermal index which also takes vernalisation into account.

STICS-IC introduces new formalisms to improve the simulations of bi-specific intercrop systems. It provides a better representation of processes of competition and dominance effects, and was recently calibrated and validated for various intercrops including wheat-pea (Vezy et al., 2023). The model is able to simulate interactions with alternate rows of each crop or equivalent designs. The variables calculated include canopy height and dominance inversion between the two species, quantity of light intercepted by each crop in the mix according to radiative transfer equations, microclimate (temperature, humidity and wetness duration) for the mixed canopy taking into account parameters such as canopy shape, growth patterns, and variables such as foliar density.

The fungal pathogen was modelled using MILA (Caubel, Launay, Lannou, and Brisson, 2012), a process oriented and mechanistic model, simulating disease dynamics with disease-specific parameters (table provided in Supplementary Material for brown rust). The MILA model simulates the different epidemiological stages of the fungus life cycle, including dispersal, interception, infection, latency, and production of secondary inoculum (Fig. 1). Individuals are spores or lesions that evolve into those different epidemiological stages in cohorts of the same age. The model computes daily transition rates allowing to quantify the number of individuals (spores or lesions) moving from one stage to another. The daily intercepted spores, organ surface covered with lesions, and severity (removed surfaces) are thus provided as outputs. In the case of a polycyclic fungus such as brown rust, the model is able to simulate the successive epidemic cycles at the crop level.

MILA was first coupled with a previous standard version of STICS, which only allowed the simulation of sole crop (SC) pathosystems (Caubel et al., 2014, 2017). In this earlier setup, STICS provided MILA with daily weather, canopy microclimate, and crop data, while MILA returned the diseased organ surface for updating the green leaf area (LAI) in STICS on the following simulation day (Fig. 1). The coupled models thus simulated the daily interactions between a single host crop and a single disease, and this framework was previously validated for several pathosystems, including wheat–brown rust (Caubel et al., 2017). MILA distinguishes the dispersal process from the interception process (Fig. 1). Brown rust is dispersed by wind and this dispersion is considered homogenous and random, therefore, the common hypothesis is that dispersion is not limited (Frézal, Robert, Bancal, and Lannou, 2009). There is also a widely used analogy between light interception and spore interception (Delatouche, Tixier, Sainte-Rose, Daribo, and Lapeyre De Bellaire, 2023; El Jarroudi, Karjoun, Hajjami, Kouadio, and El Jarroudi, 2025; Lannou, Soubeyrand, Frezal, and Chadœuf, 2008). The common hypothesis for light interception is that it is distributed randomly in space. Since the same hypothesis is considered valid for aerial fungal spores, the optical porosity of the canopy to light photons is taken as a proxy for physical porosity to spores. Hence, the fraction of absorbed photosynthetic radiation (*fAPAR*) is a predictor of the fraction of available spores in the crop system that are intercepted by the canopy. As for other disease processes (infection, latency and sporulation), MILA uses microclimate variables computed in STICS via an energy balance approach (global radiation, temperature and ETP): canopy temperature,

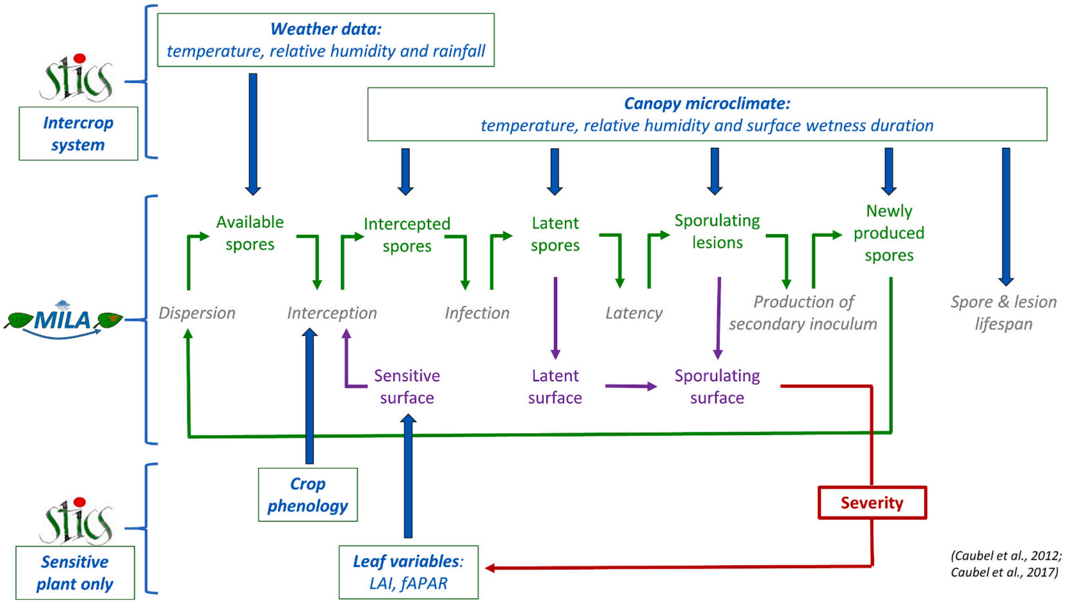

Fig. 1. Architecture of the MILA-STICS modelling framework. In blue, variables taken from the crop model STICS' outputs and used as inputs in the pathogen model MILA. In green, pathogen spore cohorts in sequential states according to the transition rates calculated in the process modules in grey. In purple, the surfaces calculated from the spore and lesion cohorts. In red, a severity index which is fed back to STICS to reduce the green leaf surface accordingly.

relative humidity and wetness duration, as well as climate variables such as precipitations, temperature and humidity. In intercrop systems, additional processes must be considered when simulating disease development: dilution, barrier, and microclimate effects. Dilution and barrier effects influence the pathogen population at the dispersal stage, particularly spore interception by plant tissues. To extend spore interception to intercrops, the original version of STICS was replaced by STICS-IC, which accounts for multiple species and mixed canopies. By replacing STICS sole crop with the new version of STICS-IC, light interception is calculated through radiative transfer equations, a more appropriate approach for mixed canopies (Vezy et al., 2023) since it computes the light environment of each plant species separately. The model simulates radiative microclimates according to the dominance and shaded/sunny parts of the two plants. The assumption for thermal and humidity microclimate is that the mixed canopy is homogenous enough to be considered the same for the 2 species.

The coupling process itself remains essentially unchanged, except that the exchange of plant variables is now restricted to those of the crop species susceptible to the considered disease, while microclimate data continue to represent the entire canopy. MILA receives the daily *fAPAR* of the susceptible crop, ensuring that competitive interactions in intercrops are accounted for in the calculation of spore interception by host leaf surfaces. Microclimate effects are directly represented in the canopy-scale outputs of STICS-IC.

2.2. *In silico experimental design*

The experimental design consisted in first selecting an intercrop situation and then combining parameters to simulate different spatial arrangements. The intercrop field experiment, which had already been studied and simulated and was chosen for the current study, was fully detailed by Vezy et al. (2023) in their work on calibration and validation, and is briefly described in Section 2.2.1 below. In Vezy et al. (2023) the STICS-IC model provided a simulation of this wheat–pea field experiment; however, neither the field trial nor the modelling study included any disease occurrence. In our study, we simulated this intercrop situation, introducing a brown rust epidemic. To account for mean trends and interannual variability, we used 30 years of reference daily weather data (1991–2020).

2.2.1. *Intercrop situation*

The model inputs for our case study were based on an experiment conducted at the INRAE research station in Auzeville (43°31′N, 1°30′E) in Southern France, on durum wheat (*Triticum turgidum* L., cv. Nefer) as a sole crop and intercropped with winter pea (*Pisum sativum* L., cv. Lucy), as fully described in Vezy et al. (2023). The field design was a 50–50 crop mix in alternate 29 cm rows with a wheat density of 140 plants.m^{-2} and a pea density of 36, sowed during autumn The soil was characterised as a deep loamy soil and assumed to be non-limiting in terms of nutrient availability. All model input files on soil, plants and farming practices were readily available and considered to be reliable to form the basis of our exploratory work. These input files were only modified to simulate different levels of row spacing, plant density and species proportion (spatial arrangement). A list of relevant plant parameters and their values is available in Supplementary Material.

2.2.2. *Spatial arrangements*

Three factors were considered to design a variety of virtual fields, i.e. species proportion, total plant density and row spacing, in order to highlight the effect of the three mechanisms involved as described below:

- dilution effect alone: this is when we dilute a 100% wheat crop, i.e. when we decrease plant density and/or increase row spacing, thereby only reducing the availability of plants susceptible to infection per unit of soil surface,
- dilution and barrier effects together: This is when we implement a wheat/pea IC with the same factors as in dilution but with added variations in species proportion, thereby introducing different levels of physical barrier to the dilution effect,
- microclimate effect: microclimate variables (canopy temperature, humidity and wetness duration) are calculated in STICS-IC based on canopy geometry (density, shape) which takes into account the specificities of heterogeneous canopies.

In order to implement this experimental design, parameters of the STICS-IC model were modified to implement variations in three factors: distance between rows, sowing density and species proportion. In order to maximise the level of control in our experiment, emergence was forced to 100% and frost sensitivity disabled in order to obtain a total plant density equal to the chosen sowing density This is to remove the effect of yearly differences in post-emergence densities, or sensitivity to species-dependant stress, to better highlight the effects of plant competition in our simulations.

In effect, species proportion varied from 25 to 100% of wheat (i.e. 75 to 0% of pea). Total sowing density varied from very low to very high at field level, in five classes according to combinations of values for the wheat and pea sowing densities (Table 1). At very low field density, SC wheat and SC pea densities were respectively set at 140 and 36 plants. m-^{2}. The densities of wheat and pea in intercrops were calculated as the product of wheat and pea proportions by their SC density. Accordingly, the parameter *densitesem* was set to values indicated in Table 1. This unique parameter enables us to manage two factors (proportion and density). It translates in some of the equations into a distance between plants on the row. For species proportion, it is the relative sowing densities of the two species which enable to design fields with pea being added or substituted to wheat. We repeated this design for five levels of row spacing (parameter *interrang*): 10, 20, 30, 40 and 50 cm, at each of the previous total densities and proportions. This resulted in a full factorial experiment with 150 combinations (5 row spacing(s) x 6 species proportions x 5 densities) representing a variety of designs.

2.2.3. Weather data

To identify general trends and focus on output averages, we ran the 150 combinations described above using 30 years of daily weather data (4500 simulations) based on a reference period going from 1991 to 2020, providing the experimental design with a varied mix of yearly climates (Supplementary material). Data was extracted from the SAFRAN database (grid cell 9010 for Auzeville, France), daily weather variables provided by Météo-France and downloaded via the SICLIMA service platform (AgroClim-INRAE, 2025).

2.3. Simulation results analysis

2.3.1. Output variables and characterisation of the pathosystem

In order to analyse the simulation results, we focused on a selection of output variables for the coupled model for three phenological stages which mark out the different changes in trends observed during the crop cycle, namely stem elongation, flowering and physiological maturity.

The variables selected correspond to the three mechanisms of interest (dilution, barrier and microclimate) and their impact on the susceptible plant, namely diseased surface, plant green leaf surface, spore interception and canopy microclimate (Table 2).

We defined the operational onset of the epidemic as the date when severity reaches 5% of leaf area, consistent with typical agronomic management threshold for fungicide application and economic injury levels.

Table 1
Values for the sowing density of each crop (plants.m-2) to reflect the different levels of total densities (from very low to very high) and species proportion, repeated for the five levels of row spacing. For example, using a 50% wheat with a 50% pea at a normal level of plant density means that sowing density was 140 plants per m^2 for wheat and 36 plants per m^2 for pea.

field density level	wheat/pea proportions (%)					
	25/75	**33/66**	**50/50**	**66/33**	**75/25**	**100/0**
very low	35/27	46/24	70/18	93/12	105/9	140/0
low	53/43	70/38	105/27	140/18	158/14	210/0
normal	70/54	93/48	140/36	186/24	210/18	280/0
high	88/68	116/60	175/45	231/30	263/24	340/0
very high	105/85	140/71	210/54	277/36	315/27	420/0

Table 2
description of acronyms and output variables used in our analysis. All variables were calculated for each year of simulation and then averaged over the 30 year period used as reference.

Abbreviation	unit	Definition and interest
AUDPC	na	Area Under Disease Progress Curve reached at a given stage (from emergence), characterising the intensity of the disease
infrate	%	Mean of daily infection rate when different from 0, representing the proportion of pathogen spores deposited on wheat susceptible surface which germinate and enter latency, according to canopy temperature and leaf wetness duration (details about the response curve available in Caubel, Launay, Lannou, and Brisson (2012))
infrateDays	number of days	Mean number of days where the infection rate is different from 0
sporesLAI	Spore count.m^{-2} of green leaf	Cumulative number of spores intercepted per unit of LAI of wheat, reached at a given stage, as an indicator of intensity of dilution and barrier effects.
DateSev5	Na	Date on which severity reaches 5%, indicator of disease earliness (Magarey et al., 2005)
LAImax	$m_2.m^{-2}$	Maximum leaf surface reach at a given stage, equivalent to green photosynthetic leaf surface, indicator of plant vigour
SWD	hours	Mean daily leaf surface wetness duration within the sole crop and intercrop canopy, a key microclimate variable in the disease infection process
Temp	degrees °C	Mean daily temperature within the sole crop and intercrop canopy, a key microclimate variable in all disease processes

Microclimatic variables relevant to brown rust are surface wetness duration (SWD) and canopy temperature (Temp). When the text of this paper mentions “microclimate”, it refers to the combination of these two variables. Thus, microclimate can be favourable when the combination of the two variable produces an aggregated result which favours disease development.

2.3.2. Quantification of the respective contributions of dilution and barrier effects

The dilution and barrier effects disrupt the movement and deposition of spores in the canopy of the susceptible plant. In order to quantify the relative weight of dilution and barrier effects, we calculated percentages of reduction in the cumulative number of spores intercepted per unit of LAI (*sporesLAI,* Table 2) as follow, similarly to the approach used by Levionnois, Pradal, Sanner, Saint-Jean, and Robert (2023) on their analysis of AUDPC in IC versus SC.

We transformed the raw output giving the daily number of spores intercepted and divided it by the LAI of each day in order to obtain a form of normalisation. Our aim was to be able to compare situations that are different, and remove effects of known influences. Indeed, crop development and growth are the result of many interactions, particularly in terms of compensating for LAI at different plant densities, for example through tillering. Doing this for daily outputs also has the advantage of taking into account the dynamic of crop and pathogen growth together. Since the number of spores intercepted is directly dependant on leaf surface available, dividing this variable by the LAI provides insights independent from this relation. We can separate the effects of deposition resources from the effects of regulation mechanisms on severity/AUDPC, both indicators dependant on LAI.

The daily normalised number of intercepted spores was then cumulated over the crop cycle, from emergence to physiological maturity, for each combination of the three factors (density, row spacing, species proportion) and average over the 30 years of simulations.

The chosen reference situation ($sporesLAI_{ref}$) is the wheat SC at the highest density (420 plants.m^{-2}) and at the lowest row spacing (10 cm), considered as the most beneficial to disease development (i.e. where *sporesLAI (Table 2)* is the highest, see supplementary material). The cumulative number of spores intercepted per unit of wheat LAI for this reference situation is then used to calculate a percentage of reduction for all other combinations.

The dilution effect (SC wheat) is quantified according to this equation:

$$dilution\ effect\ size_{r,d} = \frac{sporesLAI_{ref} - sporesLAI_{r,d}}{sporesLAI_{ref}}$$

where $sporesLAI_{r,d}$ is the cumulated number of spores intercepted for each level of density d and row spacing r, averaged over 30 years (Table 2) and $sporesLAI_{ref}$ the reference situation as described above.

The total effect (dilution and barrier effects together in a wheat and pea IC) is quantified as follows:

$$dilution\ x\ barrier\ effect\ size_{r,d,p} = \frac{sporesLAI_{ref} - sporesLAI_{r,d,p}}{sporesLAI_{ref}}$$

where $sporesLAI_{r,d}$ is the cumulated number of spores intercepted for each level of density d, row spacing r, and proportion p, averaged over 30 years (Table 2).

From this overall effect, and based on the assumption that effects are linear, we deduced the barrier effect size by subtracting the dilution effect size from the overall effect for each proportion p.

$$barrier\ effect\ size_{r,d,p} = dilution\ x\ barrier\ effect\ size_{r,d,p} - dilution\ effect\ size_{r,d}$$

The dilution effect is therefore quantified as a reduction percentage in the cumulative number of spores intercepted for each unit of susceptible LAI when plant density is reduced and/or distance between rows increased. The barrier effect is evaluated as a reduction percentage following an increase of either plant density, distance between rows or pea proportion.

Further to this, we included a measure of uncertainty in the quantification of the reduction in spores intercepted ($dilution\ x\ barrier\ effect\ size_{r,d,p}$) by using propagation of uncertainty (effect on a function of the variables' uncertainty using the standard deviation) usign the standard deviation of sporesLAI over 30 years in the following equation:

$$\sqrt{\left(\frac{SDsporesLAI_{r,d,p}}{SDsporesLAI_{ref}}\right)^2 + \left(sporesLAI_{r,d,p}\ \frac{SDsporesLAI_{ref}}{sporesLAI_{ref}{}^2}\right)^2}$$

Where *sporesLAI* is the 30-year average of the cumulated number of intercepted spores (emergence to physiological maturity) per unit of LAI, and *SDsporesLAI* is its standard deviation.

3. Results

Disease intensity, quantified by the AUDPC, was compared between the wheat sole crop (SC) systems and the wheat/pea Intercrops (IC); it highlighted the different mechanisms (dilution, barrier, microclimate) and processes (spore interception, infection, latency, sporulation, crop growth) at play in a brown rust epidemic during the crop cycle. The impact of IC on disease intensity is significant but nuanced according to spatial arrangements, i.e. combinations of row spacings, sowing densities and species proportions. After a preliminary overview of disease intensity over the whole wheat cycle (from emergence to maturity), results are presented separately in three phases marked by the following stages: emergence, stem elongation, flowering and maturity. Stem elongation is an important transition phase for plant height dynamics, particularly impacting the barrier effect (taller wheat means less barrier). Flowering: critical stage in yield formation in terms of grain numbers and filling. The quantity of disease at this stage is crucial for determining yield. Indeed, different patterns were observed during each period which highlight the major processes involved over time.

3.1. Spatial arrangement and crop phenology effects: Impact on disease regulation

Disease intensity varies greatly according to the crop system (SC versus IC) and spatial arrangement (Fig. 2). The pattern in disease development was split in three phases according to wheat phenology. At the stem elongation stage, the two crop systems do not show differences in disease outcomes except at the lowest inter row where AUDPC in SC is higher than all AUDPC in IC (Fig. 2A). Differences start to appear in the second part of the cycle (from stem elongation to flowering) with IC clearly beneficial in terms of disease control (Fig. 2B). At maturity, the benefits are still present for IC except for shorter distances between rows (Fig. 2C).

3.1.1. From emergence to the start of stem elongation: Early species competition initiated a positive effect of IC on spore interception

When the stem elongation stage was reached, the AUDPC was very small as expected early in the season (Fig. 2A). There was a slight advantage for IC at the shortest interrow distance and for the lower proportion of wheat, leading to a maximum decrease of 30%. It is important to note that despite this advantage, absolute values remain very small at this stage, with severity reaching a maximum of 1% at this stage. The LAI in the IC was markedly stable and unresponsive to the row spacing at this stage (Fig. 3A). At comparable sowing density and row spacing, the presence of pea hinders the growth of wheat with a reduction in LAI from 25 up to 40%. This decrease in susceptible surface available for the pathogen resulted in fewer spores intercepted by wheat (Fig. 3A). Despite the lack of effect of row spacing on the wheat LAI in IC, there was an effect on light interception and by extension on spore interception. In particular, increasing row spacing led to a greater interception of rust spores by pea or bare soil.

However, results found for AUDPC (Fig. 2A) were not fully aligned with those obtained for spore interception (Fig. 3A). For example, the difference in spore interception for a 20 cm row spacing did not translate into a difference in AUDPC. It suggests IC impacted other disease processes, particularly infection. Indeed, we observed a higher mean infection rate in the IC (Fig. 5A) during this early period. In the model, the infection rate is calculated using the leaf wetness duration (*SWD*) and the canopy temperature (*Temp*) (see response curve provided in Supplementary Materials). Despite the notable reduction in SWD in the IC, temperatures were slightly higher (Fig. 4A) which provided favourable conditions for infection and hence reduced the difference in terms of AUDPC between SC and IC, compared to the difference in terms of spore interception. Because there is a smaller LAI in the IC, air can circulate more freely in the canopy, and therefore is drier and warmer (Fig. 4A). In both systems however, the levels of SWD reached were above the saturation threshold thus with no impact on infection rates. Instead, despite the low temperature range, it was located on the steep part of the response curve of infection to temperature (provided in Supplementary Materials). At this stage, there was no difference between SC and IC for other disease processes such as latency and sporulation (provided in Supplementary Materials).

In summary, variations in disease intensity during stem elongation are primarily caused by two factors: early crop competition, which tends to reduce disease levels, and differing canopy microclimates, which often promote disease development. Inter-rows of at least 20 cm or low plant densities in the field brought the most beneficial conditions for disease regulation. Reducing the proportion of wheat in the mix was less important at this stage, except for a 10 cm interrow.

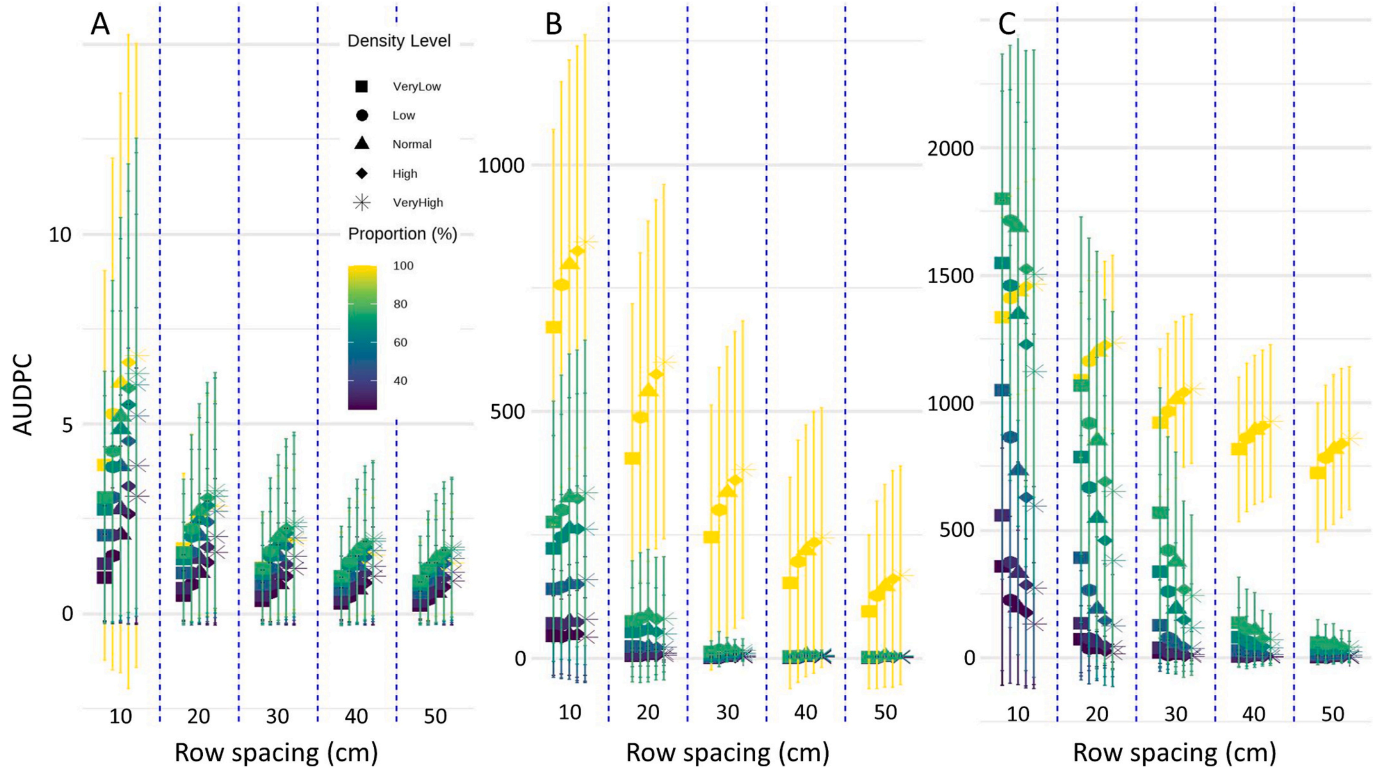

Fig. 2. Mean brown rust disease intensity over 30 years of simulations, as quantified by the AUDPC for each combination of row spacing, plant density and species proportion, reached at each of the following wheat phenological stages: stem elongation (A), flowering (B) and physiological maturity (C). The X axis represents distance between rows. The colours represent wheat proportion in the species mix and shapes the level of total plant density. Error bars represent standard deviations.

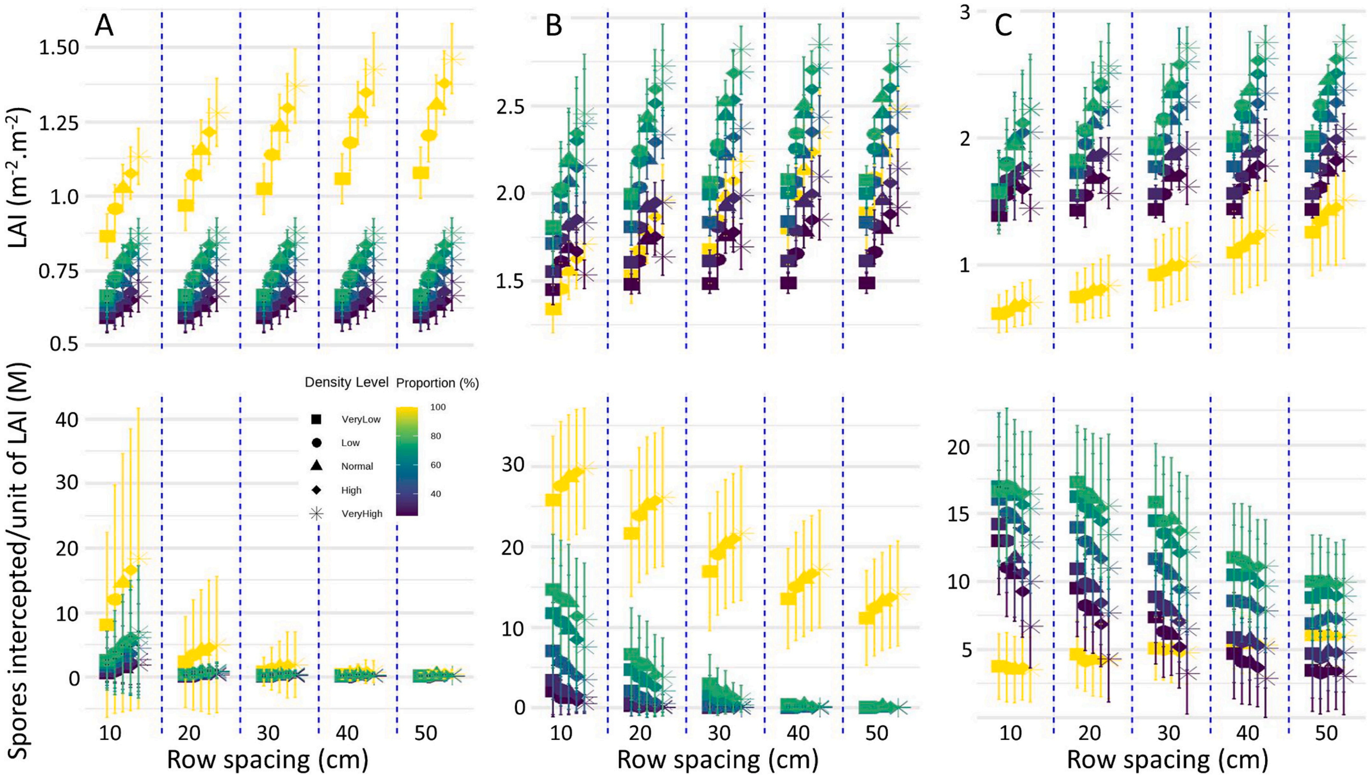

Fig. 3. Mean maximum wheat green leaf surface ($m^{-2}.m^{-2}$) (top), and mean cumulative number of spores intercepted per unit of leaf surface (millions of spores.m^{-2}) over 30 years for each combination of row spacing, plant density and species proportion, reached at each of the following wheat phenological stages: stem elongation (A), flowering (B) and physiological maturity (C). The X axis represents distance between rows. The colours represent wheat proportion in the species mix and shapes the level of total plant density. Error bars represent standard deviations.

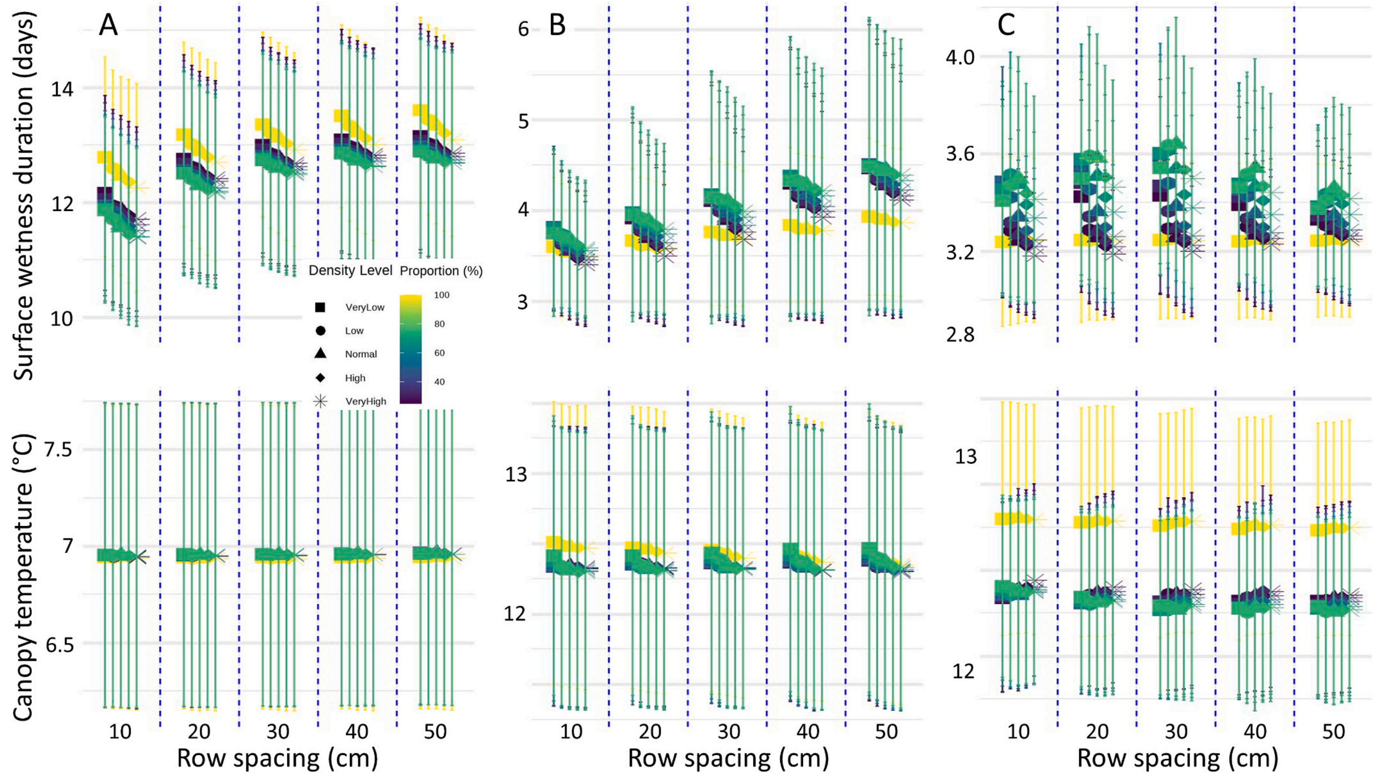

Fig. 4. Mean microclimate variables (SWD and canopy temperature) over 30 years, for each combination of row spacing, plant density and species proportion, reached at each of the following wheat phenological stages: stem elongation (A), flowering (B) and physiological maturity (C). The X axis represents distance between rows. The colours represent wheat proportion in the species mix and shapes the level of total plant density. Error bars represent standard deviations.

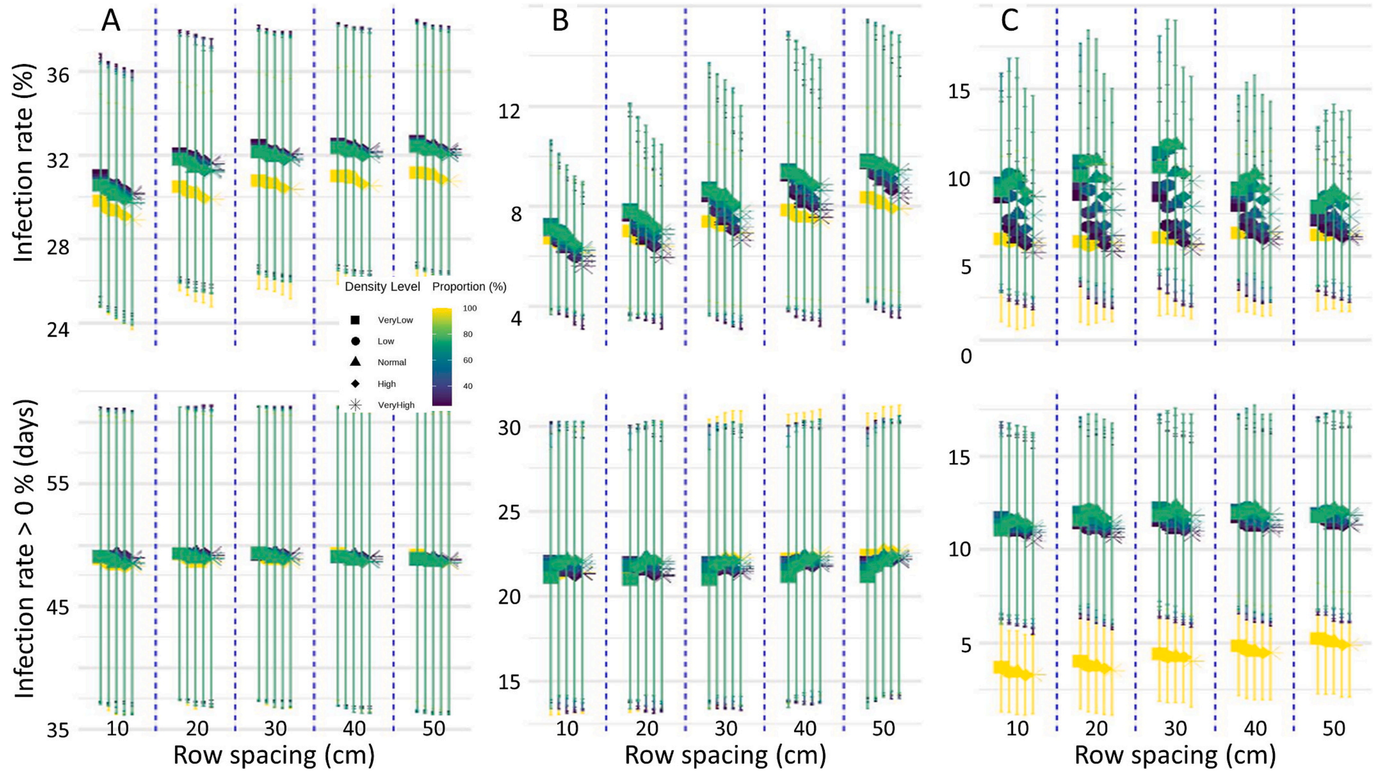

Fig. 5. Mean infection rate (top), and mean number of days with an infection rate strictly over 0% (bottom) over 30 years, for each combination of row spacing, plant density and species proportion, reached at each of the following wheat phenological stages: stem elongation (A), flowering (B) and physiological maturity (C). The X axis represents distance between rows. The colours represent wheat proportion in the species mix and shapes the level of total plant density. Error bars represent standard deviations.

3.1.2. From the start of stem elongation to flowering: The height dominance of pea over wheat enables the dilution and barrier effects to compensate microclimatic conditions more favourable to disease

As wheat transitioned from stem elongation to flowering, the dynamics of the disease intensity shifted. During this phase, the presence of pea began to exert a more pronounced regulatory effect on disease as illustrated by the reduction of at least an 80% in AUDPC (Fig. 2B) and at least a 6-fold reduction in cumulative spore interception (Fig. 3B). The simulations showed that with wider rows, the number of spores intercepted by wheat could fall to nearly 0. The benefit of IC was also found in the LAI (Fig. 3B) catching up to the same or higher levels as the SC with potential benefits for grain development and harvest levels.

The dilution and barrier effects provided by IC remained beneficial, even though an increase in wetness duration inside the IC canopy has lessened these advantages by promoting microclimate conditions more favourable to disease. As the pea LAI grew, the SWD increased from 3.6–3.8 h in SC to 3.7–4.4 h in IC (Fig. 4B), which could have led to an increase in infection rate. However, because the temperature tended to be colder in the IC (Fig. 4B), the impact on infection rate was mitigated (Fig. 5B). The impact of microclimate on other processes such as latency and sporulation was still minimal (Supplementary Materials).

In summary, differences in disease intensity at flowering were related to the dilution and barrier effects brought by the pea domination largely offsetting the negative effect of longer leaf wetness duration in IC. This suggests that while competition may initially hinder growth and increase disease pressure in IC during the juvenile phase, the development and growth of the pea created conditions conducive to disease regulation. Indeed, the barrier and dilution effects induced a clear reduction in spore interception which varied according to the spatial arrangement. To bring beneficial conditions for disease regulation, the most influential lever at this stage was to increase the distance between rows. As a second lever to play with, decreasing wheat proportion and/or total plant density increased the effect of distance between rows.

3.1.3. From flowering to maturity: Spatial arrangement is critical to avoiding the negative effect of IC on microclimate

In this last part of the wheat cycle, there was an inversion in the pattern of spore interception compared to the previous phases: more spores were intercepted in the IC than in the SC (Fig. 3C). The LAI in the IC overtook the LAI in the SC (Fig. 3C) due to earlier leaf senescence in the latter, enabling longer spore interception in IC. This translated into situations for which a SC is more advantageous than an IC but only for extreme spatial arrangements such as a 10 cm row spacing (see AUDPC Fig. 2C).

The microclimate, particularly SWD, is increasingly favourable to disease development as shown with higher infection in IC compared to SC (Fig. 5C). The mean infection rates between SC and IC systems show small differences but the number of days with an infection (rate different from 0) are clearly higher in the IC with 11 days relatively to about 4 days in the SC over a one-month period. However, this degradation of microclimatic conditions in IC is not enough to counter the effects of dynamics of spore interception initiated earlier in the crop cycle (see AUDPC, Fig. 2C).

Overall, fewer spores are intercepted throughout the crop cycle in IC compared to SC, leading to a reduction in disease intensity. This suggests that dilution and barrier effects play a significant role in regulating disease development, even though IC systems often create more conducive microclimates to pathogen proliferation, particularly in the later stages of the crop cycle. Furthermore, spatial arrangement variables—such as plant density, row spacing, and species proportion—can either mitigate or exacerbate disease progression. This underscores the importance of mobilising these agronomic levers, which can be adjusted to enhance disease control in intercrop systems.

3.2. Timing effect: Disease precocity is strongly related to levels of disease intensity

There was a clear relationship between the date on which severity reaches 5% and max AUDPC (Fig. 6). The later the epidemic starts, the lower the disease severity at the end of the crop cycle. All SC data points appear before the average date of flowering, showing that 5% severity is attained earlier in the crop cycle compared to IC. In the IC, only the highest wheat proportion (at least 66% of wheat) for the shortest row spacing (10 cm) attained 5% severity before flowering. On average, IC introduced a significant delay in the phenology of the pathogen, about 37 days on average (with a standard deviation of about 18 days). This beneficial effect of the combination on epidemic delay is visible as soon as the inter-row distances are greater than 10 cm or the proportion of wheat in the mix is less than or equal to 50%. Under these conditions, the wheat crop flowers before severity reaches 5%, thus prolonging photosynthesis at a time when grains are developing and protecting the potential harvest. Even with 20 cm row spacing and 75% wheat in the mix, the benefit in terms of LAI exceeded a five-fold increase (Fig. 3C).

3.3. Quantification of dilution and barrier effects

Dilution and barrier effects were quantified separately over the whole crop cycle for spore interception (Table 3 and Fig. 7) to show the impact of spatial arrangement on these two mechanisms. The figure illustrates the relative role of the reduction in surface susceptible to infection (dilution effect) and the physical alteration in spore movement (barrier effect) in one of the major and earliest processes in disease development, namely spore dynamics, calculated as the percentage of reduction in spores intercepted.

In terms of the total number of spores intercepted between emergence and maturity, the general trend for the total effect is an increase in spore reduction with variations in factors.

The dilution effect (orange bars in Fig. 7) responded as expected:

- The magnitude of the dilution effect increases when plant density decreases,
- It increases when row spacing increases,
- There is an interaction between the two factors: the effect of plant density is reduced with increasing row spacing.

The barrier effect (blue bars in Fig. 7) responded as expected with increases in pea proportion. However, the results are more nuanced with the other two factors:

- Increasing row spacing can either increase or decrease the barrier effect depending on wheat proportion,
- The barrier effect diminishes with fewer plants in the field.

Overall, the highest reduction in spores occurs at a row spacing of 30 cm with more limited benefits after this value. It reaches 75% when wheat/pea proportions reach 50% of each species.

4. Discussion

The in silico experiment detailed in this paper demonstrated that our model is able to represent the primary mechanisms and processes involved in disease regulation in intercrops, along with their dynamics, as identified in published literature. Combining the dynamics of the pathogen, host plant and non-host plant from a mechanistic perspective reflects theoretical empirical knowledge and highlights phenomena which other modelling approaches cannot describe. For example, competition mechanisms between the two crop species reduce the surface available for infection and consequently disrupt the spore dynamic cycle, translating into a delay in the start of the epidemics. This facilitates the lowering of the AUDCP in IC compared to SC (Fig. 8).

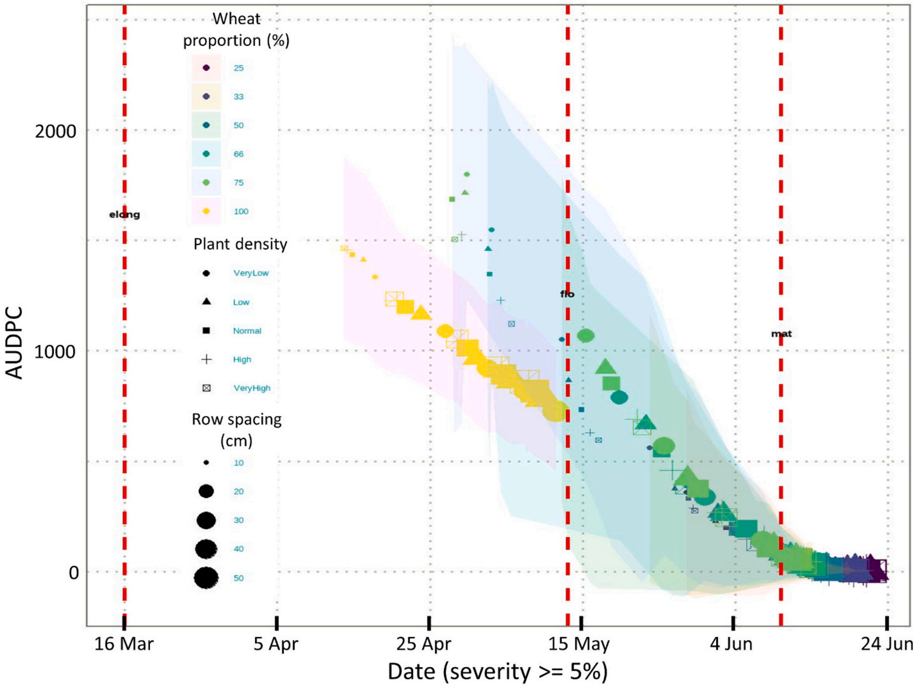

Fig. 6. Disease intensity (AUDPC value reached at maturity) as a function of disease precocity (date when the severity reaches 5%, considered the start of the epidemics). The colours represent wheat proportion in the species mix, shapes the level of total plant density and size of the shapes the distance between rows. The ribbons represent standard deviations for each level of species proportion.

Table 3
Summary table of the quantification of the dilution and barrier effects indicating the direction of variation in the reduction of cumulated intercepted spores per unit of LAI. Direction of variation for the three factors correspond to theoretical knowledge: diluting wheat means decreasing plant density and/or increasing row spacing. Same for the barrier effect with the increase of pea proportion. Ranges of variation of the effects are indicated in square brackets.

Levers to regulate disease / Effects on spore reduction	Increase pea proportion (0 to 75%)	Increase row spacing (10 to 50 cm)	Decrease plant density (Very low to very high, levels of plants.m^{-2} soil)
Dilution (%)	Stable [0;50]	Increase [0;50]	Increase [0;10]
Barrier (%)	Increase [0;40], especially at low interrow	Increase (high wheat proportion) [0;30] Decrease (low wheat proportion) [25;80]	Decrease, especially for low pea proportion [0;80]
Total (%)	Increase due to barrier effect [0;90]	Increase especially for high wheat proportion [0;90]	Decrease in IC [0;90] Increase in SC
Relative contribution barrier/ dilution (%)	Increase	Increase (low wheat proportion) Decrease (high wheat proportion)	Decrease

Additionally, it emphasised which species arrangement in the mix promotes disease regulation.

4.1. Spatial arrangement as an agronomic lever to manage disease outcomes

Our results showed that the model was able to simulate the effect of the species mix on pathogen dynamics, and how it can be modulated by spatial arrangement. Modifying the proportion of species in the mix and/or the distance between rows enables control of the beneficial effect of IC on disease regulation. Once the desired proportion of wheat in the mix has been determined, the inter-row spacing can be modified to best control the disease (Fig. 8A). Moreover, our results highlight the following expected effects:

- decreasing the sowing density and/or increasing the distance between rows in SC favoured disease control with a reduction of at least 50% in the AUDPC at maturity, in the case of a five-fold increase in row spacing, and a 25% reduction when sowing density is reduced by 50%;
- increasing the proportion of pea in the mix also reduced AUDPC at maturity of at least 80% between a 75% wheat-25% pea mix and a 25% wheat-75% pea mix.

The model outputs also highlight less expected results:

- shortening the distance between rows can make the SC less vulnerable to disease than the IC when wheat constitutes at least two-thirds of the mix (Fig. 8A, see for example that with an inter-row distance of 10 cm and 75% wheat, AUDPC is higher than with 100% wheat);
- decreasing plant density in the IC can lead to more disease than in the SC, depending on the proportion of pea in the species mix, highlighting the need for finding the best combination of spatial arrangement parameters;
- the trends in yield for wheat (Fig. 8B) with regards to species proportion showed that growing an IC offered a better yield than a wheat SC, despite higher levels of AUDPC at the end of the crop cycle. A 75% wheat/25% pea IC produced a yield 1.5 times greater than a 100% wheat SC for the same total field surface (dry wheat grains in t.ha^{-1}), suggesting that trade-offs could be found in spatial arrangement to manage both wheat disease and yield. There is a threshold after which further reducing wheat proportion (around

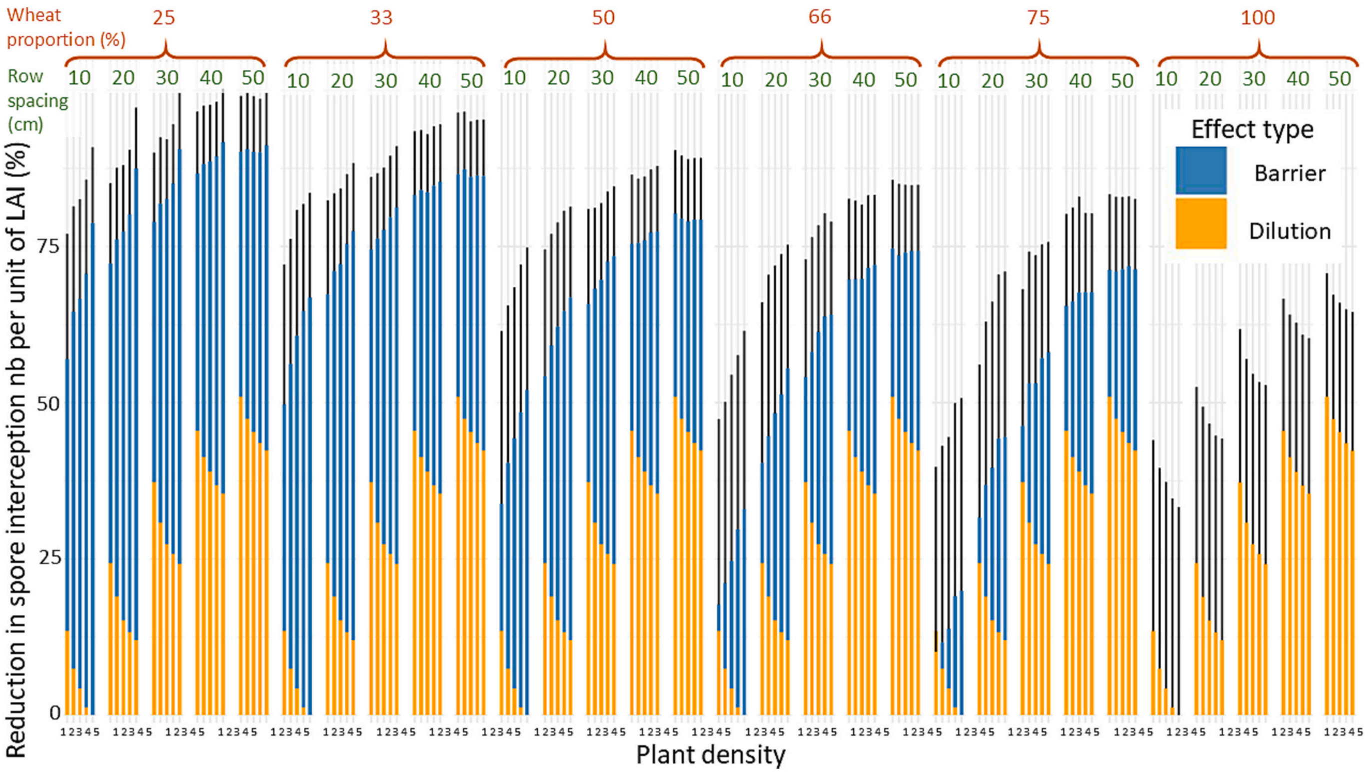

Fig. 7. Quantification of the dilution (in yellow) and barrier (in blue) effects as a percentage of disease reduction using the cumulative number of intercepted spores per unit of LAI over the whole crop cycle until physiological maturity. Error bars represent the propagation of uncertainty in the calculation of the percentage to show the variability in the results over the 30 years of simulation.

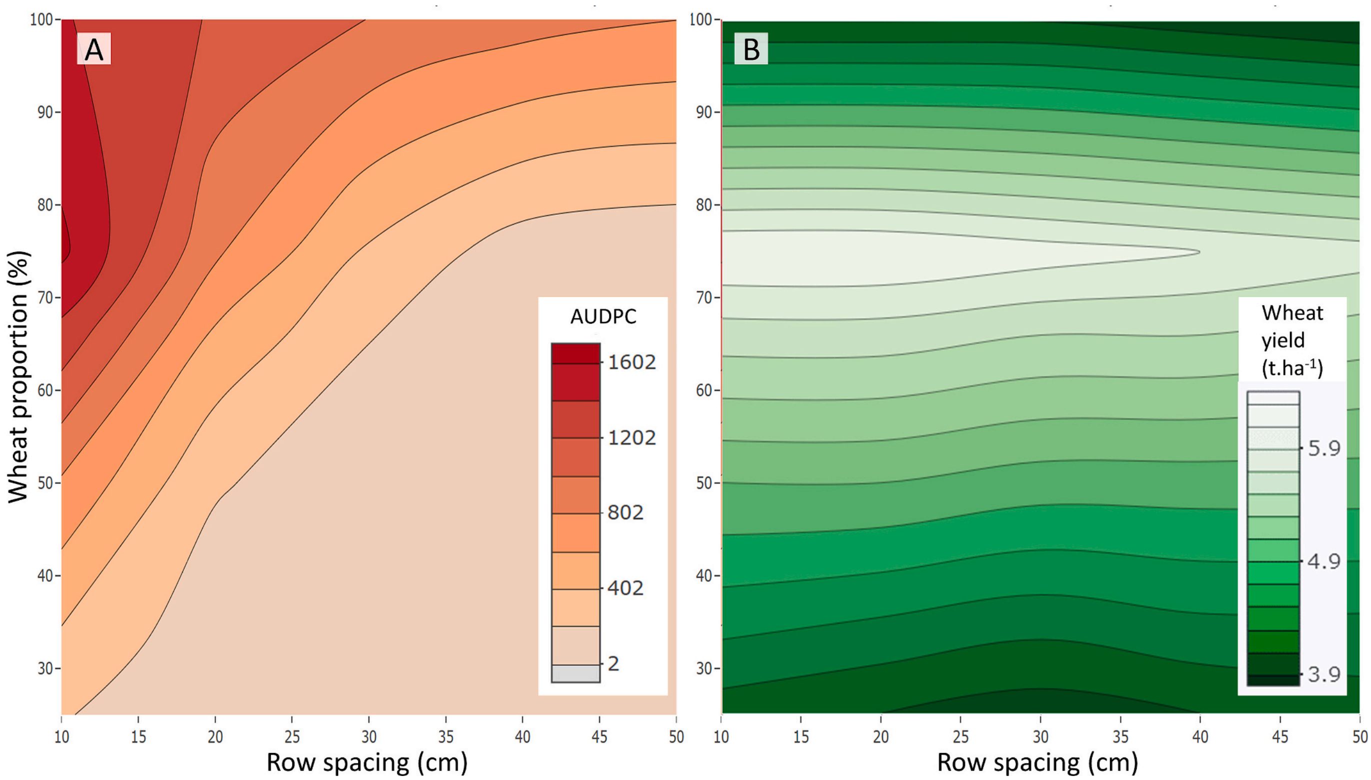

Fig. 8. A) contour graph of mean AUDPC at physiological maturity (30-year average for plant densities). B) contour graph of the mean yield for wheat at physiological maturity (30-year average for plant densities). The x axes represent distance between rows and the y axes represent proportion of wheat in the mix.

60%) does not bring more benefits in terms of production nor disease regulation.

Other published works focused in general on fewer factors compared to our experiment. Therefore, we discuss below available elements factor by factor, before offering a more global analysis.

4.1.1. Plant density

Plant density is the most studied factor in previous research. Decreasing plant density was found to generally bring positive outcomes in terms of disease control (Bondad, Harrison, Whish, Sprague, and Barry, 2023), a phenomenon we also have observed in our simulations. However, there are exceptions depending on yearly weather conditions, potted versus field experiments, types of diseases (Finckh et al., 2000); and when a reduction in disease intensity is observed, the range in relative reduction is very large (Finckh and Gacek, 1999). Moreover, when considering disease incidence, Douma and Noordhoek (2025) in their meta-analysis found no correlation between disease incidence and plant density. They emphasised that a more thorough investigation into the fundamental mechanisms and interactions involved was essential.

Our model and simulation results showed that the impact of plant density on disease intensity is dependent on yearly weather. Although we chose to focus on a 30-year average, there was a high standard deviation for important variables such as AUDPC and spore interception early in the crop cycle. It has been previously suggested that this is due to the amount of primary inoculum available at sowing and on epidemics earliness (Finckh and Gacek, 1999). But in our simulations, the amount of primary inoculum available at the beginning of each year was fixed, suggesting that it may not be the only explanation behind the link between disease response and weather. Microclimate variables also varied according to intra-annual weather variability with a clear important temporal aspect; indeed, patterns changed during the crop cycle, i.e. reducing density was more positive at the beginning than the end, revealing changes in species dominance and architecture. A modelling study using a Functional-Structural Plant Model suggested links between plant density and canopy architecture (Baccar et al., 2011).

In IC, results can be different, even contradictory, depending on the combination of plant densities and species proportions (Garrett and Mundt, 2000). In our results, we did find that decreasing density may lead to negative outcomes depending on pea proportion, seemingly due to a reduction in spore interception, concurrently to a decrease in infection rate. In designs where pea is added to wheat, the density of susceptible plants remains constant, but the density of associated plants changes. Therefore, changes in overall plant density modify either spore dispersal (the barrier effect) and/or the microclimate. Conversely, in designs where wheat is replaced by pea, changes in the density of susceptible plants may influence disease outcomes (dilution effect) more than the presence of the resistant crop (Boudreau, 2013). Our quantification of dilution versus barrier effects supports the principle that any disruption in spore dispersal will bring the strongest results in the end.

Finally, the relationship between density and disease intensity could very well be a non-linear one with a threshold effect which would depend on plant growth and phenology. If the plant cycle can outrun the disease cycle, then the consequences at harvest will be minimised (Ferrandino, 2008). Thanks to a dynamic modelling approach, we were able to identify phenological periods that delimit different patterns in our results. Based on 30-year averages, these global trends may however vary from one year to the next which needs further research.

4.1.2. Distance between rows

This is where our work brings novel results, as studies on fungal diseases, experimental or model-based, are sparse and often compare different arrangements based on composition (random mix versus strips or rows) rather than spatial distribution (Sapoukhina, Durel, and Le Cam, 2009). While random mixes are usually found to be more performant in maximising the heterogeneity of the canopy (Mundt, 2002), their practical implementation is limited due to the reliance of agriculture on standardised machinery. Therefore for row or strip cropping, which is the focus of our study, inter-row distance is a worthwhile lever to use (Gardarin et al., 2022). Reducing distance between rows in cultivar mixes reduced the benefits brought by the diversification for short distance dispersal of spores (Sapoukhina, Tyutyunov, Sache, and Arditi, 2010). This was also the case in our simulations, especially up to the flowering stage of the susceptible crop.

Whether in interspecific or intraspecific mixes, distance between plants is more studied for its wider effects on crop growth and structure than disease management. Indeed, this lever modifies radiation interception as well as nutrients and water uptake (Bedoussac et al., 2015; Thorsted, Olesen, and Weiner, 2006). However, all these aspects can have indirect impacts on diseases via the development of the susceptible host plant, thereby impacting both the fitness, and potential resistance of the plant to infection, as well as the availability of habitat for the given pathogen (Tibi, Martinet, and Vialatte, 2023).

4.1.3. Species proportion

The great majority of published studies shows that introducing a companion species brings beneficial outcomes on disease control and leads to a significant reduction in diseases (Boudreau, 2013). The necessary quantity of companion species is not always clearly addressed. The relative proportion of species in the mix was found here to be the most impactful lever overall, generally with a threshold effect after which no further benefit is observed from increasing the proportion of resistant plants.

For example, Levionnois, Pradal, Sanner, Saint-Jean, and Robert (2023) demonstrated through modelling that the proportion of the companion crop of 25% had the strongest effect on disease severity, which was reduced by 50%. Précigout, Renard, Claessen, and Robert (2023) found an 85% reduction in AUDPC when adopting a mix of 60% susceptible host - 40% resistant host, a threshold after which no further improvement was observed. When studied alongside density, proportion of susceptible plants is still the most important factor in designing fields for maximising disease control (Gigot, de Vallavieille-Pope, Huber, and Saint-Jean, 2014). Vidal et al. (2020) also showed that this is quite robust when there are marked contrasts between cultivars' canopy architectures. In comparison, our results comfort these findings and contribute to expose the underlying mechanisms behind these observations:

- The threshold effect is mostly felt in the microclimate where there is a clear separation between SC and IC,
- Proportion had a non-linear relationship with disease severity particularly when combined with other factors such as inter-row distance and density.

These preliminary comments on spatial arrangement can now inform the discussion on the core topic of the mechanisms involved, namely dilution, barrier and microclimate.

4.2. The relative contribution of the dilution, barrier and microclimate mechanisms

A central aim of this work was to further investigate the three main mechanisms at play in disease regulation when intercrop systems are implemented. The objective was to quantify their respective weight in the processes involved in an epidemic. There is an inherent difficulty in separating these mechanisms, and by extension, in identifying the main drivers behind their inner workings, because of their interconnectedness.

Previous studies have made the hypothesis that dilution, as a reduction in density of susceptible hosts, hence limiting suitable habitat for the pathogens, is the main factor behind the improvement in disease epidemics control (Newton and Skelsey, 2023). These findings need to be put in perspective with several key intertwined elements:

- The pathogen considered and its mode of dispersal (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024; Burie and Ducrot, 2014), with for example a potentially reduced effectiveness for rain splashes (Borg et al., 2018) or enhanced effectiveness for wind dispersed spores (Calonnec et al., 2012);
- The relative timing in crop and pathogen physiologies (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024), depending for example, on the concurrent LAI dynamic in both crops (Précigout, Renard, Claessen, and Robert, 2023), and on a potential reduction in plant growth (competition) (Calonnec et al., 2012);
- The indirect impact of dilution on canopy microclimate which could either reinforce or counter its benefits (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024).

In contrast, the barrier effect has been widely evaluated as always being beneficial in controlling epidemics (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024; Calonnec et al., 2012; Homulle et al., 2025; Ratnadass, Fernandes, Avelino, and Habib, 2011; Schoeny, Jumel, Rouault, Lemarchand, and Tivoli, 2009; Schoeny, Jumel, Rouault, et al., 2010; Villegas-Fernández, Amarna, Moral, and Rubiales, 2021; Xu, 2011). Physical obstacles to spore movement, especially in the early days of the crop cycle, reduce the deposition of primary inoculum (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024; Finckh et al., 2000). Questions remain on the strength of the barrier effect as it depends on field design, particularly species proportion or whether the plants are arranged as a random mix or as rows (Borg et al., 2018; Levionnois, Pradal, Sanner, Saint-Jean, and Robert, 2023; Newton and Skelsey, 2023).

As a general trend in our simulations, the contribution of the barrier effect relative to the dilution effect increases with increase in pea proportions and higher plant densities. Its response to row spacing is modulated by species proportion. Different spatial arrangements can yield similar outcomes in terms of reduction effect. For example, an IC system with 75% of wheat at normal plant density and with rows 40 cm apart further reduces spore interception by 50% compared to the SC, which is equivalent to an IC system with only 50% of wheat at normal density but with rows 20 cm apart. However, this translates into a total LAI (photosynthetic surface) for wheat of 2.6 and 2 $m^2.m^{-2}$ respectively, compared to around 1 in the SC.

In summary, IC associated with field design optimisation could protect photosynthetic capacity of wheat for longer during the crop cycle, mainly through the alteration in the movement of spores (barrier effect) in systems with wheat proportions below 75% and row spacings below 30 cm; and through reduced habitat availability (dilution effect) for lower plant densities, lower wheat proportion and rows further apart. It provides potential explanation as to what yielded variable results in other research works as described above.

Spore dynamics is driven by both dilution and barrier effects, while the other diseases processes are driven by microclimate effects. In our results, microclimate was the mechanism with the smallest but most negative effect on disease regulation from the start of the crop cycle. Particularly, the increase in SWD late in the crop cycle which led to an notable increase in infection rates, despite a colder temperature in the IC canopy. This is consistent with selected experimental studies (Schoeny, Jumel, Rouault, Lemarchand, and Tivoli, 2009; Vidal et al., 2017) on similar pathosystems. Other works have shown that the effect of IC on microclimate is not straightforward and can lead to either a reduction or an increase in SWD and/or in temperature depending on the crops and the timing of growth in terms of height and canopy density (Affichard, Jacquelin, Khalil, Andrivon, and Le May, 2024; Calonnec et al., 2012; Homulle et al., 2025; Ratnadass, Fernandes, Avelino, and Habib, 2011).

All in all, the IC remained an advantageous option for controlling disease by tempering with the dynamic in spore interception early in the crop cycle, limiting the number of spores and lesions which can develop thanks to the favourable microclimate created by the mixed canopy. In particular, a significant delay in the disease onset reduced the final damage in IC. The sensitivity of the three mechanisms to agronomic levers such as inter-row, plant density and species proportion depended on many factors related to the pathosystem considered. From our results, we concluded that modelling had the potential to become a useful tool to assess and sort many different possible scenarios offered by diversification in the field.

4.3. *Perspectives and limitations*

A high-level comparison with published field experiments conclusions showed that modelling can inform the design of more sustainable agrosystems by testing many different IC strategies. Modelling indeed allows for a feasible quantification of the mechanisms and their interactions, for a variety of situations in terms of field design and weathers. Particularly, our model can do so dynamically for the pathosystem as a whole, which means the pathogen in interaction with the crops and all in interaction with a pedo-climatic context as well as farming practices. Moreover, beyond disease control alone, it can include other considerations such as consistent production and reduced inputs. The model can also be used to evaluate optimal spatial arrangements in the context of a future climate, where nutrient and water availability will inevitably constrain system design.

As with any modelling work, formalism and analysis assumptions are a key driver of results. Here we would like to mention a few to raise awareness:

- Formalism assumption about spore interception and its reliance on light interception,
- Homogeneity of canopy for thermal microclimate, good with random, close individual plants, less so with plants further apart and in row,
- Linearity assumption about dilution and barrier effects and its effect on the additive potential of the two effects.

To go further, thanks to the genericity of the model's formalisms, the method can be applied to other pathosystems and pedoclimates to provide resources to disentangle the multiple combinations of crops, proportions, and techniques available to farmers. Such a coupled model could conceivably translate disease severity into yield losses, thus enabling the impact of IC on reducing pesticide use to be quantified (Zhang, Zhang, Cong, Bedoussac, and Munier-Jolain, 2025).

Furthermore, by using other complementary modelling approaches such as 3D canopy descriptions (Gaudio et al., 2022), we could further identify which detailed aspects really impact mechanisms at finer spatio-temporal scales. Conversely, by coupling this model with landscape models, we could upscale to the ecosystem level and consider the complex and diverse agroecosystems involved in the agroecological transition at a regional scale.

Despite its initial validation on sole crops for MILA, and without disease for STICS-IC, the coupled model framework has not yet been confronted to experimental data which includes both disease and intercrop measurements. It will be indeed the next step in the model development to ensure a satisfactory performance for further usage.

Our study highlighted the complexity of the interactions between diseases and intercrops. Our work remained essentially qualitative given the levels of interactions between factors and interannual variability. We advocate for a more comprehensive analysis with more robust mathematical tools which can deal with dynamic, multi-variable modelling (including intermediary and state variables).

5. Conclusion

Thanks to the coupling of two validated models, we were able to simulate an intercrop pathosystem in a coherent manner and to bring elements of understanding which should help unlock some of the obstacles to the study of diseases in species mixes. This is an essential first step in validating this novel coupling of a crop model with a disease model in an intercrop situation, before formal confrontation to experimental datasets.

In particular our study confirms that, when looking at the crop cycle as a whole, IC is generally beneficial in terms of disease control. We found lower AUDPCs at maturity in 93% of cases compared to SC, with exceptions typically occurring at the shortest inter-row distance. This benefit was primarily driven by the dilution and barrier effects which introduced a delay in the disease onset and limited spore interception. While the effect of IC on canopy microclimate was favourable to disease development, it does not offset the overall benefits on spore dynamics.

These mechanistic insights highlight the importance of spatial arrangement in maximising the benefits of IC on disease regulation. Particularly, increasing the distance between rows emerges as a potentially effective strategy, although not all combinations of sowing density, species proportion and inter row distance were conducive to regulating pathogen population and disease severity. Optimal IC strategies require to consider interannual variability which brings a significant element of uncertainty in disease outcomes from one year to the other, as shown in most previous studies with year-to-year comparisons (Finckh and Gacek, 1999; Homulle et al., 2025; Précigout, Renard, Claessen, and Robert, 2023). Our study provides supporting evidence that modelling is a useful reflexion tool to simulate a variety of scenarios for further research, including the stability of disease regulation under future climate conditions.

Data and sources statement

The source code of STICS IC coupled with MILA, as well as all Input and output files, are available in open access on a Zenodo archive (Deheinzelin, Vidal, Lecharpentier, Bancal, and Launay, 2026).

CRediT authorship contribution statement

Audrey Irene Deheinzelin: Writing – original draft, Project administration, Data curation, Conceptualization. **Tiphaine Vidal:** Writing – review & editing, Validation, Supervision, Project administration. **Patrice Lecharpentier:** Writing – review & editing, Software, Resources, Methodology. **Marie Launay:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Marie-Odile Bancal:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Audrey Irene Deheinzelin reports financial support was provided by European Research Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.agsy.2026.104717.

Data availability

Deheinzelin, A. et al. (2026). Data, code and software to reproduce the article [dataset]. Zenodo. https://doi.org/10.5281/zenodo.18700622

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