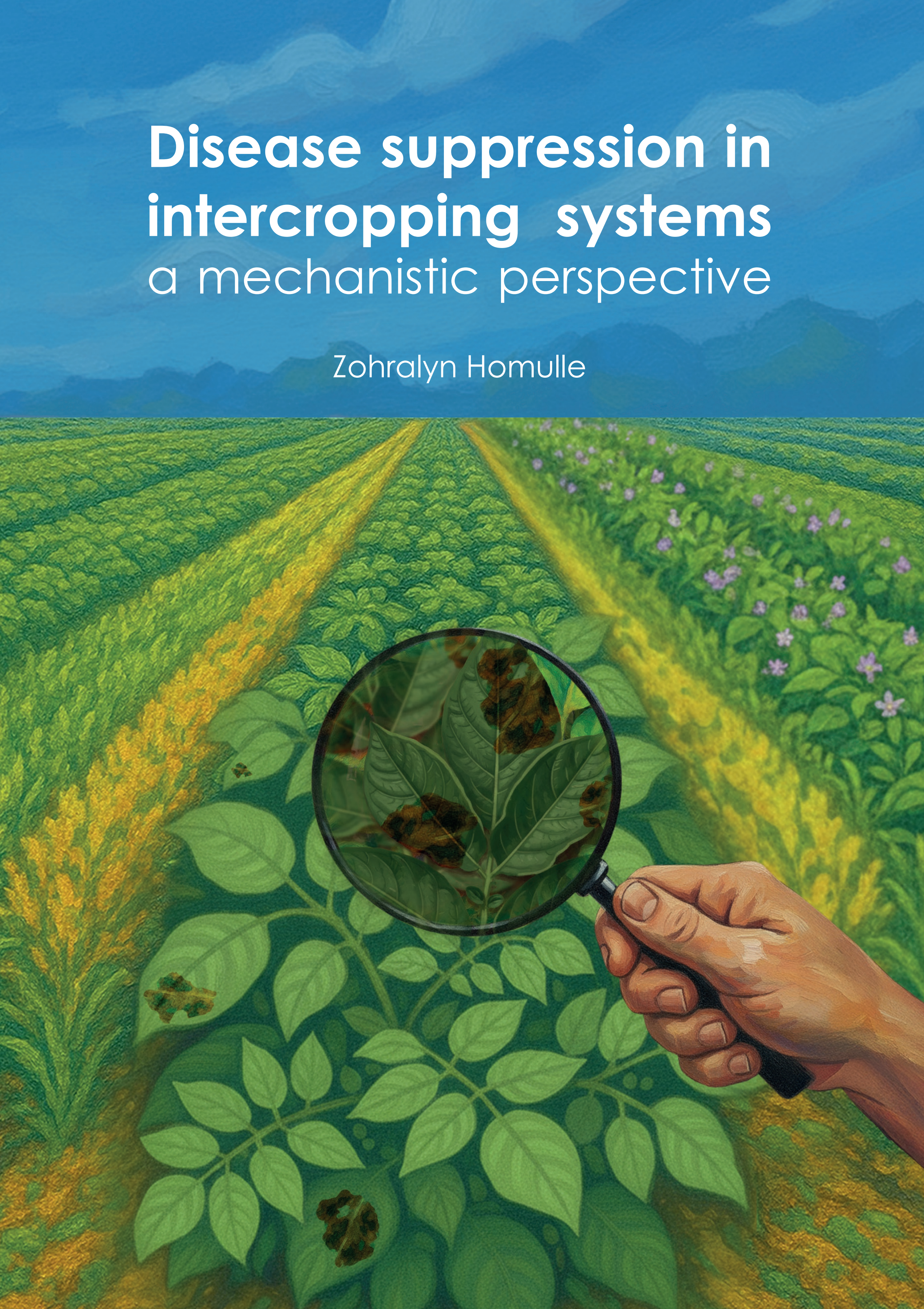
Disease suppression in intercropping systems

a mechanistic perspective

Zohralyn Homulle



Propositions

1. Understanding one system’s mechanisms is more effective for designing disease-suppressive strategies than looking for general patterns across systems.
   (this thesis)

2. The most sustainable method to reduce *Phytophthora infestans* is to greatly reduce the area of potato production.
   (this thesis)

3. If all farmers in the Netherlands would adopt strip-cropping, the reduction in synthetic inputs will be minimal.

4. Research focusing on improving industrial agriculture diverts resources from research on long-term sustainable practices.

5. Educating students to collaborate and work transdisciplinary is more important than fostering independent researchers.

6. The projected rise in human population is wrongly equated with the need to increase food production.

7. Recycling perpetuates a throwaway culture.

8. People who do not like driving are not driving the right car.

Propositions belonging to the thesis, entitled

Disease suppression in intercropping systems: a mechanistic perspective

Zohralyn Homulle
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Disease suppression in intercropping systems: a mechanistic perspective

Zohralyn Homulle

Thesis committee

Promotors
Prof. Dr N.P.R. Anten
Professor of Crop and Weed Ecology
Wageningen University & Research

Co-promotor
Dr J.C. Douma
Quantitative Researcher Nature and Sustainable Agriculture
Rabobank, Utrecht

Other members
Dr F.J.J.A. Bianchi, Wageningen University & Research
Prof. Dr M. Höfte, Ghent University, Belgium
Dr M.M. Riemens, Wageningen University & Research
Dr J. van Dijk, Utrecht University

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Contents

Chapter 1

General Introduction

The current Dutch countryside is a landscape where fields, farmland, meadows, and nature come together. It is characterised by its flat terrain and extensive agricultural use, where fields are divided into large, rectangular plots. The land is intensely managed, machines cultivate the fields with precision, resulting in crops lined up in neat, geometrically precise rows. There is little room for anything outside of the planned crops; wild plants, flowers, or hedgerows are kept to a minimum. There are occasional trees around fields and farms, along with some scattered fragments of wooded areas. Overall, the countryside is a well-structured, cultivated environment, with little diversity.

Fig. 1.1 Impression of the Dutch countryside. (A) large, rectangular plots (Noordoostpolder), (B, C) managed fields with neat rows and no room for plants other than the main crop, (D) satellite images of rectangular fields (Noord Brabant).

These (large-scale) fields, where a single crop type is grown, are often called monocultures. The term monoculture can refer to either repeated cultivation of the same crop in the same field from season to season (Power & Follett, 1987), or to fields where a single crop type is grown at a particular time (spatial monoculture), which can have a crop rotation in time (Franco et al., 2022). Throughout this thesis, monoculture means the latter: a (large-scale) field cropped with a sole crop. It is commonly observed that compared to more species-rich systems, monocultures are relatively vulnerable to pests and diseases (Kaur et al., 2024; Venbrux et al., 2023). Due to the low plant diversity, a single pathogen can spread relatively unhindered, potentially destroying the whole crop (McDonald & Stukenbrock, 2016; Zhan et al., 2014). Yet, agricultural landscapes have not always been dominated by monocultural fields. Before industrialised agriculture, farmers commonly used diverse cropping systems (Liebman, 1996; Vandermeer, 2009), which are thought to contribute to the regulation and suppression of plant disease epidemics (Altieri, 1999, 2018). These diverse cropping systems, known as polycultures, mixed cropping or intercropping, involve growing two or more crop species together in the same field (Altieri, 1999; Liebman, 1996; Vandermeer, 1992). To understand the current western farming and food system, its challenges, and potential solutions, it is important to understand the historical context of how monocultures became the dominant form of production. The context of this thesis is industrialised, mechanised farming systems, particularly within the European and Dutch agricultural context, where farming practices are based on, and tailored to, monocultures.

1.1 The sources of industrial agriculture

Modernised farming in Europe began during the Agricultural Revolution(s) of the 17th, 18th and 19th centuries (Chorley, 1981; Thompson, 1968). Improvements in agricultural techniques, such as new equipment, scientific breeding methods, improved drainage, and experimentation with new crops and systems of crop rotation increased agricultural efficiency and food production. By the 20th century, European agriculture further modernised with the introduction of chemical fertilizers, pesticides, and motorised machinery (Martín-Retortillo & Pinilla, 2015). Land consolidation, by reducing the number of parcels and improving their shape, further stimulated the trend towards mechanisation, intensification and monoculture cropping. By growing just one crop species in a field at a time, monocultures enabled farmers to use even larger machinery, increasing the efficiency of activities like planting and harvesting. Institutional efforts to resolve the food shortages at the end and shortly after World War II led to policies supporting agricultural intensification, such as the Common Agricultural Policy (CAP) (Martín-Retortillo & Pinilla, 2015). These policies, along with subsidies, market demands, international trade and economies of scale (cost advantages from large-scale production), further reinforced the shift towards large-scale monoculture farming. As a result, intensive, monoculture-based farming is a widely used method of crop cultivation in Europe.

Although agricultural intensification, specialisation, and mechanisation, have significantly improved efficiency, leading to higher yields — for instance, in the Netherlands, the yield (kg/ha) of major crops like potatoes and wheat has nearly doubled over the past decades (FAO, 2023) — agriculture has many negative side effects. Agricultural areas contribute to the widespread loss and degradation of ecosystems and biodiversity (Dudley & Alexander, 2017; Lanz et al., 2018; Sánchez-Bayo, 2011). A major driver of this degradation is the heavy reliance on chemical inputs such as pesticides, fertilizers, and fossil fuels. Pesticides harm non-target organisms by disrupting their survival, growth, reproduction, and behaviour (Elhamalawy et al., 2024), and cause long-term changes in habitats and food chains (Isenring, 2010; Sánchez-Bayo, 2011). Numerous studies have reported significant declines in abundance, diversity, and biomass of insects, such as butterflies (Fox et al., 2015; Maes & Van Dyck, 2001; Thomas, 2016; Wepprich et al., 2019), bees (Goulson et al., 2008; Nicholson et al., 2024; Nieto, 2014; Winfree et al., 2009), and moths (Conrad et al., 2002; Dennis et al., 2019). A well-documented example is the 76% decline in airborne insect biomass over the past 27 years in nature protection areas in Germany (Hallmann et al., 2017). Declines extend beyond insects; also birds, mammals, amphibians, and fish are affected through reduced food resources, poisoning by (accumulated) pesticides and spillover of pesticides into surface waters (Hallmann et al., 2014; Isenring, 2010; Ortiz-Santaliestra et al., 2018). Additionally, pesticides pose health risks to humans due to occupational exposure or spillover of pesticides to residential areas (European Environment Agency, 2023; Navarro et al., 2023; Ottenbros et al., 2023).

Next to biodiversity loss, excessive chemical use reduces soil fertility and soil life, and pollutes air, water, and soil, thereby affecting soil health and reducing ecosystem resilience (Mandal et al., 2020; Pahalvi et al., 2021; Tripathi et al., 2020). Additionally, the use of fossil fuels in agricultural practices contributes to greenhouse gas emissions, further exacerbating environmental degradation and climate change. Manufacturing of fertilizers, through ammonia (NH_3) synthesis via the Haber-Bosch process, is currently one of the largest global energy consumers and greenhouse gas emitters, responsible for an estimated 1.5% of all anthropogenic CO_2 emissions (International Fertilizer Association, 2022; Tubiello et al., 2022)

Throughout this thesis, the term ‘pesticides’ refers to all types of chemical substances used to control pests, including insecticides, herbicides and fungicides. Unless otherwise specified, it primarily refers to synthetic chemical pesticides.

1.2 Diversifying the agricultural system

Sustainable solutions are thus urgently required to cultivate crops while reducing the impact of agricultural systems on the environment and human health (Godfray et al., 2010). Diversification of cropping systems is expected to lead to more resilient food systems. Increasing crop diversity through intercropping, the simultaneous cultivation of multiple crop species (Vandermeer, 1992), is a relatively simple and effective agroecological practice (He et al., 2019). Intercropping systems have been used by smallholder farmers in Africa, Latin America and parts of Asia for centuries (Lithourgidis et al., 2011). For instance, before European settlement, many Native American nations intercropped maize, common bean and squash, commonly called the “Three Sisters”, a system in which each crop performed multiple roles and in which the three species complemented each other, resulting in a stable and productive system (Mt. Pleasant, 2006). In contrast, in modern mechanised agricultural systems, intercropping is rarely practised, because it is generally incompatible with standard machinery (Bedoussac et al., 2015). However, there is a renewed interest in intercropping, because of its better environmental performance than modern intensive agriculture (Belstie, 2017; Lithourgidis et al., 2011; Weih et al., 2022).

The reported benefits of intercropping are many and diverse. The most common advantage of intercropping is the production of greater yield on a given piece of land by making more efficient use of the available resources, by combining crops of different rooting traits, canopy structure, height, and nutrient requirements, allowing them to complement each other in their resource utilisation (Li et al., 2020b, 2023; Lithourgidis et al., 2011; Yu et al., 2015). Moreover, intercropping improves soil health and quality by increasing soil organic matter and fostering a healthy community of soil microorganisms, which enhances nutrient cycling and soil structure (Cong et al., 2015; Layek et al., 2018; Tang et al., 2021). Intercropping also enhances biodiversity in cropping systems, which can lead to the suppression of weeds (Gu et al., 2021), pests (Chadfield et al., 2022; Dassou & Tixier, 2016) and diseases (Boudreau, 2013; Zhang et al., 2019)

Intercropping can be practised in varying spatial configurations. In mixed intercropping, multiple crops grow simultaneously with no distinct row arrangements. Row intercropping is the cultivation of crop species in alternating rows. Relay intercropping consists of multiple crops or living mulches grown in sequence with some overlap in their growth cycle. Lastly, the crop species can be grown in alternating multi-row strips, known as strip cropping. In strip cropping, the strips are wide enough to be operable using equipment that is currently available on modern mechanised farms (Ditzler et al., 2021; van Oort et al., 2020), but narrow enough for crops to ecologically interact. With the use of precision technologies such as GPS-tracking, farmers can make straight tracks when sowing, harvesting, fertilising or spraying, making the implementation of strip cropping possible (Bulten et al., 2022). In practice, a strip width of 3 meters or more is used due to limitations set by available equipment (Ditzler et al., 2021).

1.3 Disease suppression in intercrop systems

Ample evidence has been gathered over the years attesting to the disease-suppressive potential of intercropping. Literature searches overwhelmingly indicate that intercropping generally reduces diseases. Out of 206 studies examined, 73% reported a reduction in disease due to intercropping (Boudreau, 2013). In a different study out of 101 papers, 79% reported decreased disease severity or incidence in the intercrop (Stomph et al., 2020). The disease-suppressive effect of intercropping (i.e., relative to monocropping) is the result of a complex interaction between the focal crop, the pathogen, the companion crop species and the abiotic and biotic environment, both at field and landscape scale.

Despite the overwhelming evidence that intercropping suppresses disease, it is not clear which management practices, pathogen traits or host or companion crop characteristics influence the strength of the suppression. Several mechanisms contributing to disease suppression in intercrop systems have been proposed and include the companion species acting as a barrier for the dispersal of disease propagules (hereafter referred to as the ‘barrier effect’), an altered microclimate in the host canopy (‘microclimate effect’), a resistance response in the host elicited by the presence of the companion crop (induced host resistance or host susceptibility), and altered plant morphology and canopy structure of the host due to interactions with the companion crop (‘morphological effect’) (Boudreau, 2013). Additionally, in replacement-type intercrop systems, i.e. mixtures created by replacing plants of one crop species with those of another such that the relative plant density total stays constant (van der Werf et al., 2021), the density of the host crop is reduced, which may, in turn, reduce the chance that a given pathogen propagule reaches a host crop (‘dilution effect’) (Boudreau, 2013; Hiddink et al., 2010).

The different mechanisms may act alone or in combination and can be influenced by the type of companion crop species. For example, in tomato intercropped with marigold or pigweed, both companion species acted as a barrier for spore dispersal and reduced the relative humidity in the tomato canopy, leading to the suppression of tomato early blight (Gómez-Rodríguez et al., 2003). Additionally, marigold exhibited allelopathic effects that inhibited in-vitro spore germination. In another study, in a pepper-maize intercrop, maize formed a barrier for anthracnose spores, which resulted in a reduction of spore density of *C. scovillei* in the intercrop, which was significantly associated with a reduction in anthracnose disease incidence (Gao et al., 2021). In a pea-cereal intercrop, reduction in *Ascochyta* blight was explained by host dilution, lowered relative humidity, and reduced splash dispersal (Schoeny et al., 2010).

While modern mechanisation makes strip cropping more feasible than mixed or row intercropping, increasing strip width would reduce some of the benefits of intercropping, such as overyielding, because the species complementarities that drive some of these advantages depend on the proximity of the different species (van Oort et al., 2020). However, for disease suppression, mechanisms such as host dilution and barrier effects could still play a role in strip crop systems with wider strips. There is, however, little information on the effectiveness of disease control in strip cropping systems. Secondly, although disease-suppressive mechanisms have been hypothesised and studied, it is largely unknown whether and how the mechanisms can be influenced by the identity and traits of the companion species, and how the effects of different mechanisms work out in combination (i.e., there being trade-offs or synergies). Such knowledge, though, could help our understanding of why certain crop combinations are more effective at disease suppression than others, and could thus provide vital knowledge needed to improve intercrop designs to enhance disease management.

1.4 Potato late blight as a case study

Europe has a long tradition of potato cultivation and consumption (Love et al., 2020). From the seventeenth to the twentieth century, the potato crop (*Solanum tuberosum* L.) developed progressively from a staple to a cash crop all over Europe (Goffart et al., 2022). Potato is an important cash crop for farmers and the whole potato value-chain. Currently, about one quarter of the global potato production originates from Europe (van Loon et al., 2025).

Among the various potato pathogens of fungal, bacterial and viral origin, *Phytophthora infestans*, the causal agent of potato late blight, is considered the most devastating. *P. infestans* is an oomycete, a fungus-like organism belonging to the group of water moulds. Leaves, stems and tubers are all susceptible and the disease can spread very fast under suitable conditions and kill the crop entirely (Fry, 2008; Wu et al., 2020). *P. infestans* is widespread throughout the world and causes serious tuber yield losses (Majeed et al., 2017). This pathogen caused late blight epidemics which led to the Irish potato famine in the 1840s (Andrivon et al., 2003; Fry, 2008). Even today, it continues to pose significant challenges. In the Netherlands, where conditions are often favourable for late blight epidemics during the growing season, late blight is of major concern for potato growers (Ditzler et al., 2021; Haverkort et al., 2008).

Currently, a combination of different methods is used to manage the disease, including eliminating on-farm sources of the pathogen before planting, using resistant cultivars or early-maturing cultivars to reduce the duration of the epidemic, and applying fungicides (Bouws & Finckh, 2008; Fry, 2008). The use of fungicides continues to be the most common strategy for late-blight control (Campos & Ortiz, 2020). Besides the high costs incurred (Haverkort et al., 2008), challenges are arising concerning fungicide resistance (Brylińska et al., 2016; Runno-Paurson et al., 2010) and environmental sustainability (Majeed et al., 2017). In organic agriculture, where the use of pesticides is not allowed, diseases can significantly reduce crop yields. Thus, exploring additional methods for the integrated control of *P. infestans* is necessary for both conventional and organic growers.

P. infestans primarily spreads through the dispersal of spores. Primary infection sources of *P. infestans*, such as infected seed tubers, unharvested tubers or harvested tubers dumped on refuse piles, produce spores that can be dispersed by wind or rain to healthy potato plants (Fig. 1.2) (Zwankhuizen et al., 1998). *P. infestans* spores have a potential for long-distance wind dispersal to other fields (Fry, 2008). Under conducive conditions, the spores then germinate, infect, and generate new spores, thereby initiating additional disease cycles and repeating the infection cycle multiple times within a single growing season. Disease development during the growing season is influenced by temperature and relative humidity (optimum temperatures between 10 and 27°C and relative humidity > 90%; Zwankhuizen & Zadoks, 2002).

An agronomic control measure for potato late blight, beyond those previously mentioned, could be strip cropping. If potato were strip-cropped, the previously discussed disease-suppressive mechanisms could be activated. A tall companion crop species could act as a barrier for the initially incoming spores that start an epidemic, thus limiting initial primary infection, as well of the spores produced by the in-field infections, thus limiting spread within the field. In contrast, a short companion crop species could potentially change the microclimate in the host canopy to be less conducive for infection, lesion growth and sporulation. Both tall and short companions would provide a dilution effect for the within-field spread of the disease across strips. The magnitude of these effects has not yet been studied. Experiments comparing strip cropping with different companion species offer insights into which companions can provide effective disease suppression.

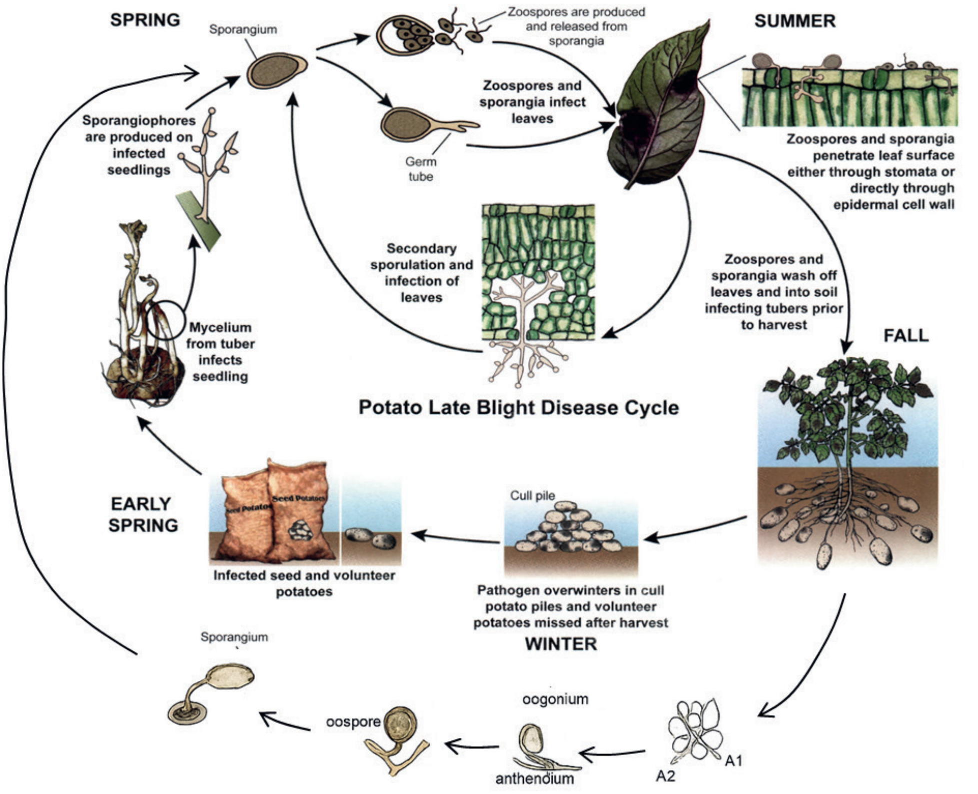

Fig. 1.2 The disease cycle of the late blight pathogen, *P. infestans* (Kirk et al., 2015). *P. infestans* overwinters in infected seed tubers, unharvested tubers or harvested tubers dumped on refuse piles. In early spring, these sources will produce spores, which can be dispersed by wind or rain to healthy potato plants. Under favourable conditions, spores germinate, grow, and produce new spores, to initiate new disease cycles. At the end of the growing season, in fall, spores can wash into the soil and infect tubers. The pathogen will again overwinter in infected tubers, starting the cycle again in the next year. *P. infestans* can also reproduce through a sexual cycle (bottom of figure), in which oospores are formed, which can overwinter in the soil, initiating new infections under favourable conditions.

1.5 Research objectives

The overarching objective of this research is to improve our understanding of disease-suppressive mechanisms in (strip)intercrop systems. Although the literature has provided extensive evidence of the disease-suppressive potential of intercropping, there is substantial unexplained variation in the reported effectiveness. Furthermore, there is limited understanding of the specific mechanisms underlying disease suppression, particularly how the mechanisms are influenced by the identity and traits of the companion species and how different mechanisms work out in combination.

We used a two-fold approach to improve our insight into what drives disease suppression in intercropping. First, we used a quantitative synthesis method – meta-analysis – to identify patterns across these different systems and to gain insights into the disease-suppressive mechanisms at play across these systems. Although this approach provides insights into general patterns (or lack of patterns), it does not allow for a detailed examination of the specific mechanisms and their interactions. Therefore, I followed this meta-analysis with a more in-depth study of one specific system, namely potato late blight in strip cropping.

The specific research objectives of this thesis are to:

- Identify factors that drive the variability in disease suppression in intercropping systems by synthesizing published experiments across all types of intercrops and pathosystems (Chapter 2).
- Investigate the effect of strip cropping potato with companion crop species of different stature (grass, faba bean, maize) on the epidemic development of *P. infestans* and tuber yield (Chapter 3).
- Assess how these different companion crop species mediate various disease-suppressive mechanisms (Chapter 4).
- Quantify the relative importance of individual mechanisms to overall disease suppression using a modelling approach, drawing on the case study and data from Chapters 3 and 4 (Chapter 5).

1.6 Outline of the thesis

To address the research objectives, this thesis presents the results of a combination of meta-analysis, field experiments, and a modelling approach. The thesis consists of four research chapters, each addressing disease suppression in (strip)intercrops.

In this chapter (**Chapter 1**), I have provided the context and background necessary to understand the scope of this research. The following chapters will each present a distinct research aspect. The thesis begins with a broad investigation of disease suppression in intercrop systems. **Chapter 2** analyses published experiments on disease suppression across various intercrop combinations and pathosystems, to identify patterns across these different systems and to gain insights into the disease-suppressive mechanisms at play across these systems. Although this approach provides insights in general patterns (or lack of patterns), it does not allow for a detailed examination of the specific mechanisms and their interactions driving disease suppression. Therefore, I followed this meta-analysis with a more in-depth study of one specific system. The subsequent chapters focus on this specific system, namely potato late blight in strip cropping. **Chapter 3** presents data from three years field experimentation on disease suppression and yield in potato strip cropping in Wageningen, the Netherlands. The experiments tested the effect of strip cropping potato with companion crops of different stature, each planted in alternating 3-meter wide strips, on the epidemic development of *Phytophthora infestans* and tuber yield. This chapter confirms that strip cropping has the potential to suppress disease. **Chapter 4** delves deeper into the mechanisms underlying disease suppression. In the field experiments described in Chapter 3, we measured various factors related to disease-suppressive mechanisms, such as microclimate, spore dispersal, and host resistance. This chapter explores how different companion crops influence these factors. Investigating these disease-suppressive mechanisms helps to understand how intercropping suppresses disease, demonstrating that different companion crops can reduce disease pressure even if the mechanisms operate differently. Finally, in **Chapter 5** we go one step further and use the findings from the field experiment in a modelling approach to quantify the relative importance of individual mechanisms in overall disease suppression, and the interactions between mechanisms. This modelling framework can be used to explore how intercrop design affects disease suppression and can also be applied to test the potential dynamics of other pathosystems within an intercrop.

The thesis concludes with a general discussion (**Chapter 6**), summarising the findings from each chapter and reflecting on their implications for sustainable disease management. I conclude by identifying further research to expand the contribution of crop diversity to sustainable disease management.

Chapter 2

Drivers of disease suppression in intercropping, a meta-analysis

Zohralyn Homulle[1], Wenfeng Li[2], Wopke van der Werf[1], Tjeerd Jan Stomph[1], Niels P.R. Anten[1], Jacob C. Douma[1]

[1]Centre for Crop Systems Analysis, Wageningen University, 6700 AK, Wageningen, the Netherlands

[2]Faculty of Mechanical and Electrical Engineering, Yunnan Agricultural University, Kunming, 650201, China

Abstract

Intercropping, the practice of growing multiple crop species together, is drawing interest as an option for ecological intensification of agriculture. The disease-suppressive potential of intercropping has been often attested, but there is little insight into how different factors influence disease suppression. Here, we synthesised results of 54 papers, together reporting results of 108 experiments on disease incidence in intercrops. Specifically, we analysed how variability in disease suppression is affected by factors such as companion crop traits, management choices, and pathogen characteristics. Compared to sole crops, intercropping reduced disease incidence by 33%, lowering both the initial disease incidence and the apparent infection rate. This shows that intercropping suppresses both initial and secondary infections. The average disease suppression was independent of pathogen type (fungus, bacteria, or virus) and their characteristics, host density, intercrop design, and relatedness between focal host and companion crop. While the majority of data records (91%) showed disease reduction in intercrops, improved yield was demonstrated in only 40% of the records. Disease suppressive potential has been observed in many studies, but does not seem to arise from one or a few key mechanisms. Rather we suggest that the magnitude of disease suppression depend how the companion crop interacts with the traits of the hosts, the pathogen, and the environment. Disease control in intercropping hence does not arise by one or few key overriding mechanisms but emerges from a multitude of mechanisms with varying effect sizes in different studies.

Key words: crop diversity, intercropping, crop mixtures, disease, disease suppression

2.1 Introduction

Intensified agricultural systems currently require high levels of agrochemicals (Aktar et al., 2009; Hedlund et al., 2020) to ensure high crop yields (Spielman & Pandya-Lorch, 2009; Woodhouse, 2010). The use of chemical inputs can cause environmental problems, such as loss of biodiversity and associated ecosystem services (Dudley & Alexander, 2017; Lanz et al., 2018; Sánchez-Bayo, 2011), and are increasingly recognised to have negative health effects (Kalyabina et al., 2021; Kim et al., 2017; Rani et al., 2021). Sustainable solutions are thus urgently required to protect crops while reducing the negative impact of agricultural systems on the environment and human health (Godfray et al., 2010). Intercropping (the practice of growing multiple crop species together (Vandermeer, 1992)) has gained increased societal and scientific interest, because of its better environmental performance compared with modern intensive agriculture (Belstie, 2017; Lithourgidis et al., 2011; Weih et al., 2022). The reported benefits of intercropping are many and diverse, such as improved land-use efficiency and yield gain (Li et al., 2020b, 2023; Yu et al., 2015), soil health and quality (Cong et al., 2015; Layek et al., 2018; Tang et al., 2021), resource-use efficiency (Glaze-Corcoran et al., 2020), as well as reduced weed, pest and disease pressure (Boudreau, 2013; Chadfield et al., 2022; Dassou & Tixier, 2016; Gu et al., 2021).

Ample evidence has been gathered over the years attesting to the disease-suppressive potential of intercropping. Literature searches overwhelmingly indicate that intercropping reduces diseases. Out of 206 studies examined, 73% reported a reduction in disease due to intercropping (Boudreau, 2013), and in a different study out of 101 papers, 79% reported decreased disease severity or incidence in the intercrop (Stomph et al., 2020). More recently, a quantitative analysis has been performed on the disease control effectiveness of intercropping. Intercropping was found to significantly reduce disease incidence from an average of 36% in sole cropping to an average of 22% in intercropping (Li et al., unpublished manuscript). The disease-suppressive effect of intercropping was successful irrespective of region or pathogen taxon, indicating that intercropping results in disease suppression in a wide range of crops, environmental conditions and for a wide range of pathogens. Nevertheless, substantial variation in the achieved level of disease suppression existed, ranging from a slight increase in disease incidence in the intercrop, to a control effectiveness of almost 100% (Li et al., unpublished manuscript).

Various mechanisms can contribute to disease suppression in intercrop systems. Mechanisms that are thought to play an important role include: the companion crop species providing a physical barrier against pathogen dispersal, alteration of microclimate within the host canopy due to species mixing, and decreased host density (Boudreau, 2013). Certain characteristics of the companion crop species (e.g. its height) could influence to which extent it acts as a physical barrier for incoming propagules, but it can also determine how it modifies the microclimate in the neighbouring host canopy. Furthermore, mixtures with more closely related crop species might be less effective in reducing disease pressure, since closely related plants are more likely to become infected by the same pathogens (Gilbert et al., 2015; Gilbert & Webb, 2007; Yguel et al., 2011). Alternatively, mixtures with somewhat related species could expose a focal crop to a pathogen that, while not genetically compatible, still triggers resistance responses (Chadfield et al., 2022; Finckh et al., 2000; Finckh & Tamm, 2017). Choosing one companion crop species could thus potentially lead to greater disease suppression than choosing another species (Cao et al., 2015; Sahile et al., 2008), however it is unclear to which extent across studies, different characteristics of the companion crop species affect their efficacy.

Furthermore, crop management practices can influence the level of disease suppression provided by different mechanisms. An early-sown companion crop might be tall enough to act as a physical barrier against pathogen dispersal before the host crop emerges, while a later sown companion species might be less effective, but this effect of relative sowing date on barrier effects is likely to interact with the relative tallness of the focal and companion species. The spatial arrangement of the crops in the intercrop system, such as complete mixture, row or strip intercropping, could also affect the level of disease suppression provided by barrier effects or companion crop effects on microclimate in the focal crop. Although it is often assumed that a finely grained mixing of the crop species is more effective at reducing disease, the specific outcomes may be variable (Boudreau et al., 2016; Enikuomehin et al., 2010; Fininsa & Yuen, 2002; Lai et al., 2019). A reduced number or density of susceptible hosts in the mixture, compared with monoculture, may lead to decreased disease pressure, because disease propagules have a higher chance of encountering a non-host, lowering the number of subsequent infections (Burdon & Chilvers, 1977; Mundt, 2002; Schoeny et al., 2010). For example, in cultivar mixtures of susceptible and resistant cultivars, the proportion of resistant cultivars has been shown to have a clear effect on the level of disease reduction achieved, in both field and simulation studies (Finckh et al., 2000; Garrett & Mundt, 1999; Leonard, 1969; Mundt, 2002; Munk et al., 1998; Skelsey et al., 2005, 2010). In theory, one would expect that reducing host density also may play a role in mixtures of different crop species because the encounter rate with hosts may depend on their density, particularly for spore-dispersed pathogens. However, for vectored diseases, the ratio of plant to vector density may be more important than host density per se. Therefore, while the mentioned mechanisms are broadly recognised as relevant, they are likely to interact and they may differ between pathogens with different ecology.

The effectiveness of intercropping may differ depending on the dispersal characteristics of the pathogens involved. For instance, pathogens dispersing aboveground by wind may be differently affected by intercropping than soil-borne pathogens that spread in the soil, e.g. as a result of hyphal growth or through soil tillage.

Disease suppression can be caused by a delay of the onset of the disease (Boudreau et al., 2016; Fernández-Aparicio et al., 2010), or a reduced disease progress rate (Fondong et al., 2002; Guo et al., 2021), or both (Fininsa & Yuen, 2002), though all mechanisms are likely to be potentially effective both in changing the prevalence of primary infections and the rate of spread.

Lastly, plant pathogens can cause significant yield losses (Oerke, 2006; Savary et al., 2012), so when intercropping reduces disease incidence, it can be expected to lead to increased yields, with stronger disease reduction correlating with higher yield gains. For example, in variety mixtures of glutinous and hybrid rice, panicle blast severity on the glutinous varieties averaged 20% in monocultures, but was reduced to 1% in the mixtures, which coincided with on average 89% greater grain production per hill of glutinous varieties in mixtures than in monoculture (Zhu et al., 2000). While reduced disease severity likely contributed to this yield gain, other factors such as competition or complementarity between the crops in the intercrop likely also played a role. Niche complementarity for resources has been shown to be an important cause of overyielding in mixtures (Li et al., 2020a; Vandermeer, 1992; Yu et al., 2016), even if there is no effect on disease in the mixture, therefore the contribution of disease reduction to yield effects in intercropping may be difficult to quantify. While the effect of disease-suppression on yield gain might not be as straightforward, investigating this pattern could be interesting.

Here, we synthesize a large number of published experiments on disease suppression in intercropping (of mixtures of two different crop species). We aim to find out what drives the variability in disease suppression in intercrop systems. Specifically, we asked: 1) do specific characteristics of the companion crop species and focal host influence the intercropping effect on disease incidence?; 2) how do certain management choices influence disease suppression and how does the disease-suppressive effect translate to enhanced yields?; 3) how do characteristics of the pathogen influence the disease-suppressive effect of intercropping?; and 4) to which extent is disease suppression by intercropping caused by a delay of the onset of the disease or a slower spread of the disease compared to a corresponding sole crop?

2.2 Methods

2.2.1 Study selection

A literature search was conducted on Web of Science on 27 October 2022. Key words for intercrop systems, including different ways of writing, and names of diseases were included in the search terms to ensure the most inclusive amount of suitable papers. See supplementary method S2.1 for details of the search criteria and screening process.

After selection based on these criteria, 54 publications remained. The paper selection process is further detailed in the PRISMA diagram in supplementary method S2.1. The list of selected papers is given in supplementary method S2.2. The 54 identified publications together described the results of 108 experiments from which 476 data records were extracted for intercrop systems and 247 for the corresponding sole crops.

2.2.2 Data extraction

Publications often report the results of several experiments. An experiment was defined as a unique combination of site and year, a paper could thus provide data for two or more experiments if more than one site or year was reported. One experiment can include different treatments such as different crop species, species densities, fertiliser rates, or other factors. We extracted results for each treatment in each experiment separately. When disease incidence was observed on both species in a mixture, data for each crop species were extracted separately along with data on the corresponding sole crop. When multiple diseases were monitored in the same experiment, data were extracted for each disease separately, yielding separate records.

A unique number was assigned to each study and experiment such that ‘study’ and ‘experiment’ could be used as random factors. If data from the same experiment (e.g. on two different diseases) were reported in several papers, data from both papers were included under the same experimental number. A data record of disease incidence was created for each unique disease and treatment combination in an experiment and study. Data were extracted from the text, tables, or from figures using the software GetData Graph Digitizer (http://getdata-graph-digitizer.com/).

Either disease incidence, defined as the proportion of diseased plants or leaves out of all sampled plants or leaves, or the area under the disease progress curve (AUDPC, i.e. the integration of disease intensity between two or more time points (Campbell & Madden, 1990)), were extracted from the papers, depending on which variable was reported. Papers using a disease rating scale were not included. If papers reported disease incidence at multiple time points throughout the epidemic, all incidence data and the corresponding time points, measured in days after planting and days after the first disease observation, were extracted. These data were used to analyse disease progression over time. 14 articles reported disease incidence over time, consisting of 32 experiments. In analyses that did not require time dependent data, we combined three types of data: (1) measurements at a “snapshot” moment in time, chosen by the investigators, (2) a seasonal average reported by the investigators, of (3) an average incidence calculated by dividing the AUDPC by the time duration over which the AUDPC was calculated. For papers that reported both the final incidence and AUDPC, the calculated average incidence was used in the analysis.

2.2.3 Explanatory variables

Various independent variables were either directly extracted from the papers, calculated based on information provided in the papers, or additional literature was used if it was missing from the primary papers. These variables were: 1) height of the companion crop, 2) genetic relatedness of focal host and companion, 3) spatial arrangement of the intercrop system, 4) difference in sowing time between focal host and companion, 5) host density (plants per m^2), 6) type of pathogen, 7) life cycle of pathogen, 8) trophic style of pathogen, 9) dispersal modes of pathogen, 10) survival strategy of pathogen (Table 2.1).

Table 2.1 Variables used to explain the disease-suppressive ability of intercrops. For an explanation see main text.

Variable	Distinction
Height of the companion crop species	(1) shorter than host, (2) same as host, or (3) taller than host
Relatedness of focal host and companion	The phylogenetic distance between each host-companion pair
Phylogenetic relatedness	(1) focal host and companion belong to the same plant family, (2) they belong to different plant families
Spatial arrangement of the intercrop system	(1) mixed, (2) row, (3) row/strip, (4) strip/row, or (5) strip
Difference in sowing time	The difference in days between sowing of the focal host and the companion crop
Host density	The density of host plants in mixture compared to the total plant density in the mixture (scaled relative density)
Type of pathogen	(1) bacteria, (2) virus, or (3) fungi and oomycetes
Life cycle	(1) monocyclic or (2) polycyclic

Trophic style the of pathogen (only for fungi and oomycetes)	(1) biotrophic, (2) necrotrophic, or (3) hemibiotrophic
Dispersal modes of pathogen (during growing season)	(1) wind, (2) water, (3) wind and water, (4) vector, or (5) soil
Survival strategy of pathogen (in absence of host)	(1) soil survivor (2) debris- and/or seed-borne, or (3) vector-borne

Height of the companion crop

Since only two papers mentioned both the height of the focal crop and the companion crop species, it was decided to classify crop pairs into classes characterising the height difference between the species as (1) similar height; (2) host is taller, and (3) companion crop is taller. The classification was made on the basis of ranges in final plant height reported by Small (2009) and Elzebroek & Wind (2008). Species were considered similar in height if the ranges reported in the literature overlapped. Otherwise they were classified as “host is taller” or “companion is taller”, depending upon which species was the taller one.

Relatedness of the focal host and companion crop species

We furthermore assessed phylogenetic relatedness between the focal and companion crop species to assess whether and how this affected disease suppression by intercropping. For this, we generated a phylogenetic tree of all the crop species in the database (both focal hosts and companions) with the phyloT online tool (phylot.biobyte.de) (Fig. S2.2). The patristic distance (i.e. the sum of the lengths of the branches) between each host-companion pair was then calculated using the function ‘distTips’ in the R package ‘adephylo’ (Jombart et al., 2010). For instance, an intercropping system with wheat (*Triticum aestivum*) and faba bean (*Vicia faba*) has a patristic distance of 27. Intercropping wheat with another Poaceous crop, such as barley (*Hordeum vulgare*), will have a patristic distance of only 6. Additionally, we tested whether the crop species in the mixture belonging to the same plant family or different families influenced disease suppression.

Spatial arrangement of the intercrop system

Five types of spatial arrangements of the intercrop systems were distinguished: mixed, row, row/strip, strip/row, strip (Table 2.1). Mixed intercropping consists of an intercrop design without a distinguishable pattern due to random sowing. Row intercropping consists of arrangements whereby the focal crop and companion crop species are most often grown in alternating single rows. In row/strip intercropping the focal crop is grown in single rows, while the companion crop is grown in strips that consist of multiple rows of that crop. Contrary, in strip/row intercropping the focal crop is grown in strips while the companion crop is grown in single rows. Lastly, in strip intercropping both the focal crop and the companion crop are grown in strips.

Sowing time

For each experiment, the sowing date of both species was extracted if available, and the difference in sowing time (days) was calculated. A negative time difference means that the companion species was planted before the focal host, whereas a positive time difference means the companion was planted later.

Host density

We assessed the effect of the plant density of the focal host crop in the mixture compared to the total plant density in the mixture, using the scaled relative density (Li et al., 2020a; van der Werf et al., 2021). The scaled relative density of the host in the intercrop was calculated as: $SRD = \frac{RD_1}{RD_1+RD_2}$, where RD_1 and RD_2 are the relative densities of the host and the companion crop species, respectively, and relative density is the density of a species in the intercrop divided by the density in the sole crop. For example, in a sole crop, wheat would be grown with a density of 200 plants m^{-2} and faba bean with a density of 20 plants m^{-2}. If in a mixture of these two crops, a density of 100 wheat plants m^{-2} and 10 faba bean plants m^{-2} would be used, which corresponds to a relative density of 0.5 for both crops, the scaled relative density would be $\frac{0.5}{0.5+0.5} = 0.5$. If in the intercrop the wheat had been grown at a density of 150 plants/m^2, the relative density of wheat would be 0.75, and the scaled relative density for wheat would be $\frac{0.75}{0.75+0.5} = 0.6$ and for faba bean $\frac{0.5}{0.75+0.5} = 0.4$. The SRD is a measure of focal host dilution at field scale. One could argue that the effect of host dilution may be relevant at smaller spatial scales, due to the limited dispersal capacity of the pathogen. For this reason, we tested a range of other proxies for host density, see Supplementary Methods S2.3.

Classification of diseases

The pathogens in the database were classified in groups according to five criteria: 1) type of pathogen, 2) lifecycle, 3) trophic style (only for fungi and oomycetes), 4) dispersal mode, and 5) survival strategy (Table 2.1).

The first classification was based on the phylogeny of pathogen: bacteria, fungi, oomycete or virus. As there were only two data points for oomycetes they were merged as a single group with fungi. This grouping makes ecological sense because oomycetes and true fungi, while phylogenetically distinct, share ecological and functional characteristics, such as hyphal growth and spread by spores (Money, 1998). The second classification was based on the length of the lifecycle of the pathogen compared to that of the crop: either monocyclic or polycyclic. Monocyclic pathogens have only one generation per growing season in a crop and many are introduced into a crop from outside sources, though they can also originate from soil or planting material (Zadoks & Schein, 1979). Polycyclic pathogens have multiple generations (cycles of infection) in the crop during the growing season. Infections that are caused by propagules produced within the same crop are called secondary infections, while those originating from outside sources or from soil or planting material are called primary infections. Many important crop diseases (rusts, mildews, oomycetes, viruses) are polycyclic, though some are monocyclic.

The fungi and oomycetes were further classified based on their trophic style: biotrophic, necrotrophic or hemibiotrophic (Vega et al., 2019). Biotrophs obtain nutrients from living cells (e.g. powdery mildews and rusts), while necrotrophs must kill the cells of their focal host to obtain nutrients (e.g. rots and wilts). Hemibiotrophs are characterised by having two phases of infection, first the pathogen feeds on living cells (biotrophic phase) while later, it kills the cells of the focal host and uses their nutrients (necrotrophic phase). Although these terms are well-known and frequently used, for some pathogens there is ongoing discussion to which class they belong (Oliver & Ipcho, 2004). See Table S2.1 for the classification we used.

We further classified the pathogens based on their main dispersal mode during the growing season: wind, water (i.e. rain splash), wind and water, vector or soil. Lastly, pathogens were classified based on survival strategy: soil survivor, debris- and/or seed-borne, or vector-borne (Vega et al., 2019). Soil survivors are able to survive in the soil without the presence of host tissue. Debris- and/or seed-borne pathogens survive for relatively long periods in host tissues (from months to a few years), but for very short periods in soil (from days to a few weeks). Vector-borne pathogens survive on insect vectors when the plant host is absent.

2.2.4 Statistical analysis

Models for disease incidence in mixtures and sole crops

The relationship between disease incidence and these predictor variables was analysed using generalized linear mixed models (GLMMs) with the variability modelled according to the beta distribution (Douma & Weedon, 2019) (Table 2.2). Not all articles reported standard errors or the number of replicates, we therefore did an unweighted analysis in which all experiments had equal weight. The R package glmmTMB was used for fitting the models (Bolker, 2016; Magnusson et al., 2017). Because of the logit link function, records reporting zero incidence in either intercrops or sole crops were replaced by a value of 1/sample size. To keep things equal, the disease incidence value of the corresponding sole crop or intercrop was also increased by 1/sample size. For records reporting 100% incidence, these were replaced by 1 – 1/sample size, and again the incidence of the corresponding monocrop records was also reduced by 1/sample size. Publication and experiment were defined as random effects, with experiment nested in publication. Interactions between random and fixed effects were tested, but did not, or only marginally, impact the model fit. To account for heteroscedasticity between sole crops and intercrops, '*Treatment*' (e.g. intercrop or sole crop) was added in the *dispformula* argument of the glmmTMB function (Brooks et al., 2017).

Models for the strength of disease suppression

The strength of disease suppression by intercropping was captured by calculating from corresponding observations of disease incidence in the mixture and sole crop the log odds ratio (LOR) (Table 2.2, model 3, 5, 7). The LOR is calculated as the difference in the logits of disease incidence in the intercrop and the sole crop (Borenstein et al., 2009; Hedges et al., 1999):

$$\mathrm{LOR} = \mathrm{logit}(x_{\mathrm{ic}}) - \mathrm{logit}(x_{\mathrm{sc}}) = \ln\left(\frac{x_{\mathrm{ic}}}{1 - x_{\mathrm{ic}}}\right) - \ln\left(\frac{x_{\mathrm{sc}}}{1 - x_{\mathrm{sc}}}\right) = \ln\left(\frac{\left(\frac{x_{ic}}{1 - x_{ic}}\right)}{\left(\frac{x_{sc}}{1 - x_{sc}}\right)}\right)$$

where x_{ic} is disease incidence in the intercrop and x_{sc} is disease incidence in the corresponding sole crop. For the statistical analyses using the LOR, a gaussian distribution was used (Table 2.2). Also in these analyses, we did not use weights, because of missing data. We first determined the effect of each explanatory variable in simple linear regression models, however if no significant effect was found, we tried to improve the model by adding variables and comparing AIC values (Table S2.2, S2.3, S2.4).

Data records with missing values of an explanatory variable were omitted from analyses requiring that variable.

Models of intercropping effects on disease progress

To analyse to which extent intercropping causes a delay in the onset of the disease or a slower spread of the disease compared to sole cropping, disease incidence was analysed over time (Table 2.2, model 12) for a subset of studies providing information on disease incidence over time. For this model, a model selection was performed by testing beta regression models using timepoint in either days after planting (DAP), or days after first disease observation (DAFO). Study was used a random intercept and random slope to capture variation across studies in the onset and slope of disease progression (Zuur et al., 2009). Furthermore, we compared different functional forms (logit, gompertz) for the link function, and used model comparison to eliminate unnecessary random effects (Table S2.5).

Models for the yield effect of intercropping

Most papers that provided information on yield, only presented the yield of the focal host, and few papers also included the yield of the companion crop. Therefore, we decided to focus on the net effect ratio (Li et al., 2023) of yield in the focal host, which was calculated as follows:

$$NER = \frac{Y_{IC}}{pi * Y_{SC}}$$

with Y_{IC} and Y_{SC} the yield of the host in the intercrop and sole crop, respectively, and pi the relative density of the host in the intercrop (van der Werf et al., 2021). The relationship between LOR and NER was analysed using a Chi-Square test of independence.

Table 2.2 Summary of the fitted models for the comparison of intercrop systems with their corresponding sole crops. + means additive effects are assumed, while * means main effects and interactions are estimated. A slash / before a random effect means that it is nested in the preceding random effect to the left.

Model #	Response variable	Distribu-tion	Link function	Predictors	Random effects	Dispersion parameter
1a	Incidence	Beta	logit	Height companion crop	Study/ experiment	~Height companion crop
1b	Incidence	Beta	logit	Height companion crop * Dispersal mode pathogen	Study/ experiment	~Height companion crop
2	LOR	Gaussian	-	Relatedness of host and companion	Study/ experiment	~ Relatedness
3	LOR	Gaussian		Same or different family	Study/ experiment	~ Same or different family
4	Incidence	Beta	logit	Spatial arrangement	Study/ experiment	~Spatial arrangement
5	LOR	Gaussian	-	Difference in sowing time	Study/ experiment	-
6a	Incidence	Beta	logit	Scaled relative density	Study/ experiment	~Scaled relative density
6b	LOR	Gaussian	-	Scaled relative density	Study/ experiment	~ Scaled relative density
8a	Incidence	Beta	logit	Taxon * Treatment	Study/ experiment	~Taxon * Treatment
8b	LOR	Gaussian	-	Taxon	Study/ experiment	~Taxon
9a	Incidence fungi and oomycetes	Beta	logit	Trophic style * Treatment	Study/ experiment	~Trophic style * Treatment
9b	LOR fungi and oomycetes	Gaussian	-	Trophic style	Study/ experiment	~Trophic style
10a	Incidence	Beta	logit	Life cycle * Treatment	Study/ experiment	~Life cycle * Treatment
10b	LOR	Gaussian	-	Life cycle	Study/ experiment	~Life cycle
11a	Incidence	Beta	logit	Dispersal mode pathogen * Treatment	Study/ experiment	~ Dispersal mode pathogen * Treatment
11b	LOR	Gaussian	-	Dispersal mode pathogen	Study/ experiment	~ Dispersal mode pathogen
12a	Incidence	Beta	logit	Survival strategy pathogen * Treatment	Study/ experiment	~ Survival strategy pathogen * Treatment
12b	LOR	Gaussian	-	Survival strategy pathogen	Study/ experiment	~ Survival strategy pathogen

13	Incidence	Beta	logit	Treatment * DAFO	DAFO | Study/experiment/ ID	~Treatment

Note: *Treatment* has two levels; intercrop and sole crop. *Study* is paper from which data are extracted. *Experiment* represents a unique combination of site and year within a study. *ID* represents the series of associated observations across time. *DAFO* is days after first observation, i.e. the days at which the disease assessments were made, expressed as days after the first observation.

2.3 Results

Disease incidence was significantly reduced through intercropping, by 32.5%, compared with sole crops. The estimated average disease incidence in intercrops across all records was 26.4% (n = 467; 95% CI: [21.2, 32.4]) and that in the sole crops was 40.9% (n = 257; 95% CI: [33.9, 48.5]).

2.3.1 Height of the companion crop

The height of the companion crop species relative to the focal crop did not significantly influence the level of disease suppression in the intercrop overall (Fig. 2.1A, B). However, for pathogens spread by vectors, intercrop systems with a companion crop taller than the focal host had a significantly lower disease incidence (16.0% (95% CI: [8.4, 28.5])) than systems with a shorter companion (incidence of 31.1% (95% CI: [21.1, 40.7]), p = 0.01), or a companion similar in height to the host (incidence of 32.1% (95% CI: [21.7, 42.3]), p = 0.002) (Fig. 2.1C). Focal species in intercrops with a companion species shorter than the focal host or similar in height to the focal host, had significantly 31.3% and 29.3% (LOR of -0.85 and -0.52) lower incidence of vectored diseases than the corresponding sole crops. Focal species in intercrops with companion crop species taller than the focal host had significantly 64.7% (LOR of -1.60) lower incidence of vectored diseases than the sole crop (Fig. 2.1D).

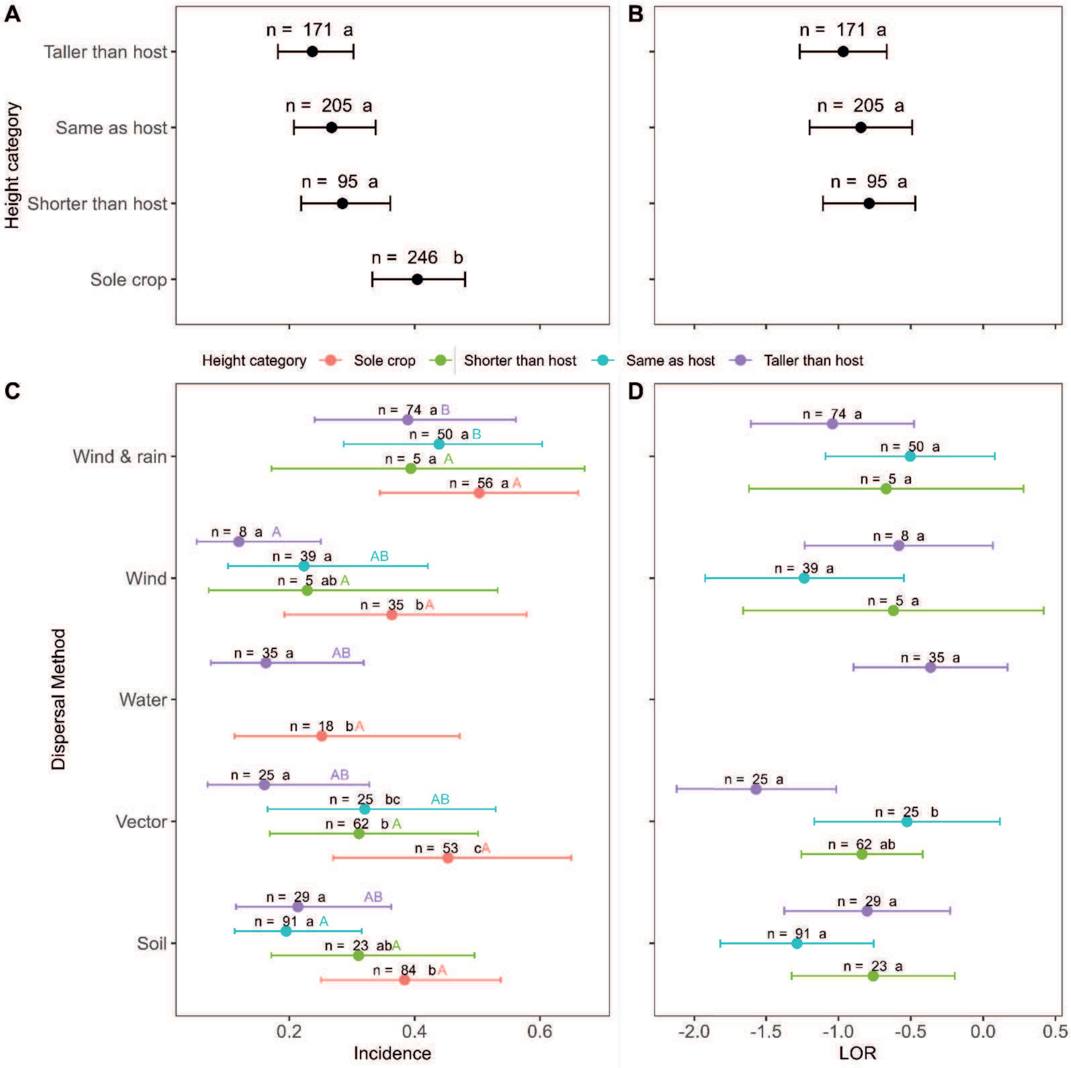

Fig. 2.1 Panels on the left give the incidence (proportion) in sole crops and intercrops while panels on the right give the reduction in intercrops compared to sole crops, expressed through LOR. (a) Estimated disease incidences for three different categories of the companion crop species (taller than, as tall as, or shorter than the focal host) in the intercrops and incidence in the sole crop (model 1a in Table 2.2), and (b) the corresponding reduction achieved by intercropping expressed through LOR. (c) Estimated disease incidences for pathogens with different dispersal methods, across the three height categories (model 1b in Table 2.2). Small black letters indicate differences within each dispersal category, whereas capital coloured letters indicate differences between dispersal categories per height category, and (d) the achieved reduction expressed through LOR. Points and horizontal bars indicate the mean incidences and the 95% confidential intervals, respectively. *n* indicates the number of records for each design. Letters indicate differences between groups within each plot based on pairwise comparisons ($p < 0.05$).

2.3.2 Relatedness of focal host and companion

We found no significant relationships between the LOR (the difference in the logit of disease incidence in the intercrop and the sole crop) and the patristic distance between the host and companion crop ($p = 0.785$) (Fig. 2.2A). Likewise, the reduction achieved by intercropping expressed as LOR was similar for intercrops of two species from the same or from different plant families (Fig. 2.2B).

2.3.3 Sowing time

In the majority of studies, the two crops were sown simultaneously in the mixture. In 16 studies comprising 33 experiments, the companion crop was, however, sown before the focal host (negative relative sowing time; Yu et al., 2016). In four studies, consisting of seven experiments, the companion crops were sown after the host (positive relative sowing time). We found no effect of the time of sowing of the companion species on the LOR ($p = 0.493$) (Fig. 2.2C).

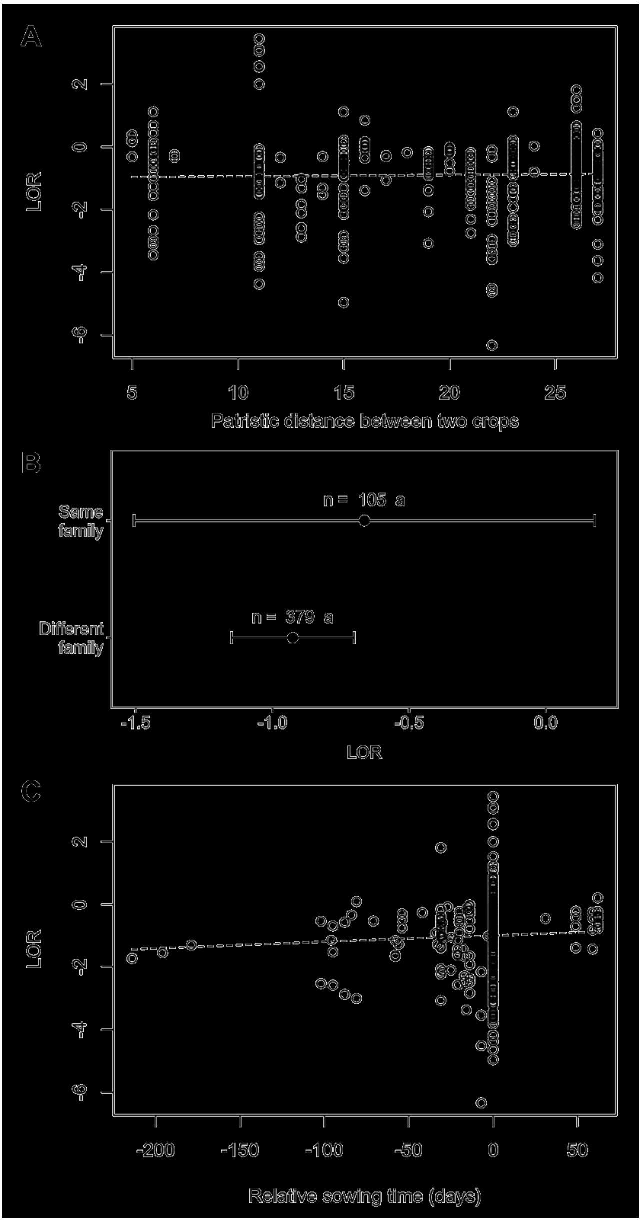

Fig. 2.2 (a) Relationship between LOR and the patristic distance between each focal host-companion pair (p = 0.785) (model 2 in Table 2.2). A larger patristic distance means the host and the companion crop species are less closely related. (b) Comparison of LOR for intercrops with two species from the same family or different families (p = 0.541) (model 3 in Table 2.2). (c) Relationship between LOR and the relative sowing time; the difference in days between sowing of the two crops in the mixture (p = 0.493) (model 5 in Table 2.2). A negative time difference means that the companion crop was sown before the focal host, which might be conducive to achieving a greater barrier effect against primary or secondary infections.

2.3.4 Spatial arrangement of the intercrop system

Five different intercropping patterns were distinguished in this analysis, namely mixed, row, row/strip (focal host crop grown in single rows, companion grown in strips), strip/row (host grown in strips, companion in single rows), and strip. Mixed intercrop systems were the most common, accounting for 180 data records (Fig. 2.3A). Strip/row designs were least represented, being only 6% of the records (n = 28). All designs significantly reduced disease incidence compared with a sole crop (Fig. 2.3A, B). We found similar disease incidence reduction across the different intercropping patterns.

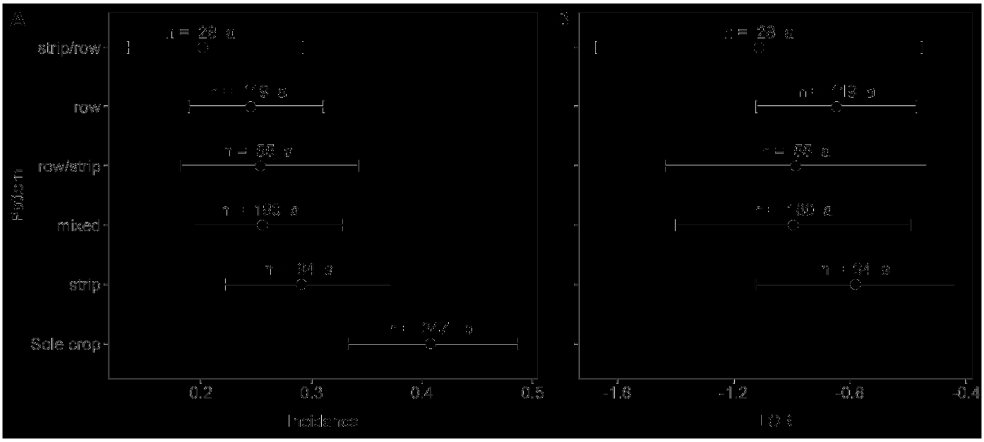

Fig. 2.3 (a) Estimated disease incidences for five different types of intercropping patterns (mixed, row, row/strip, strip/row, strip) and their corresponding sole crops (model 4 in Table 2), (b) the achieved reduction expressed as LOR. In row/strip intercropping the focal crop is grown in single rows, while the companion crop is grown in strips that consist of multiple rows. Contrary, in strip/row intercropping the focal crop is grown in strips while the companion crop is grown in single rows. Points and horizontal bars indicate the mean incidences and the 95% confidential intervals, respectively. *n* indicates the number of records for each design. Letters indicate differences between groups within each plot based on pairwise comparisons ($p < 0.05$).

2.3.5 Host density

Comparing the proportion focal host in the total plant population, excluding sole crops, no significant relation between proportion and disease incidence was observed (Fig 2.4, dashed line). However, when including sole crops, a significant increase in incidence was observed with an increase in focal host proportion in the total plant population (Fig 2.4); the incidence increased 1.02 on a logit scale per unit increase in fraction hosts ($P < 0.001$).

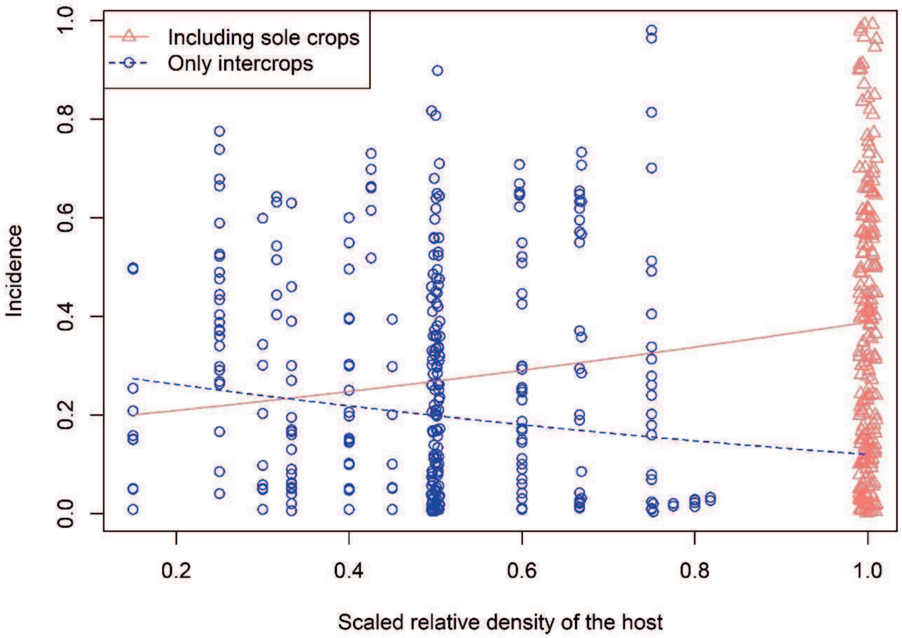

Fig. 2.4 Relationship between incidence and the scaled relative density (model 6a in Table 2.2). A scaled relative density of 1 means a sole crop (triangles). Points at relative densities of 0.5 and 1 are jittered to show the many experiments with these relative densities. The red solid line represents the relationship including the sole crops ($p < 0.001$). The dashed line represents the relationship if only intercrop data is used ($p = 0.51$).

We found no significant relationship between the scaled relative density and the LOR (Fig S2.3, model 6b in Table 2.2). Fitting different relationships per survival mechanism, dispersal modes or life cycle of the pathogen did not change this conclusion; the AIC was marginally lower compared to the baseline model (Table S2.2). Also for the other methods of calculating host density no significant relationship between LOR and host density was found (Supplementary information Results S2.1, S2.2). Thus, the published data do not support a dilution effect of intercropping on plant disease incidence.

Eight studies were identified in which different densities of the focal crop in their experiment were tested. When only analysing these studies, again no significant overall relationship between the scaled relative density of the focal host in the intercrop system and the disease incidence was found (Fig. S2.8).

2.3.6 Characteristics of the pathogen

Despite differences in the absolute incidences found between pathogen types, the disease-suppressive effect of intercropping (expressed through the LOR) was not significantly different for the three phylogenetic groups of pathogens distinguished (bacteria, fungi and oomycetes, and viruses) (Fig. 2.5B). Pathogens with polycyclic or monocyclic epidemics were suppressed to similar degrees by intercropping (Fig. 2.5D).

Fungi and oomycetes with a necrotrophic style had a lower disease incidence in intercrops (19.9% 95% CI: [11.5, 32.2]) than those with a hemibiotrophic style (38.9% 95% CI: [21.8, 59.1]) (Fig. 2.5E). Those with a biotrophic style were intermediate and not significantly different from the other two styles (incidence of 37.8% 95% CI: [15.2, 67.4]). However, all three types of pathogens were equally suppressed by intercropping (e.g. no significant difference in LOR between the three types) (Fig. 2.5F).

Pathogens that mainly spread in the soil (not through the air) during the growing season caused an incidence of 36.8% (95% CI: [22.6, 53.8]) in sole crops, which was reduced to 20.2% (95% CI: [11.4, 33.1]) in intercrops, a difference in the logit of disease incidence (LOR) of -1.28 (95% CI: [-1.69, -0.88]) (Fig. 2.5G, H). Significant relative reductions in incidence compared with sole cropping were also observed for pathogens dispersed by vectors (LOR of -0.94 (95% CI: [-1.36, -0.51])), through wind (LOR of -0.81 (95% CI: [-1.29, -0.34])) or by both wind & rain (-0.70 (95% CI: [-1.09, -0.31])). Intercropping did not significantly reduce disease incidence for pathogens dispersing mainly through water splashes (LOR -0.38, p = 0.2).

Pathogens surviving in the soil caused a disease incidence of 31.6% (95% CI: [20.4, 45.4]) in sole crops, which was reduced to 16.4% (95% CI: [10.0, 25.7]) in intercrops, a difference in the logit of disease incidence (LOR) of -1.23 (95% CI: [-1.56, -0.90]) (Fig. 2.5I, J). Pathogens surviving on plant debris or seeds caused a significantly higher disease incidence in both the sole crop (p = 0.002) and intercrop (p = <0.001) than soil surviving pathogens, and were on average less suppressed by intercropping than pathogens with other survival modes. Pathogens surviving on crop debris or seed caused a disease incidence of 47.4% (95% CI: [33.2, 62.1]) in sole crops, which was reduced to 36.3% (95% CI: [24.5, 50.0]) in intercrops, a difference in the logit of disease incidence of -0.59 (95% CI: [-0.87, -0.30]). Pathogens surviving in vectors were also reduced by intercropping with a LOR of -0.94 (95% CI: [-1.09, -0.31]).

We classified pathogens according to taxon, life cycle, trophic style, dispersal and survival mechanism, and found correlations between traits (Table S2.6, S2.7, S2.8). For instance, pathogens spreading through the soil, are also surviving in the soil. All viruses disperse through a vector, whereas none of the fungi used vectors to disperse. Therefore, there is some overlap in the analysis of intercropping effects related to these different characteristics of the pathogens.

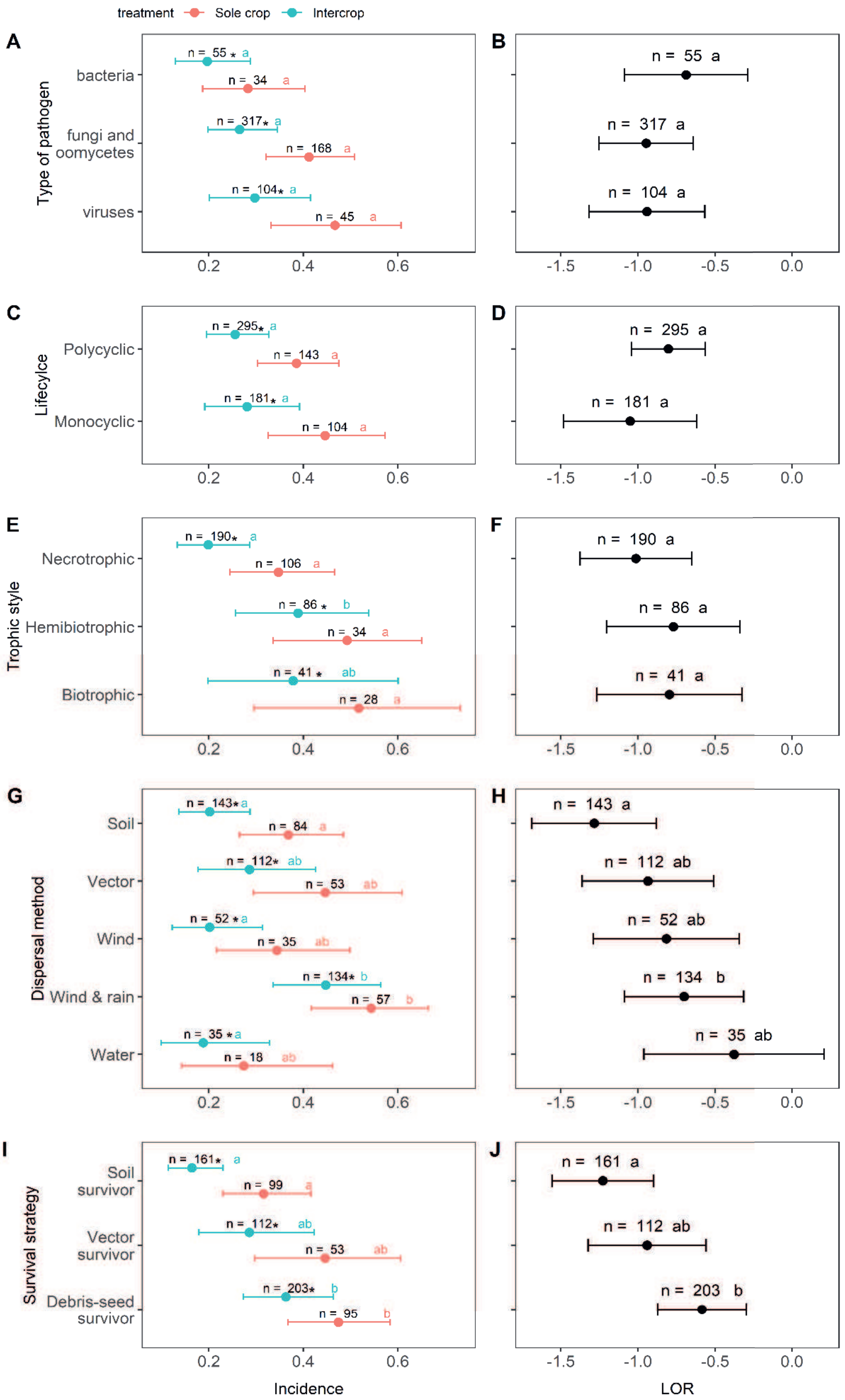

Fig. 2.5 Estimated disease incidences in the intercrops and their corresponding sole crops according to five classifications of pathogens, according to (A, B) different

phylogenetic group (bacteria, fungi and viruses) (models 8a and 8b in Table 2.2), (C, D) different epidemiology (monocyclic of polycyclic) (model 10a and 10b in Table 2.2), (E, F) different trophic styles – only for fungi and oomycetes (necrotrophic, hemibiotrophic and biotrophic) (models 9a and 9b in Table 2), (G, H) dispersal (models 11a and 11b in Table 2), and (I. J) survival strategy (models 12a and 12b in Table 2.2). Panels on the left give the incidence (proportion) in sole crops and intercrops while panels on the right give the reduction in intercrops compared to sole crops, expressed through LOR. Points and horizontal bars indicate the mean incidences and the 95% confidential intervals, respectively. *n* indicates the number of records for each category. Asterisks (in the left panels) indicate if the disease incidence in the intercrop is significantly different from the corresponding sole crop ($p < 0.05$). Coloured letters indicate differences between either the intercrops or the sole crops, within each plot ($p < 0.05$).

2.3.7 Disease onset and progress rate

Fourteen studies reported disease incidence over time (Fig. S2.9). Across these studies, the rate of disease progress (*r*) in sole crops was significantly higher than in the intercrops ($p < 0.001$) (Fig. 2.6). The rate of disease progress in the sole crops was on average 0.097 (± 0.014) day^{-1}, while that in the intercrops was 0.076 (± 0.013) day^{-1}. Furthermore, the incidence at the first observation day was significantly higher in the sole crops (13.8%) than in the intercrops (6.7%) ($p < 0.001$). Based on the fitted models, and due to the lower initial incidence and reduced disease progress rate, the intercrop would take on an average 16 days longer than the sole crop to reach 50% incidence (Fig. 2.6).

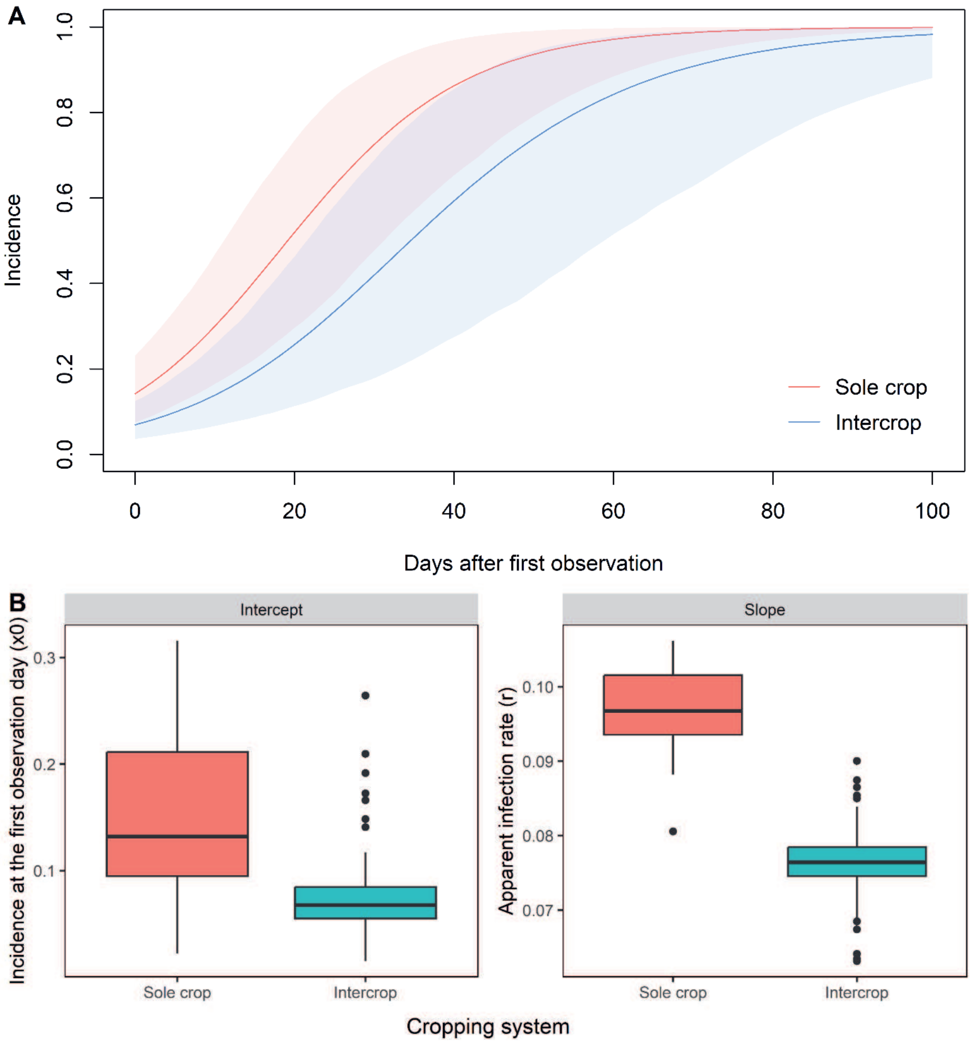

Fig. 2.6 (a) Average estimated disease progress curves for disease incidence for sole crops (red) and intercrops (blue) (model 13 in Table 2), and (b) boxplot of the estimated random-effects intercept and slopes for sole cropped (red) and intercropped (blue) crops, based on data over time from fourteen studies. Disease observations of all experiments are set to begin on the first observation day in panel a. The coloured bands around the lines represent the 2.5% and 97.5% quantiles, which represent the uncertainty in the fixed effects (see Supplementary information Method S2.4 for more information).

2.3.8 Yield

The majority of LORs (211/234) represent a reduction in disease incidence and a minority (23/234) an increase (Fig. 2.7). Out of the 211 cases that disease incidence was reduced, there were 119 cases of a yield decrease (trade-off type 1, where disease suppression is achieved at the expense of yield of the host crop) and 92 cases of yield increase (win-win, both reduced disease and increased yield). In the 23 cases of an increase in disease incidence in intercropping, there were 19 cases of yield decrease (lose-lose) and 4 cases of yield increase (Trade-off 2, increased disease and increased yield). A Chi-Square test of independence revealed a significant association between disease incidence and yield, $\chi^2(1, N = 234) = 4.86$, $p = 0.028$. However, the Pearson correlation test indicated no statistically significant linear relationship between the two variables ($r = 0.104$, $p = 0.112$). This suggests that while disease incidence and yield are associated, their relationship may not be linear.

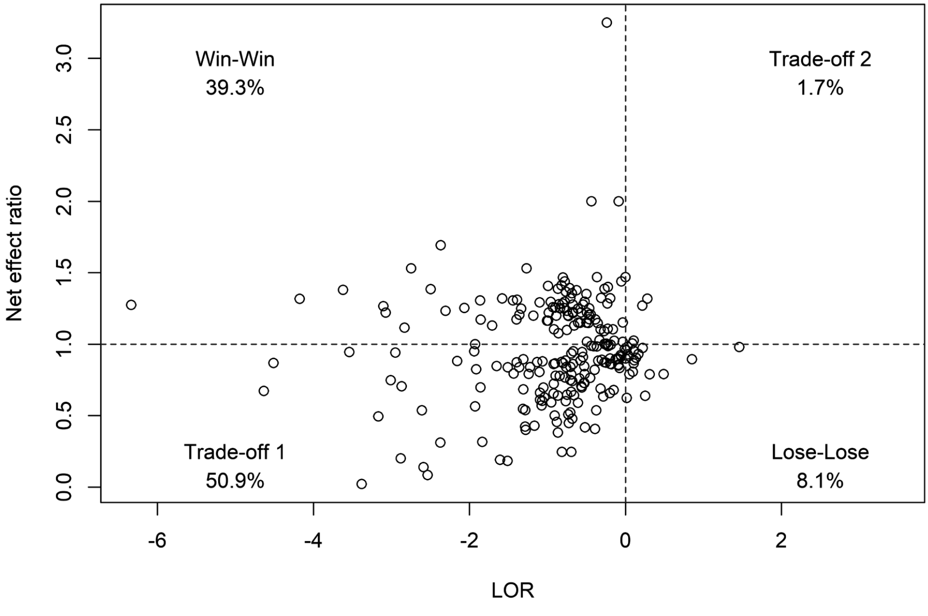

Fig 2.7 Relationship between net effect ratio (NER) and LOR. Net effect ratio measures the ratio of yield in the intercrop and expected yield in the intercrop. NER<1 indicates a yield reduction due to intercropping. LOR indicates the difference in logit of disease incidence in the intercrop and sole crop. An LOR < 0 indicates that intercropping reduces disease incidence. For 211 out of 234 data points the intercrop had a lower disease incidence than the corresponding sole crop (LOR <1), however, this did not consistently translate to a higher yield in the intercrop than the corresponding sole crop.

2.4 Discussion

Intercropping reduces disease incidence but the degree of suppression varies greatly between different studies. The objective of this study was to find factors that explain the observed variation. After analysing a large number of published experiments on disease suppression in intercrops, we found that contrasting intercrop systems in terms of companion crop characteristics, crop species combinations, and intercrop design were all able to suppress various pathogen types. This indicates that disease-suppressive effects of intercropping are rather ubiquitous, being effective against a wide variety of pathogens and not very sensitive to specific crop choices or management practices in our dataset. We identified two factors that were associated with variation in disease incidence reduction and that suggest an underlying mechanism that is operative across studies. First, tall companion crops suppressed pathogens spread by vectors more than companions that were either shorter or similar in height to the host. Second, soil-borne pathogens were more suppressed by intercropping than those dispersing through wind and rain, or surviving in host tissue. Other than that, no systematic differences in the level of disease suppression were found between intercrop systems with different companion crop heights (relative to the focal host), or between intercrop systems with different relatedness between the two different crop species in the mixture. Different types of pathogens caused varying levels of disease incidence, but this did not lead to differences in disease suppression by intercrops. Different intercrop management practices (e.g. intercropping pattern or relative sowing time of the focal species and the companion crop) did not have a significant influence on the level of disease suppression. Surprisingly, we found no relationship between the density of the focal host and disease suppression, nor did we find a difference between monocyclic or polycyclic pathogens. Instead, we found that intercropping suppressed disease incidence, but with great variation that was largely unexplained by the explanatory factors that we used. Collectively, these results are potentially important as they underscore the consist effect of intercropping in reducing disease incidence.

2.4.1 Monocyclic and polycyclic pathogens

Interestingly, no difference in disease suppression was found between pathogens with a monocyclic or polycyclic lifecycle. We expected that polycyclic pathogens, which have several infection cycles during the growing season, would be suppressed more by intercropping than monocyclic pathogens (which only produce one generation of inoculum and one cycle of infection during a single growing season), because disease-suppressive mechanisms could result in large cumulative effects by interference with the pathogen during multiple disease cycles (Leonard, 1969; Mundt, 2002). Furthermore, for polycyclic pathogens, a reduced host density in the intercrop could reduce the amount of inoculum produced each cycle (e.g. Gao et al., 2021). Therefore, intercropping was expected to lead to more effective suppression for polycyclic than monocyclic pathogens as the infection is a multiplicative process at the start. These expectations were not confirmed.

2.4.2 Reducing host density

Mixing the focal host with a non-host by introducing a companion crop is expected to reduce the efficacy of spread due to propagule deposition on non-hosts. Reduced host density is often mentioned as one of the most important mechanisms behind disease reduction in intercrops (Boudreau, 2013; Hiddink et al., 2010; Skelsey et al., 2005; Zhang et al., 2019), and was clearly demonstrated in cultivar mixtures (Finckh et al., 2000; Garrett & Mundt, 1999; Leonard, 1969; Mundt, 2002; Munk et al., 1998; Skelsey et al., 2005, 2010). Mixing had clearly an effect on disease incidence; systems with a greater host proportion (i.e. sole crops) had a higher incidence than those with a lower proportion of hosts (i.e. intercrops). Yet, when analysing the effect of relative density of the host in the mixture (i.e., excluding the sole crops), we found no relationship with disease suppression. Various ways to calculate the degree of mixing were tested (see Supplementary information Fig. S2.3, Fig. S2.4, Fig. S2.5, or Fig. S2.6) but none showed the expected relationship with disease suppression. Also, no clear pattern was observed after examining studies which tested intercrops at two or more different relative densities of the host species (Supplementary information Fig. S2.8). One possible explanation for this lack of effect is the large variation in intercropping effects on disease incidence between studies, which could mask the effects of mechanisms across studies. In our analyses we did account for variation between studies by including random study effects, but nevertheless, we could not convincingly demonstrate an effect of host proportion or number of disease cycles. Apparently, other factors, varying between studies and not included in our fixed or random effects, predominantly determined the effect of intercropping on disease incidence. Overall, we conclude that mixing species suppresses plant disease, but the degree of mixing appears to be less important, and other mechanisms might be more important.

2.4.3 A companion crop introduces various disease-suppressive mechanisms

In this analysis we tried to isolate the effects of individual factors causing disease suppression but this appeared challenging. Three explanations can be given. Firstly, by introducing a companion crop, multiple disease-suppressive (or disease-promoting) mechanisms are introduced at the same time, and these mechanisms operate at various spatial scales. A companion crop can interfere with the dispersal of pathogens, but it may also change the microclimate in the host canopy or even the focal host itself (e.g., alter its susceptibility), or it may directly inhibit the pathogen through antagonistic chemical exudates (allelochemicals) (Boudreau, 2013; Hiddink et al., 2010). Additionally, one mechanism may increase in importance with a change in companion species while another mechanism decreases resulting in the overall effect on disease suppression remaining unchanged. For example, tall companion crops can serve as physical barriers to fungi that spread above ground (Gómez-Rodríguez et al., 2003; Schoeny et al., 2010), but they can simultaneously increase humidity in the canopy of the focal crop, creating more conducive conditions for infection (Boudreau & Shew, 2006; Fernández-Aparicio et al., 2011; Ong et al., 1991), which may partly counteract the barrier effect. On the other hand, intercropping with a short statured companion crop will promote air ventilation around the focal host plants, creating a microclimate that is less conducive to fungal infection (Guo et al., 2021; Ma et al., 2023), but will be lacking in terms of a barrier effect. Furthermore, disease suppression mechanisms operate across various spatial scales: while inhibition of pathogens through exudates happens at fine scales (e.g. at the plant-plant level) and could thus be expected to benefit more from increased interspecific interaction, host dilution primarily takes place at broader spatial scales (field level). For example, the spatial configuration of an intercrop system might affect the suppression of pathogens with short-distance dispersal. However, for pathogens that are capable of long-distance dispersal (e.g. wind-borne fungal spores), the spatial arrangement of an intercrop may not matter much for reducing spread, because these pathogens can still travel significant distances (Rieux et al., 2014), dispersing beyond the row or strip.

Next to the interaction of different mechanisms, the eventual suppression of disease also depends on specific interactions among focal hosts, companion crops, pathogens, and weather conditions. For instance, some pathogens require leaf wetness to germinate and penetrate plant tissues (Dawson & Goldsmith, 2018; Rowlandson et al., 2015), while others do not require moisture or their gemination is even inhibited by it (e.g. certain mildews (Mieslerová et al., 2022; Schnathorst, 1965)). If in a specific intercrop system humidity is reduced, this intercrop could thus be effective at suppressing pathogens that require leaf wetness but not pathogens that are less dependent on leaf wetness. The disease-suppressive effect of the companion species will also likely depend on the weather and climate of a site. For instance, certain intercrop pairs have been found to be effective at suppressing disease during one year or season, but less effective or even ineffective during another year or season, which could be due to weather variability (Ahohuendo & Sarkar, 1995; Uzokwe et al., 2016). The interactions between the traits of focal host, companion species, pathogen and the weather and climate make it challenging to identify mechanisms from disease-suppressive effects measured in intercropping system across plant and pathogen combinations and weather.

Lastly, variability in incidence data between studies affects the identification of mechanisms. For instance, the moment of scoring has an impact on the observed disease-suppressive effect of intercropping; if a study were to assess disease incidence early after the first disease observation, the suppressive effect could appear less than if assessments were done at the middle of the epidemic (see also Fig. 2.6a). Furthermore, some studies reported only the final disease incidence, whereas others reported an average of multiple measurements over a period of time (e.g. AUDPC), which complicated analyses, because it affects the observed level of disease suppression. This variability between studies in observed incidence and thus observed disease suppression makes it difficult to find clear patterns across intercrop systems.

Intercropping lowered both the apparent infection rate and the initial disease incidence compared with sole cropping. This shows that intercropping suppresses both initial infections, and secondary infections, and that disease-suppressive mechanisms are thus active throughout the season. We were not able to separate polycyclic from monocyclic disease, due to the relatively low number of studies. Intercropping will not keep crops completely disease-free, but it can still be a valuable component in integrated pest management (van der Werf & Bianchi, 2022). By delaying disease onset and slowing down disease spread, intercropping can delay when certain disease thresholds are reached. Consequently, farmers would need to take less management action, such as fungicide spraying, throughout the season.

2.4.4 Yield

In previous meta-analyses examining yield benefits from intercropping, over 80% of the data records showed a positive yield gain of intercrops (Li et al., 2020b, 2020a; Yu et al., 2016). However, in our analysis, while the majority of studies observed a lower disease incidence in the intercrop system than in the sole crop, only 40% of data points reported an increase in the net effect ratio of the focal species. This discrepancy with the previous meta-analyses could at least in part be linked to the fact that most studies in our dataset sowed both crops at the same time, while intercrop systems that have the highest yield advantage are those in which there is some temporal separation of the two crop species in the intercrop, i.e. relay intercropping (Li et al., 2020b, 2020a; Yu et al., 2016). Competition between species in the mixtures, due to simultaneous sowing, might not have been fully compensated by a reduction in disease incidence. Additionally, intercrops in our analysis may have been designed primarily for disease suppression rather than yield increase. For instance, mixtures with a tall companion species may have a disease suppressive barrier effect, but the yield of the focal crop may nevertheless be negatively affected because of shading. Because of a lack of differences in sowing time, it could not be explored to what extent disease suppression is equally effective when there is a large temporal separation of crops grown. We showed that intercrops can exhibit both synergies and trade-offs between yield stimulation and disease suppression. The factors that determine which of the two outcomes prevails need to be explored.

2.5 Conclusion

This meta-analysis showed that intercropping consistently suppressed disease across a wide range of intercrop systems, but the extent of suppression varied considerably. Intercropping reduced both the initial incidence and the apparent infection rate, and we show that this can substantially slow down the rate at which diseases reach a certain (critical) level. Furthermore, we found that tall companion crops suppressed pathogens spread by vectors more than companions that were either shorter or similar in height to the host. Due to the interactions among traits of the focal host, companion species, the pathogen, weather and climate, and the variability in experimental design between studies (e.g. the moment of disease observation), it was challenging to tease apart the separate effects of different causal factors on plant disease incidence. Within each specific focal host-companion-pathogen combination, different disease-suppressive mechanisms are likely at play at different strengths, and different types of intercrop systems may achieve disease suppression in different ways. Across the board, this analysis shows that intercropping suppresses both initial infections, and secondary infections, and supports disease-suppression throughout the season. In the current analysis, we did not identify a clear relationship between disease incidence reduction and yield. Further work is needed to elucidate why this is the case.

Acknowledgements

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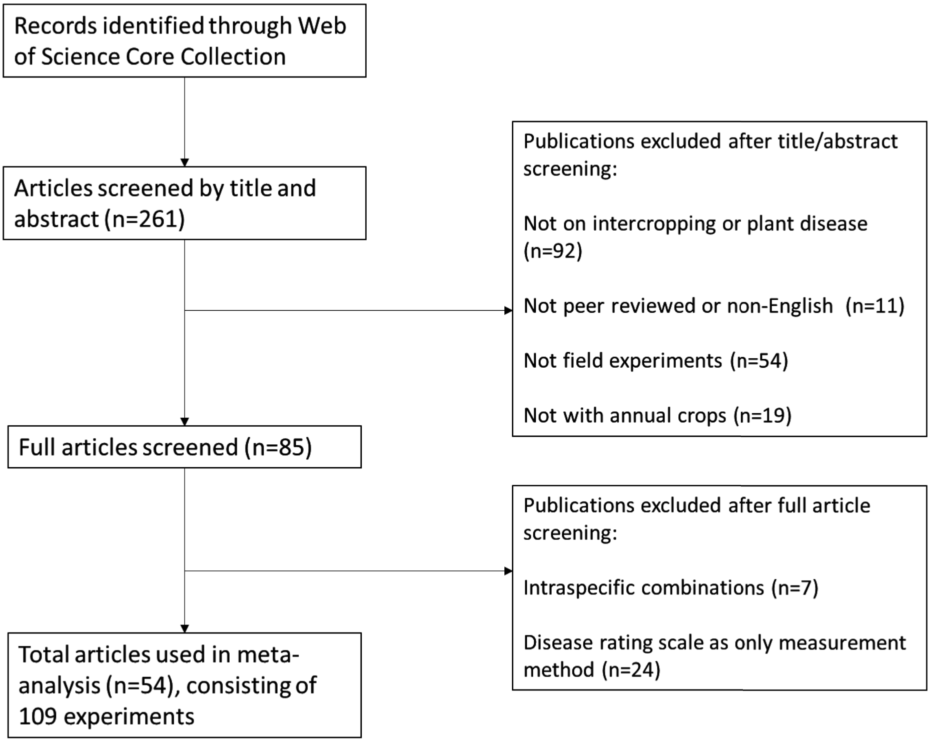
Notes

Li W.F., Douma J.C., Makowski D., Homulle Z., van der Werf W. Intercropping consistently but variably decreases plant disease incidence: a global meta-analysis. Unpublished manuscript.

Supplementary material

Methods S2.1 Prisma diagram illustrating the process of paper selection



A literature search was conducted on Web of Science on 27 October 2022. Key-words for a range of different intercrop systems, including different ways of writing, and names of diseases were included in the search terms to ensure the most inclusive amount of suitable papers. The search was performed with (“intercrop*” OR “inter crop*” OR “inter-crop*” OR “crop mix*” OR “species mix*” OR “mixed crop*” OR “mixed cultivation” OR “strip-crop*” OR “stripcrop*” OR “strip crop*” OR “crop combin*” OR “poly-cultur*” OR “polycultur*” OR “relay crop*” OR “relay-crop*” OR “relaycrop*”) in the title, and (“disease*” OR “vir*” OR “pathogen*” OR “blight” OR “rust” OR “smut” OR “mold” OR “mould” OR “wilt” OR “rot” OR “mildew” OR “blast” OR “canker” OR “scab” OR “mosaic” OR “spot” OR “infect*”) in the topic, NOT (virgatum OR mycorrhiz* OR model* OR nematod* OR fish* OR shrimp* OR tree* OR livestock).

The search yielded 261 publications, which were screened considering the following inclusion criteria: peer reviewed article in English; reporting primary data from field experiments on intercrops of annual crop, thus excluding studies conducted in pots or in glasshouses, or modelling studies; reporting data on interspecific plant mixtures, thus excluding papers using intraspecific combinations (e.g. cultivar mixtures); reporting data on plant diseases caused by viruses, fungi, bacteria or other micro-organisms, thus excluding papers reporting only on nematodes, insects or abiotic disorders; reporting quantitative data on disease incidence in both the intercrop and the corresponding sole crop under the same management, thus excluding papers using only disease rating scales, which are often different between experiments and thus not comparable.

Methods S2.2 List of publications used in the meta-analysis

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Table S2.1 Overview of the classification of the diseases present in the database

Common name of the disease	Latin name	Infected crop(s)	Type of pathogen	Trophic style	Dispersal mechanism	Survival strategy	Life cycle
Bacterial blight	*Xanthomonas axonopodis*	common bean (*Phaseolus vulgaris*) or cowpea (*Vigna unguiculata*)	bacteria		Water	Debris-seed-borne	Polycyclic
Bacterial wilt	*Pseudomonas solanacearum*	potato (*Solanum tuberosum*)	bacteria		Soil	Soil survivor	Monocyclic
Corn stunt spiroplasma	*Spiroplasma kunkelii*	maize (*Zea mays*)	bacteria		Vector	Vector borne	Polycyclic
Halo blight	*Pseudomonas syringae*	common bean (*Phaseolus vulgaris*)	bacteria		Water	Debris-seed-borne	Polycyclic
Tobacco or tomato bacterial wilt	*Ralstonia solanacearum* or *Pseudomonas solanacearum*	tobacco (*Nicotiana tabacum*) or tomato (*Solanum lycopersicum*)	bacteria		Soil	Soil survivor	Monocyclic
Angular leaf spot	*Phaeoisariopsis griseola*	common bean (*Phaseolus vulgaris*)	fungus	Hemibiotrophic	Wind & rain	Debris-seed-borne	Polycyclic
Anthracnose disease	*Colletotrichum scovillei*	pepper (*Capsicum annuum*)	fungus	Hemibiotrophic	Water	Debris-seed-borne	Polycyclic
Aspergillus flavus	*Aspergillus flavus*	groundnut (*Arachis hypogea*)	fungus	Necrotrophic	Wind	Soil survivor	Monocyclic

Table S2.1 Continued

Common name of the disease	Latin name	Infected crop(s)	Type of pathogen	Trophic style	Dispersal mechanism	Survival strategy	Life cycle
Bean rust	*Uromyces appendiculatus* or *Uromyces viciae-fabae*	common bean (*Phaseolus vulgaris*) or faba bean (*Vicia faba*)	fungus	Biotrophic	Wind	Debris-seed-borne	Polycyclic
Brown blotch	*Colletotrichum truncatum*	cowpea (*Vigna unguiculata*)	fungus	Hemibiotrophic	Water	Debris-seed-borne	Polycyclic
Brown spot	*Alternaria alternata*	tobacco (*Nicotiana tabacum*)	fungus	Necrotrophic	Wind & rain	Debris-seed-borne	Polycyclic
Cercospora leaf spot	*Cercospora sesami Zim.*	sesame (*Sesamum indicum*)	fungus	Hemibiotrophic	Wind & rain	Debris-seed-borne	Polycyclic
Chocolate spot	*Botrytis fabae*	faba bean (*Vicia faba*)	fungus	Necrotrophic	Wind & rain	Soil survivor	Polycyclic
Corn common rust	*Puccinia sorghi*	maize (*Zea mays*)	fungus	Biotrophic	Wind	Debris-seed-borne	Polycyclic
Cotton root rot	*Phymatotrichum omnivorum*	cotton (*Gossypium hirsutum*)	fungus	Necrotrophic	Soil	Soil survivor	Monocyclic
Early leaf spot	*Cercospora arachidicola*	groundnut (*Arachis hypogea*)	fungus	Hemibiotrophic	Wind & rain	Debris-seed-borne	Polycyclic

Table S2.1 Continued

Common name of the disease	Latin name	Infected crop(s)	Type of pathogen	Trophic style	Dispersal mechanism	Survival strategy	Life cycle
Fusarium wilt	*Fusarium spp*	barley (*Hordeum vulgare*), wheat (*Triticum aestivum*), oat (*Avena sativa*), common bean (*Phaseolus vulgaris*), faba bean (*Vicia faba*), soybean (*Glycine max*) or pigeonpea (*Cajanus cajan*)	fungus	Necrotrophic	Soil	Soil survivor	Monocyclic
Late blight	*Phytophthora infestans*	potato (*Solanum tuberosum*)	fungus	Hemibiotrophic	Wind & rain	Soil survivor	Polycyclic
Late leaf spot	*Cercosporidium personatum*	groundnut (*Arachis hypogea*)	fungus	Hemibiotrophic	Wind & rain	Debris-seed-borne	Polycyclic
Leaf blight	*Alternaria sesamicola Kaw.*	sesame (*Sesamum indicum*)	fungus	Necrotrophic	Wind	Debris-seed-borne	Polycyclic
Leaf spot	*Phoma sorghina*	fluted pumpkin (*Telfairia occidentalis*)	fungus	Necrotrophic	Wind & rain	Debris-seed-borne	Polycyclic
Leek rust	*Puccinia allii*	leek (*Allium porrum*)	fungus	Biotrophic	Wind	Air borne	Polycyclic
Net blotch	*Pyrenophora teres*	barley (*Hordeum vulgare*)	fungus	Necrotrophic	Wind & rain	Debris-seed-borne	Polycyclic

Table S2.1 Continued

Common name of the disease	Latin name	Infected crop(s)	Type of pathogen	Trophic style	Dispersal mechanism	Survival strategy	Life cycle
Northern leaf blight	*Exserohilum turcicum*	maize (*Zea mays*)	fungus	Hemibiotrophic	Wind & rain	Debris-seed-borne	Polycyclic
Phytophthora blight	*Phytophthora sojae*	soybean (Glycine max)	fungus	Hemibiotrophic	Soil	Soil survivor	Polycyclic
powdery mildew	*Erysiphe graminis* or *Blumeria graminis*	wheat (*Triticum aestivum*)	fungus	Biotrophic	Wind	Debris-seed-borne	Polycyclic
Pseudo-cercosporella herpotrichoides	*Pseudo-cercosporella herpotrichoides*	barley (*Hordeum vulgare*), wheat (*Triticum aestivum*) or oat (*Avena sativa*)	fungus	Necrotrophic	Wind & rain	Debris-seed-borne	Monocyclic
Red crown rot	*Cylindrocladium parasiticum*	soybean (*Glycine max*)	fungus	Necrotrophic	Soil	Soil survivor	Monocyclic
Rhizoctonia cerealis	*Rhizoctonia cerealis*	barley (*Hordeum vulgare*), wheat (*Triticum aestivum*) or oat (*Avena sativa*)	fungus	Necrotrophic	Soil	Soil survivor	Monocyclic
Rice blast disease	*Magnaporthe oryzae*	rice (*Oryza sativa*)	bacteria	Hemibiotrophic	Wind	Debris-seed-borne	Polycyclic
Sheath blight disease	*Rhizoctonia cerealis*	rice (*Oryza sativa*)	fungus	Necrotrophic	Soil	Soil survivor	Monocyclic
Stripe rust	*Puccinia striiformis*	wheat (*Triticum aestivum*)	fungus	Biotrophic	Wind	Debris-seed-borne	Polycyclic
Sugarcane smut	*Ustilago scitaminea*	sugarcane (*Saccharum officinarum*)	fungus	Biotrophic	Wind	Debris-seed-borne	Monocyclic

Table S2.1 Continued

Common name of the disease	Latin name	Infected crop(s)	Type of pathogen	Trophic style	Dispersal mechanism	Survival strategy	Life cycle
Cassava mosaic disease		cassava (*Manihot esculenta*)	virus		Vector	Vector borne	
Chilli veinal mottle virus, Pepper veinal mottle virus, Cucumber mosaic virus or Potato virus Y		pepper (*Capsicum annuum*) or hot pepper (*Capsicum chinense*)	virus		Vector	Vector borne	
Cucumber mosaic virus, Zucchini yellow mosaic virus, Papaya ringspot virus, Cucurbit leaf crumple virus, watermelon mosaic virus or Squash silverleaf		zucchini (*Cucurbita pepo*)	virus		Vector	Vector borne	
Maize mosaic virus, Maize rayado fino virus or Maize streak virus		maize (*Zea mays*)	virus		Vector	Vector borne	
potato virus y		potato (*Solanum tuberosum*)	virus		Vector	Vector borne	
Soybean mosaic virus		soybean (*Glycine max*)	virus		Vector	Vector borne	
Tobacco mosaic virus		tobacco (*Nicotiana tabacum*)	virus		Vector	Vector borne	

Methods S2.3 Different definitions of host density

To explore the potential host dilution effect we calculate the density of the host crop in the mixture. We did this by using the scaled relative density of the host in the intercrop (Li et al., 2020a; van der Werf et al., 2021; see main text). However, host density could also be defined as the plant density of the host in the intercrop in comparison to the density the corresponding sole crop:

$$RD = \frac{D_{1,IC}}{D_{1,SC}}$$

Where $D_{1,IC}$ and $D_{1,SC}$ represent the density of the host (plants m^{-2}) in the intercrop and density in the sole crop, respectively. By using this definition completely additive intercrop designs experience no host dilution.

Proportion conspecifics

Next to this definition of host density, host density on a finer scale can also be calculated. When hosts are grown in strips they will be effectively surrounded more often by the same species compared to the non-host. As such the effective host dilution may be much lower than what is expected from the relative densities. A simplified calculation of the proportion of neighbours of the same species as that of a host plant (conspecifics) was calculated based on information of the intercrop design. Only the direct neighbours were considered in this calculation, and for simplification we considered a plant to have eight neighbours (Fig. S2.1).

In row and row/strip intercrop systems, only the neighbours within the row are similar, whereas all others are dissimilar (Fig. S2.1). So, out of the total eight neighbours the proportion conspecifics was considered $\frac{2}{8}$.

In strip and strip/row intercrop systems, the middle row(s) of the strip are completely surrounded by similar neighbours, and only the outer two rows of the strip are interacting with a dissimilar neighbour (Fig. S2.1). The proportion conspecifics was calculated as follows: for plants in the outer two rows, five out of eight neighbours are of the same species and for plants in the middle row(s) only all neighbours are of the same species (Eq. 2.1).

$$\frac{2}{total\ number\ of\ rows\ in\ strip} * \left(\frac{5}{8}\right) + \frac{(total\ number\ of\ rows\ in\ strip\ - 2)}{total\ number\ of\ rows\ in\ strip} * 1 \tag{2.1}$$

In mixed intercrop systems, the proportion similar of dissimilar neighbour is different for each host plant, inherit in the randomness of the design (Fig. S2.1). On average, the proportion conspecifics dependents on the ratio of the crops in the mixture. For example, if there is 40-60% ratio of host and non-host crop, than the proportion of conspecifics for any host is on average 0.4.

Plants in pure stand are only interacting with similar neighbours, and therefore the proportion conspecifics is 1.

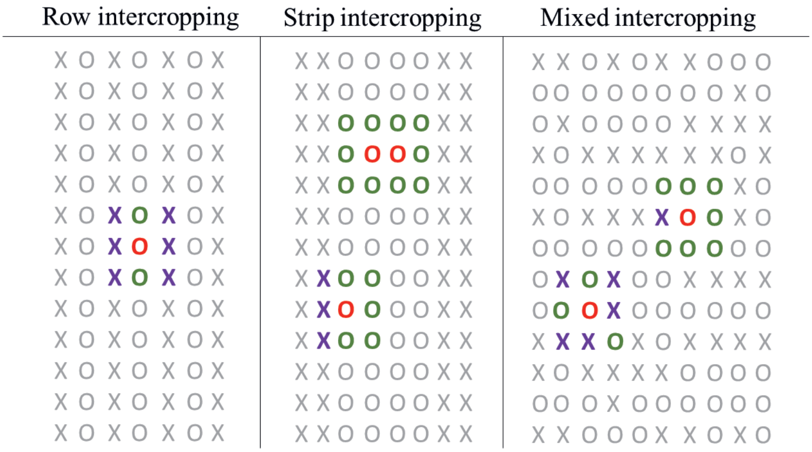

Fig. S2.1 Conceptualisation of the proportion of similar or dissimilar neighbours**.** Red circles are random host plants in the intercrop, green circles are the conspecific neighbours, and purple x’s are dissimilar neighbours. In row intercrop systems, only the neighbours within the row are similar, whereas all others are dissimilar. In strip intercrop systems, the middle rows of the strip are completely surrounded by similar neighbours, and the outer two rows of the strip are interacting on one side with a dissimilar neighbour. In mixed intercrop systems, the proportion of having similar of dissimilar neighbour is different for each host plant.

Fig. S2.2 Phylogenetic tree of all the crop species present in the database. The tree was generated with the phyloT online tool.

Table S2.2 Model selection for the relationship between the LOR and scaled relative density of the host species and possible interactions. For all models a gaussian distribution was used; nested random effects of Study/experiment were used; and 'scaled relative density' was used as a variable affecting dispersion (dispformula) (except for the intercrop-only model). + means additive effects are assumed, while * means a main effects and interactions are estimated.

Response variable	Predictors	AIC	BIC	loglik
LOR	Scaled relative density + Survival pathogen	1126.1	1157.7	-555.0
LOR	Scaled relative density * Survival pathogen	1127.2	1166.8	-553.6
LOR	Scaled relative density + Dispersal pathogen	1133.8	1173.3	-556.9
LOR	Relative density * Lifecycle pathogen	1135.3	1167.0	-559.7
LOR	Relative density + Lifecycle pathogen	1137.5	1165.2	-561.7
LOR	Scaled relative density * Dispersal pathogen	1139.0	1194.4	-555.5
LOR	Scaled relative density	1140.6	1164.3	-564.3
LOR	Scaled relative density + Height category companion	1142.1	1173.7	-563.1
LOR	Scaled relative density + Type of pathogen	1142.7	1174.3	-563.4
LOR	Scaled relative density + Observation category	1144.0	1175.7	-564.0
LOR	Scaled relative density * Height category companion	1144.7	1184.2	-562.3
LOR	Scaled relative density * Type of pathogen	1145.5	1185.0	-562.7
LOR	Scaled relative density * Observation category	1146.3	1185.9	-563.2
LOR	Scaled relative density + Intercrop pattern	1146.5	1186.0	-563.2
LOR	Scaled relative density * Intercrop pattern	1148.4	1203.8	-560.2
LOR	(intercept)	1180.9	1200.7	-585.4

Table S2.3 Model selection criteria (AIC and BIC) for the relationship between the LOR and relative density of the host species and possible interactions with pathogen traits, sorted by the AIC of the model. For all models a gaussian distribution was used; nested random effects of Study/experiment were used; and 'relative density' was used as a dispersion parameter (dispformula) (expect for the intercrop-only model). + means additive effects are assumed, while * means a main effects and interactions are estimated.

Response variable	Predictors	AIC	BIC	loglik
LOR	Relative density + Survival pathogen	1410.1	1443.5	-697.1
LOR	Relative density * Survival pathogen	1414.0	1455.7	-697.0
LOR	Relative density + Dispersal pathogen	1416.8	1458.5	-698.4
LOR	Relative density + Lifecycle pathogen	1420.0	1449.2	-703.0
LOR	Relative density * Dispersal pathogen	1420.4	1478.8	-696.2
LOR	Relative density	1420.6	1445.6	-704.3
LOR	Relative density + Height category companion	1421.4	1454.8	-702.7
LOR	Relative density * Lifecycle pathogen	1421.8	1455.1	-702.9
LOR	Relative density + Observation category	1422.2	1455.6	-703.1
LOR	Relative density + Type of pathogen	1424.0	1457.3	-704.0
LOR	Relative density * Height category companion	1425.2	1466.9	-702.6
LOR	Relative density * Observation category	1425.6	1467.3	-702.8
LOR	Relative density + intercrop pattern	1426.7	1468.4	-703.3
LOR	Relative density * Type of pathogen	1427.9	1469.6	-703.9
LOR	Relative density * intercrop pattern	1431.5	1489.8	-701.7
LOR	(intercept)	1468.3	1485.0	-730.2

Table S2.4 Model selection criteria (AIC and BIC) for the relationship between the LOR and the proportion conspecifics and possible interactions with pathogen traits, sorted by the AIC of the model. For all models a gaussian distribution was used; nested random effects of Study/experiment were used; and 'proportion conspecifics' was used as a variable affecting dispersion (dispformula) (expect for the intercrop-only model). + means additive effects are assumed, while * means a main effects and interactions are estimated.

Response variable	Predictors	AIC	BIC	loglik
LOR	Proportion conspecifics * Survival pathogen	1235.7	1275.9	-607.8
LOR	Proportion conspecifics * Dispersal pathogen	1238.7	1295.0	-605.3
LOR	Proportion conspecifics + Survival pathogen	1239.0	1271.2	-611.5
LOR	Proportion conspecifics + Dispersal pathogen	1241.4	1281.6	-610.7
LOR	(intercept)	1252.5	1272.6	-621.2
LOR	Proportion conspecifics	1253.6	1277.7	-620.8
LOR	Proportion conspecifics * Height category companion	1255.0	1295.3	-617.5
LOR	Proportion conspecifics + Height category companion	1255.9	1288.1	-619.9
LOR	Proportion conspecifics + Type of pathogen	1256.6	1288.8	-620.3
LOR	Proportion conspecifics * Type of pathogen	1257.8	1298.1	-618.9
LOR	Proportion conspecifics + intercrop pattern	1258.2	1298.4	-619.1
LOR	Proportion conspecifics * intercrop pattern	1260.1	1316.4	-616.0

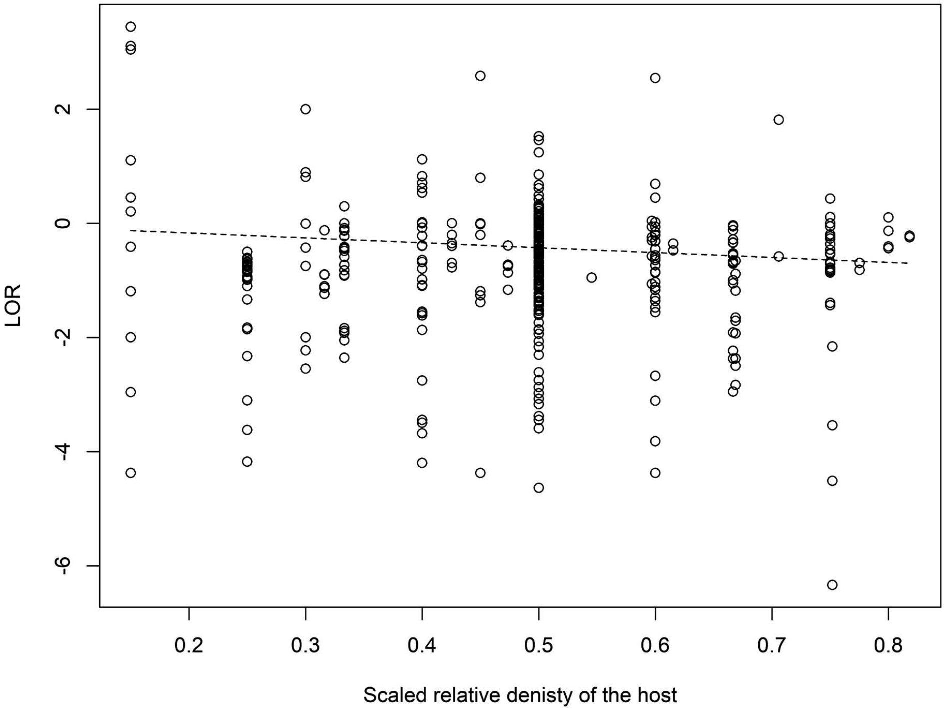

Fig. S2.3 Relationship between the LOR and the scaled relative density of hosts in the intercrop (P > 0.99).

Results S2.1 host density

Comparing the plant density of hosts on in the intercrop to the density in the corresponding sole crop (Method S2.3) showed a significant increase in the incidence with an increase in the proportion of hosts in the population (Fig. S2.4). The incidence increased 0.94 on a logit scale per unit increase in fraction hosts (P < 0.001). When excluding the sole crop, the relationship become nonsignificant (P > 0.32).

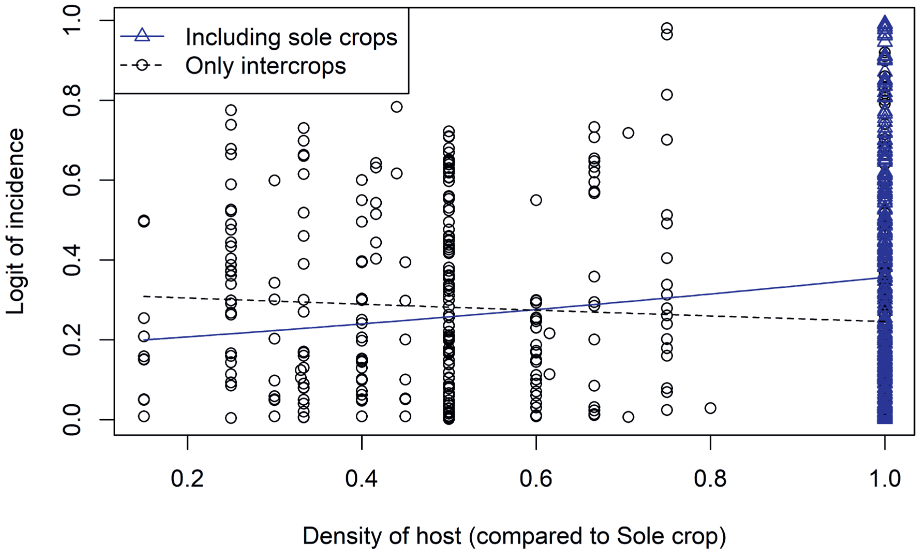

Fig. S2.4 Relationship between incidence and the density of the host in the intercrop compared with the corresponding sole crop. A density of 1 contains both incidence values from completely additive intercrops, and sole crops. The dark blue solid line represent the relationship including the sole crops (P < 0.001). The dashed line represents the relationship if only intercrop data is used (P > 0.32).

When analysing the LOR, no significant relationship between LOR and host density was found (Fig. S2.5). Again, adding either the survival mechanism, dispersal mechanism or feeding behaviour of the pathogen marginally lowered the AIC of the model (see Table S2.3), however, the relationship between host density and LOR stayed not significant (Fig. S2.5).

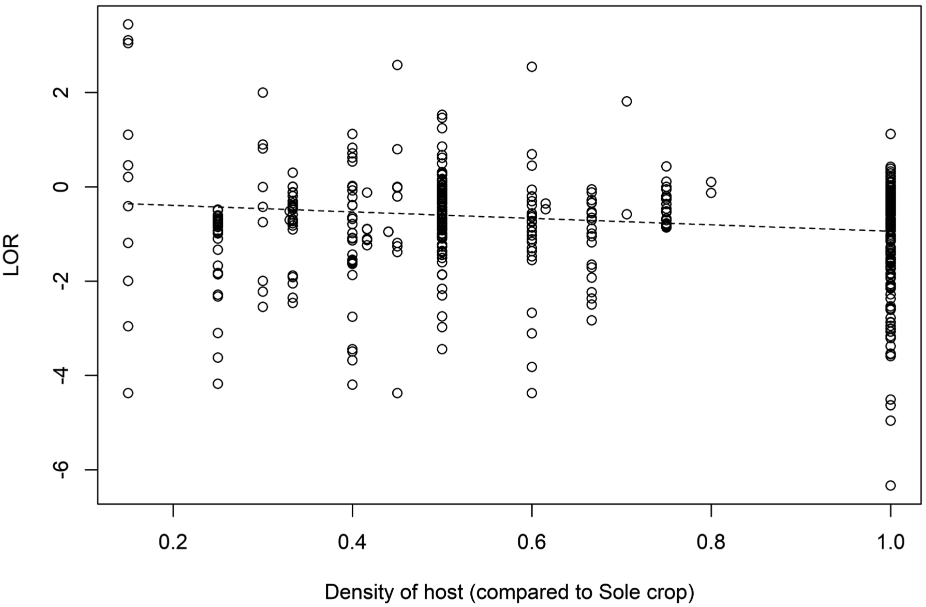

Fig. S2.5 Relationship between LOR and the density of hosts in the intercrop compared with the corresponding sole crop (P > 0.42). A density of 1 represents additive intercrop designs.

Results S2.2 proportion conspecifics

Having a higher proportion of conspecifics (Method S2.4) out of all direct neighbours increased disease incidence (Fig S2.6). When excluding the sole crop, the relationship become non-significant (P > 0.63).

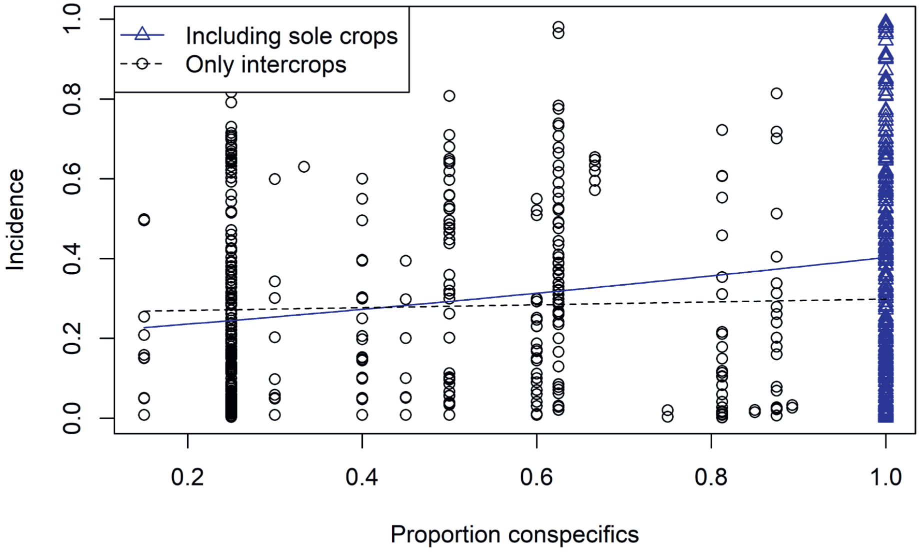

Fig. S2.6 Relationship between incidence and the proportion conspecifics out of all neighbours. All values of 1 represent the sole crops (triangles), since sole crops only have similar neighbours. The dark blue solid line represent the relationship including the sole crops (P < 0.001). The dashed line represents the relationship if only intercrop data is used (P > 0.63).

However, when only comparing the intercrop systems with each other using the LOR, an interaction with the dispersal mechanism of the pathogen was found (P = 0.03). For pathogens dispersing through the soil, the LOR decreased by -2.57 per fraction increase in similar neighbours (p <0.001) (Fig. S2.7). For pathogens dispersing via vectors, water, wind, or wind & rain, no significant relationship between the LOR and contact rate was found.

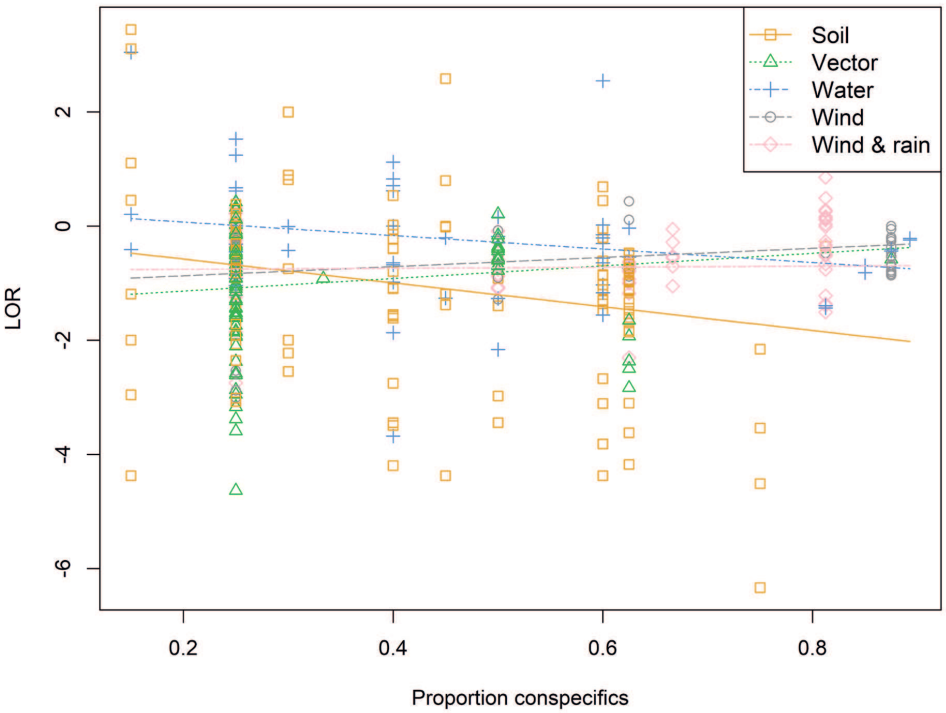

Fig. S2.7. Relationship between LOR and the proportion conspecifics out of all neighbours, for pathogens with different dispersal mechanisms. Relationship for pathogens dispersing through the soil was significant ($p < 0.001$), for pathogens dispersing via vectors, water, wind, or wind & rain, the relationship was not significant.

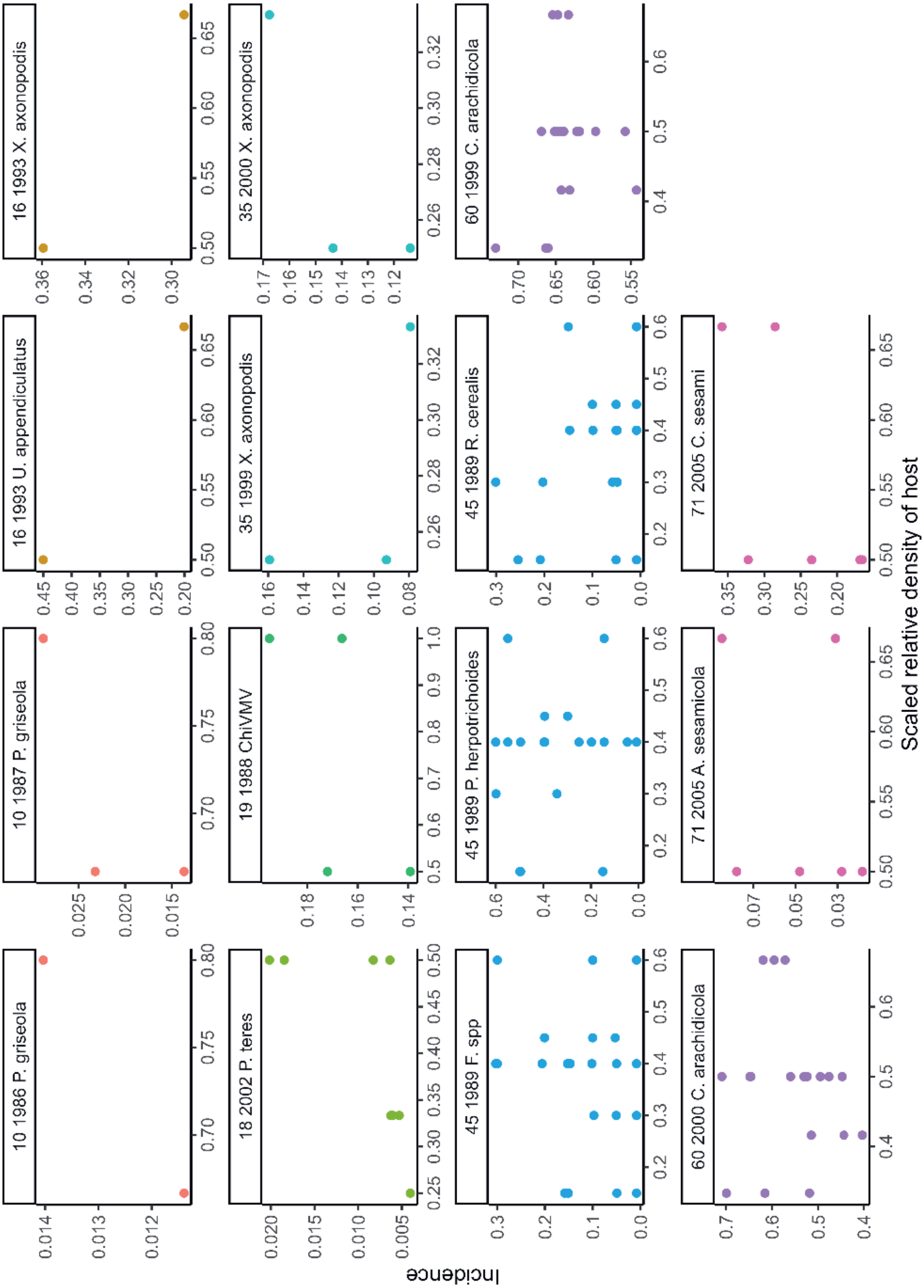

Fig. S2.8 Incidence in intercrop trials with different densities of the host (incidence in the corresponding sole crop not presented). The first number in each title is the identifier number of the study, the second number is the experimental year, and lastly the disease that was observed.

Table S2.5 Model selection for the analysis of disease incidence over time. For all models the effect of treatment on dispersion accounted for by incorporating it as a dispersion parameter (dispformula).

Response variable	Distribution	Link	Predictors	Random effects	AIC
Incidence	Beta	logit	Treatment * DAFO	DAFO | Study/experiment/ ID	-1516.9
Incidence	Beta	logit	Treatment * DAFO	DAFO | Study/experiment + (1|Study:Exp:ID)	-1514.2
Incidence	Beta	logit	Treatment * DAP	DAP | Study/experiment/ ID	-1450.7
Incidence	Beta	logit	Treatment * DAP	DAP | Study/experiment + (1|Study:Exp:ID)	-1445.1
1 - Incidence	Beta	Log-Log	Treatment * DAFO	DAFO | Study/experiment/ ID	-1417.7
Incidence	Gompertz	Log-Log	Treatment * DAP	DAP | Study/experiment/ ID	-1260.7
Incidence	Beta	logit	Treatment * DAFO	DAFO | Study/experiment	-1104.6
Incidence	Beta	logit	Treatment * DAP	DAP | Study/experiment	-1071.5

Note: *DAFO* are the days at which the disease assessments were made, in days after the first observation, while *DAP* are the days at which the disease assessments were made, in days after planting. DAP|Study/Exp/ID or DAFO|Study/Exp/ID indicates a random slope and intercept for each observation over time. (1|Study:Exp:ID) indicates only a random intercept for each observation over time.

Table S2.6 Contingency table for the classification into phylogenetic types and dispersal mechanism.

	Soil	Vector	Water	Wind	Wind & rain
bacteria	19	8	30	1	5
fungi and oomycetes	126	0	11	51	129
virus	0	104	0	0	0

Table S2.7 Contingency table for the classification into survival strategy and dispersal mechanism.

	Soil	Vector	Water	Wind	Wind & rain
Debris-seed survivor	0	0	41	48	120
Soil survivor	145	0	0	4	14
Vector survivor	0	112	0	0	0

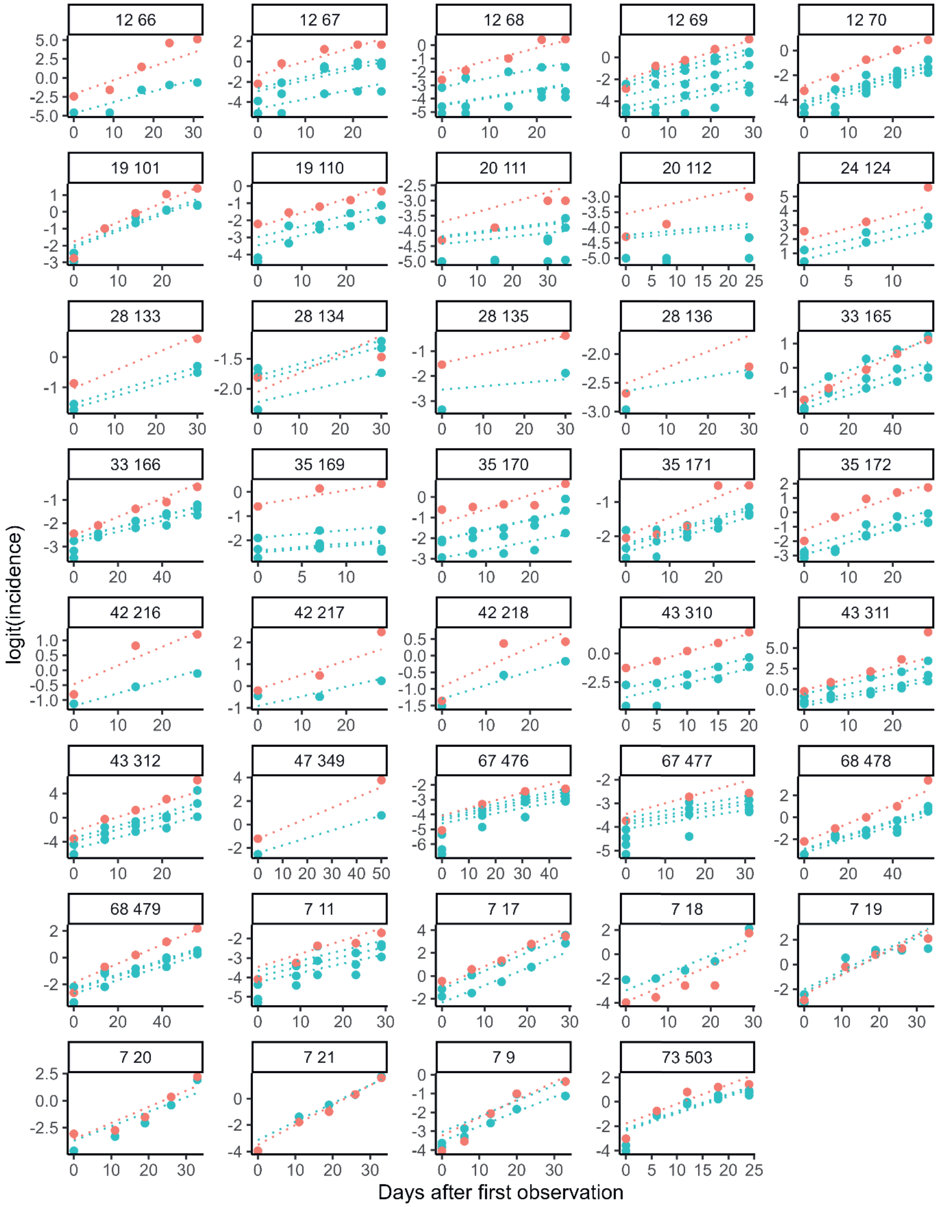

Fig. S2.9 Estimated disease progress curves for disease incidence for sole cropped (red) and intercropped (blue) crops, plotted on logit scale. Dotted lines represent the estimate curves, points are the observed incidence values which were reported in the respective papers. The first number in each title is the paper number identifier, the second number distinguishes the different experiments within a study. Disease observations of all experiments are set to begin on the first observation day.

Methods S2.4 Calculating the 2 .5% and 97.5% quantiles for the delay in crop termination

We calculated the difference in the time that potatoes in strip crops or monoculture reached given levels of severity. We also calculated the 2.5% and 97.5% quantiles of this delay, based on the uncertainty in the estimates of the logistic fit (Table 2, main text). The model coefficients along with the variance-covariance matrix of the coefficients was used to generate plausible combinations of parameter values of x_0 and r for each treatment and year. Plausible combinations (1000) were drawn randomly from a multivariate normal distribution with the means equal to the model estimates and the variance-covariance matrix of the model coefficients (Bolker, 2008). Next, quantiles were calculated representing the uncertainty in the difference in time when a given severity level is reached.

Chapter 3

The potential of strip cropping to suppress potato late blight

Zohralyn Homulle[1], Niels P.R. Anten[1], Geert J.T. Kessel[2], Tjeerd Jan Stomph[1], Wopke van der Werf[1], Jacob C. Douma[1]

[1]Centre for Crop Systems Analysis, Wageningen University, 6700 AK, Wageningen, the Netherlands

[2]Field Crops, Wageningen University & Research, Edelhertweg 1, 8219 PH, Lelystad, The Netherlands

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Abstract

Crop diversification through intercropping is known to suppress disease severity and incidence. Strip cropping is an adaptation of intercropping in which strips are made wide enough (e.g. 3 m or wider) to allow management with tractor-pulled equipment. There is, however, little evidence of the efficacy of disease suppression in strip cropping. Furthermore, it is unclear how and to which extent the choice of companion crop species affects the suppression of diseases. Here we determine how potato late blight, caused by *Phytophthora infestans*, is affected by strip cropping potatoes with three different companion crops: grass, maize or faba bean. Potato late blight severity and tuber yield were determined in field experiments in the Netherlands during three years that differed in both weather conditions and timing of the onset of the epidemic. Strip cropping with grass or maize lowered disease severity compared with potatoes grown in monoculture. Across the three years, the average severity over the observation period was significantly lower in the strip-crop with grass (0.040) or in the strip-crop with maize (0.053) than in the potato monoculture (0.105). Strip-cropping with faba bean did not significantly reduce the average severity. In 2021 and 2022, strip cropping with grass resulted in the highest potato yields (per m^2 potato area) (25.9 and 38.9 t ha^{-1} potato area in 2021 and 2022, respectively), which was 31-33% higher than the monoculture (19.8 and 29.2 t ha^{-1}). Despite the observed reduction in disease in potato strip-cropped with maize, it resulted in similar yield per unit area of potato as the monoculture, presumably due to competition for light with the taller maize plants. Together these results show that strip cropping, when integrated with other control measures, can be used to reduce late blight severity. A short non-competitive companion crop species, grass, was effective in simultaneously reducing late blight and enhancing tuber yield.

Keywords: crop diversification, crop mixtures, intercropping, disease suppression, epidemiology, potato, *Phytophthora infestans*, tuber yield

3.1 Introduction

Potato is notorious for its high reliance on fungicides for the control of late blight, caused by *Phytophthora infestans* (Goffart et al., 2022; Yuen, 2021). *P. infestans* is considered the most devastating pathogen in potato (Campos and Ortiz, 2020; Majeed et al., 2017). Leaves, stems and tubers are all susceptible and the disease can spread quickly under suitable conditions (Fry, 2008). In northwestern Europe, where conditions for late blight are often suitable, a suite of measures is taken to combat late blight, including the use of healthy seed, resistant cultivars, and the reduction of primary sources of inoculum (Cooke et al., 2011; Kessel et al., 2018). Despite these measures, potato late blight remains a big stressor for potato production, particularly in organic agriculture (Pacilly et al., 2016; Tamm et al., 2004). The use of resistant cultivars as a control measure remains limited, due to the strong market demand for already established (but susceptible) cultivars (Kessel et al., 2018; Pacilly et al., 2016) and the ability of *P. infestans* to quickly overcome host resistance, which limits the usefulness and reliability of resistance (Fry, 2008; Haas et al., 2009). Therefore, in conventional agriculture, fungicide applications remain an indispensable ingredient of the integrated control toolbox.

Although conventional growers heavily rely on fungicides to prevent and control potato late blight, there are concerns about their use. Challenges are arising concerning fungicide resistance (Brylińska et al., 2016; Fones et al., 2020), environmental sustainability (De Jong and De Snoo, 2002; Nicholson et al., 2024; Sánchez-Bayo, 2011), and human health (Tsalidis, 2022). Reducing the use and risk of chemical pesticides is essential for more sustainable food production and is a key point of discussion in agricultural and environmental policies (Finger et al., 2024; Möhring et al., 2020). Furthermore, pesticides have a high economic cost (Guenthner et al., 2001; Haverkort et al., 2008). For instance, for the Netherlands, the economic costs of chemicals to control potato late blight and their application are estimated at €115 million per year, approximately 15% of the total production value (Haverkort et al., 2008). In organic agriculture, where the use of pesticides is not allowed, diseases can reduce crop yields. For example, in Ireland, unsprayed potatoes had a 23% (10.1 t/ha) average loss in marketable yield over a 25-year period due to late blight compared to fungicide-treated crops, with yield reductions exceeding 50% in years in which the disease arrived early in the season (Dowley et al., 2008). Thus, exploring additional methods for the integrated control of *P. infestans* is necessary for both conventional and organic growers.

Farmers are implementing multiple control measures against late blight (such as the ones described above: use of healthy seed, resistant cultivars, and the reduction of primary sources of inoculum), a strategy commonly known as integrated pest management (IPM). An additional component of an IPM approach may be strip cropping. Strip cropping is a form of intercropping (Li et al., 2020b; Vandermeer, 1992), in which multiple crop species are grown in a single field at the same time in alternate, multi-row strips wide enough to be operable using equipment that is currently available on modern mechanised farms (Ditzler et al., 2021; van Oort et al., 2020). In practice, a strip width of 3 meters or more is used due to limitations set by available equipment (Ditzler et al., 2021). Some advantages of intercropping, such as overyielding, caused by niche complementarity for resource capture (Li et al., 2020a; Vandermeer, 1992; Yu et al., 2016), are lost when strip width is increased, because the species complementarities that drive some of these advantages depend on the proximity of the different species (van Oort et al., 2020). However, for pathogens that spread over larger distances, some of the key mechanisms that lead to disease suppression by species mixture, such as host dilution and barrier effects (Boudreau, 2013), could still play a role in strip crop systems with wider strips. There is, however, little information on the effectiveness of disease control in strip cropping systems.

The effect of crop diversification, including various forms of intercropping and strip cropping, for the control of potato late blight has been investigated by various researchers, all using different companion crop species and spatial configurations of potato and the companion crop species (Bouws and Finckh, 2008; Ditzler et al., 2021; Garrett et al., 2001; Kassa and Sommartya, 2006; Singh et al., 2015; Traugott et al., 2000; He et al., 2010). The majority of these studies tested either fully mixed or row intercropping systems, and only two studies were done on strip cropping (Bouws & Finckh, 2008; Ditzler et al., 2021). He et al. (2010) intercropped 2 rows of potato with 2 rows of maize and found that the average severity of potato late blight decreased by 44% compared with monocrop controls (from ~36% in the monocrop across two years to ~18% severity in the intercrop). Bouws & Finckh (2008), who examined a strip cropping system, found that cropping potato in six meter wide strips with either cereals or a grass-clover mix reduced the disease between 4 and 20% compared with potatoes grown in monoculture. They reported an area under the disease progress curve (AUDPC, a quantitative measure of the cumulative disease severity over time) of ~1470 percent-days in the strip-crop and ~1568 percent-days in the potato monoculture, across three years. The two different companion crop species had contrasting results; in one year the lowest disease levels were found in plots with cereals as the companion crop species, whereas in the other year, the reduction was greatest with grass-clover as a companion. Ditzler et al. (2021) also found that *P. infestans* infection scores were consistently lower in the strip-crop than in the potato monoculture across their six year measurement period. While these studies have provided valuable insights, demonstrating the potential of strip cropping in suppressing potato late blight, it is unclear how different companion crop species, especially those of different stature, influence the suppression of *P. infestans* in strip cropping.

The stature of the companion crop likely influences important mechanisms for disease suppression in intercrop systems, such as barrier effects and microclimate alteration (Boudreau, 2013). *P. infestans* primarily spreads through the dispersal of spores. Primary infection sources of *P. infestans*, such as infected seed tubers, unharvested tubers or harvested tubers dumped on refuse piles produce spores that can be dispersed by wind or rain to healthy potato plants (Zwankhuizen et al., 1998). Under conducive conditions, the spores then germinate, infect, and initiate new disease cycles. Disease development during the growing season is influenced by temperature and relative humidity (optimum temperatures between 10 and 27°C and relative humidity > 90% (Zwankhuizen and Zadoks, 2002)). A tall companion crop species could act as a barrier for the initial spores, and spores produced by the in-field infections, thus limiting spread within the field, whereas a short companion crop species could potentially change the microclimate in the host canopy to be less conducive for infection, lesion growth and sporulation. Both tall and short companions would provide a dilution effect in relation to within field spread of the disease across strips. Experiments comparing the effects of strip cropping with different companion species provide information on which companion species are suitable candidates for further research towards practical implementation

The objective of this study was to investigate the effect of strip cropping potato with companion crop species of different stature on the epidemic development of *P. infestans* and tuber yield. Either grass, faba bean, or maize were chosen as companion crop species, since they are shorter than potato (grass), slightly taller than potato (faba bean), and considerably taller than potato (maize). Strip cropping with maize was chosen because it may lead to more effective disease suppression than with other cereals, such as wheat. Maize is taller and has a less dense stand than wheat and could provide a barrier against incoming spores while still allowing adequate air circulation to enable drying of the potato foliage. Furthermore, earlier work on intercropping potato with maize had shown a clear reduction in disease severity (He et al., 2010). Strip cropping with grass was chosen, because its low height can facilitate more air movement in the neighbouring potato canopy than when potatoes are grown in monoculture. Improved airflow can reduce the relative humidity and shorten the leaf wetness period in the potato canopy, making conditions less conducive for the development of potato late blight. Strip cropping with faba bean was chosen because of its intermediate height between maize and grass. Furthermore, various papers have reported on disease reduction in intercrops with faba bean (Hauggaard-Nielsen et al., 2008; Luo et al., 2021; Zhang et al., 2019).

3.2 Methods

3.2.1 Field experiments

Field trials were conducted in 2021, 2022 and 2024 at the organic experimental farm of Wageningen University & Research, located in Wageningen (51.99°N, 5.65°E), The Netherlands. The fields were managed organically; organic fertilizer was used and no pesticides or irrigation (see Supplementary information Table S3.1 for detailed information). Soil at the experimental site is a sandy soil.

The summer of 2021 was warm and wet, with average daily temperatures around 18 °C during June and July and a total of 191 mm of rain (Fig. 3.1). The summer of 2022 was also warm, with the same average daily temperature of around 18 °C during June and July, but it was drier, with a total of 129 mm of rain. Important to note is the high mean temperature of 26.2 °C on 19 July 2022, with a maximum of 36.6 °C measured on that day. This is relevant because the viability of *P. infestans* lesions declines fast at temperatures above 27 °C, and no new sporangia are formed (Minogue and Fry, 1981; Rotem et al., 1970). The summer of 2024 was somewhat cooler with average daily temperatures around 17 °C during June and July and the rainfall was intermediate: a total of 157 mm.

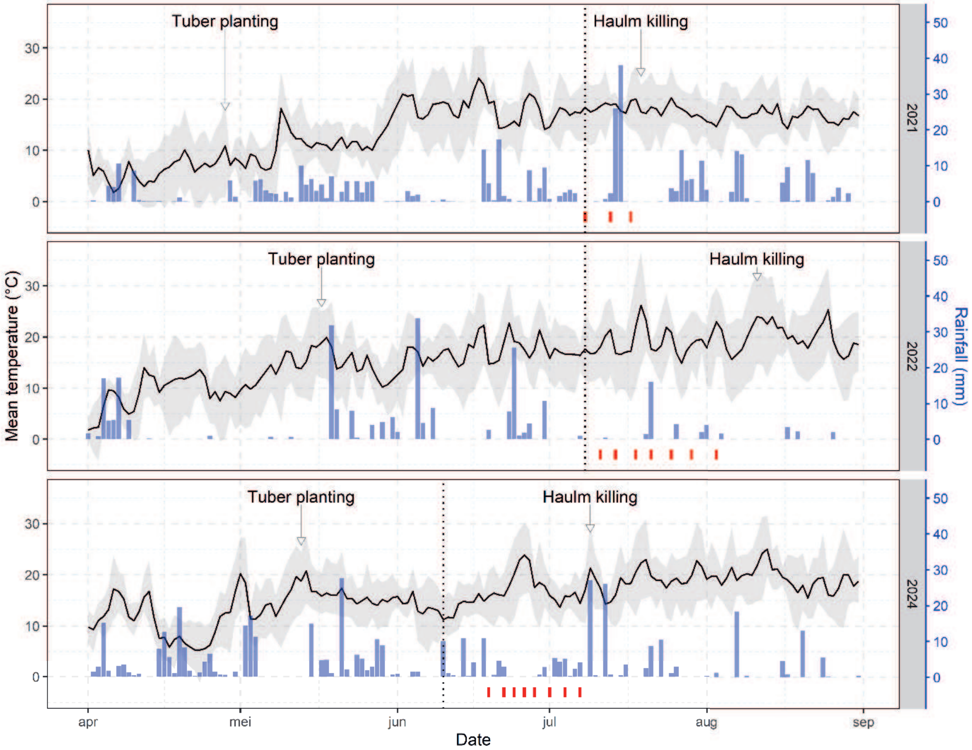

Fig. 3.1 Weather conditions during the 2021 (top), 2022 (middle) and 2024 (bottom) growing seasons. Red ticks on the x-axis mark late blight assessment dates, vertical dotted lines mark the first detection of late blight in each year. Black lines show mean temperature (degrees Celsius), grey ribbons span daily minimum and maximum temperatures, and blue bars are the total daily precipitation (mm). The dashes on the x-axis indicate the first of each month. Data was obtained from weather station De Veenkampen operated by Wageningen University, located approximately 3 km west of the experimental site.

Although the prevailing wind direction in the Netherlands is from the southwest, the wind direction during June and July was variable in the three years (Supplementary information Fig. S3.2).

Three experimental treatments were tested: potato (*Solanum tuberosum* cv. Agria) grown in monoculture, potato strip-cropped with maize (*Zea Mays*), and potato strip-cropped with English ryegrass (*Lolium perenne*) (Fig. 3.2). In 2022 and 2024, a fourth treatment was added: potato strip-cropped with faba bean (*Vicia faba* cv. Cartouche). In 2021, the maize cultivar used was Benedictio, in 2022 a mixture of two maize cultivars was used, namely 73% autens KWS and 27% LG30.179. The potato cultivar used (Agria) is moderately susceptible in the foliage and fairly resistant in the tuber to potato late blight (The European Cultivated Potato Database, 2005).

The experiment was laid out as a randomised design with two replicates of each treatment in 2021, four replicates in 2022, and two replicates in 2024, except for the strip-crop with faba bean, which had three replicates in 2024. In 2022, the experiment was split over two sites, with two replicates of each treatment at each site, and an approximate distance of 850 meter between the sites. Using two sites in the same year allowed us to explore variability of the treatment effects due to possible differences in e.g. soil humidity or initial inoculum load between the sites. Moreover, it reduced the risks associated with interplot interference, which can be substantial with *P. infestans* because of its large and rapidly expanding disease foci. Each strip-crop plot consisted of alternating 3 m-wide strips of the two species (Fig. 3.2). Strips were planted in an east-west direction, in alignment with the expected prevailing westerly wind direction (See Fig. S3.1 for the field arrangement of the plots). Each strip was 3m wide and consisted of either four rows of potato (row width of 75cm), four rows of maize, six rows of faba bean, or 20 rows of grass. The monoculture plot had a similar size as the strip-crop plots, but was planted with only potato. Plots were separated by a 6 meter strip of grass. Plots measured 21 m x 24 m.

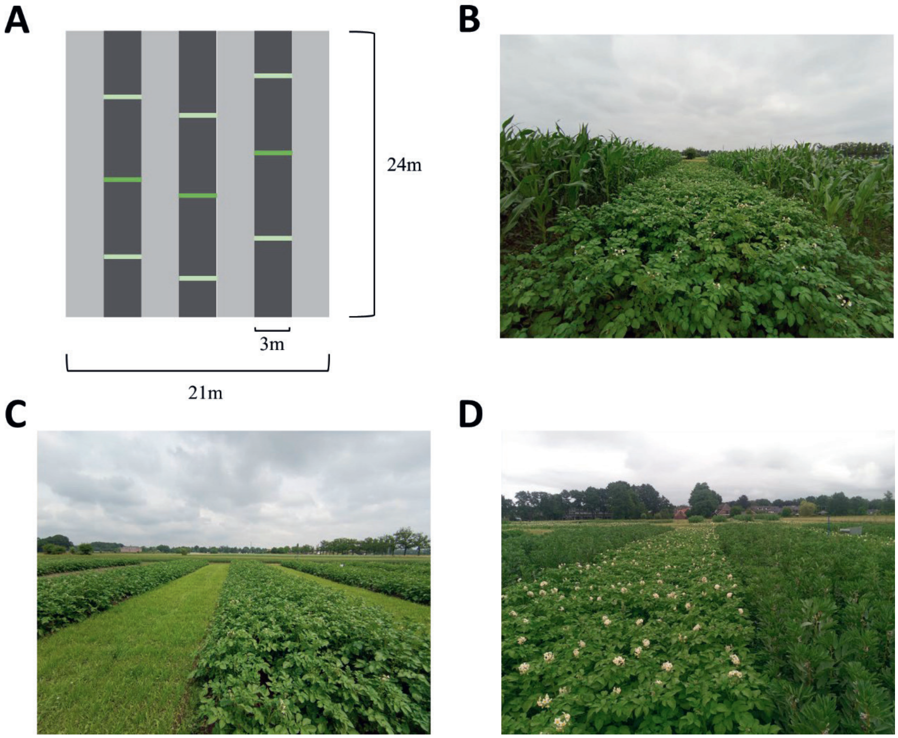

Fig. 3.2 Schematic arrangement of one experimental strip cropping plot (A), and pictures of potato strip-cropped with maize (photo taken on 16 July 2021) (B), grass (photo taken on 29 June 2021), and (C) faba bean (photo taken on 11 July 2022) (D). Strips of each crop species were 3 meter wide, and oriented east-west. The plots had a size of 21 m x 24 m. The dark grey strips in the schematic arrangement represent potato, and the light grey strip either maize, grass or faba bean. The lines perpendicular to the strips represent the transects (consisting of four plants, one per row) on which disease assessments were done. Transects were placed at random locations in each strip. We used three transects per strip in 2021 and two transects per strip in 2022 and 2024.

Potato was planted on 28 April 2021, and grass and maize were sown on 7 May 2021. Maize had not reached its final height at the time of the first late blight symptoms in 2021, therefore, to obtain a greater barrier effect in 2022, potatoes were planted later, on 17 May, in 2022. Grass and maize were sown on 29 April 2022 and faba bean was sown on 3 May 2022. In 2024, potato was planted on 13 May, faba bean was sown on 21 March, grass on 29 April, and maize on 2 May.

3.2.2 Disease assessment

Foliar late blight severity caused by natural infections was assessed in all plots, using three assessment methods: (1) counting the number of leaflets with lesions per plant, (2) estimating the percentage diseased leaf area per plant, and (3) scoring the remaining percentage green leaf area cover shortly before crop desiccation (see below). In the early stages of the epidemic, it was more accurate to count the number of leaflets with lesions per plant, rather than to estimate a very low percentage of diseased leaf area. As the epidemic progressed, counting the number of diseased leaflets was not possible anymore, due to high disease severity, and only the percentage diseased leaf area per plant was recorded, following the classification scheme of James (1971). We assessed the disease using both methods on 13 July 2021, 14 and 15 July 2022, and 24, 26 and 28 June 2024 and then performed a regression to convert the number of diseased leaflets into a percentage diseased leaf area (see Supplementary information Method S3.3). This allowed for the combination of the two assessment methods into a single metric, hereafter referred to as disease severity.

To quantify disease severity, we randomly selected in each of the three potato strips in a plot three transects perpendicular to the strip, with each transect comprising four plants (Fig. 3.2). This resulted in a total sample of 36 plants per plot for measuring blight severity. In 2021, the first late blight symptoms were observed on 8 July. Assessments were done three times (8, 13 and 17 July) from the moment the epidemic started until the haulm of the potatoes had to be desiccated (19 July) due to late blight severity passing the legal threshold. In 2022 and 2024, we quantified severity on 6 transects per plot (2 per strip), each transect consisting of 4 plants, resulting in a total sample of 24 plants per plot. In 2022, first symptoms were again observed on 8 July, and assessments were made seven times during the epidemic (on 12, 15, 19, 22, 26, 30 July and 4 August at site A, and on 11, 14, 18, 21, 25, 29 July and 3 August at site B). In 2022, the plants were desiccated on 11 August 2022. In 2024, first symptoms were observed on 10 June, and assessments were made eight times during the epidemic (on 19, 22, 24, 26, 28 June and 1, 4, 7 July). In 2024, the plants were desiccated on 9 July. In all cases, desiccation was necessary because of the legal limit to blight severity in the field (De Minister van Landbouw, Natuur en Voedselkwaliteit, 2021).

Finally, in all years, a few days before haulm killing (i.e. destruction of the potato foliage (haulm) prior to harvest), the remaining green leaf area cover (%) was assessed across the entire area of each potato plot. Per meter length within a potato row, a score was given from 1 to 5, whereby 1 represents 0-10% green soil cover, 2 = 10-50 % green, 3 = 50-90 % green, 4 = 90-99 % green, and 5 = between 99-100% green soil cover (hence note that the numbers inversely indicate percentage diseased leaf area).

3.2.3 Potato yield

Within each strip-crop plot, potato tubers were harvested from two 1.5 m-long sections in each of the three strips. Thus, per plot 27 m^2 area was harvested (3 x 2 x 1.5 x 3 m^2). Tubers were harvested separately for each of the four rows in a strip to quantify border row effects reflecting competition with the companion species (e.g. Gou et al., 2016; Zhang et al., 2007). Likewise, in the monoculture treatment, potatoes were harvested from six 1.5 m-long sections of 4 rows each, also representing a harvest area of 27 m^2 per plot. Fresh weight was converted to tons per hectare potato area (t ha^{-1}) to make the yields in the sole crop and strip crops directly comparable.

3.2.4 Data analysis

A suite of analysis methods was used to analyse the effects of treatments on disease severity, average disease severity over the observation period, green leaf area cover, and yield. The experimental data from the three years, and two sites in 2022, were analysed together as four site-years (4 levels, 2021, 2022 site A, 2022 site B, and 2024). Furthermore, differences between inner and outer rows of the strips were analysed within treatments. Inner rows are those that have only potato rows as direct neighbours whereas outer rows are those bordering the companion species.

The choice of method was determined by the type and distribution of the data and the way observations were made, taking into account nested observations by using the appropriate random effects (for fitted models see below; Table 3.1). Models were fitted in R (R Core Team, 2022).

Disease severity

The increase in proportion disease severity (*x(t),* severity/100) over time was analysed using a beta regression, using the day of the first assessment as t=0 (model 1 and 2, Table 3.1). To account for the nested structure and the distribution of the data, we used a generalized linear mixed model (GLMM), using the package glmmTMB (Bolker, 2016; Magnusson et al., 2017). We used as random effects site-year, plot, strip and transect (i.e. assessment location within the strip), with transect nested in strip, strip nested in plot, and plot nested in site-year. With these models, we estimate the parameters of the logistic function $x(t) = \frac{1}{1+\left(\frac{1}{x_0}-1\right)*exp(-r*t)}$, with x_0 the proportion disease severity at the first assessment day, and r the apparent infection rate (i.e. the relative rate of increase in proportion disease severity, day^{-1}). A beta distribution with a logit link was applied to the proportion of the severity data (Table 3.1). To avoid fitting a beta distribution model to data with zeros (which results in singularities) the observed proportions were linearly transformed according to Maier (2014) and Douma & Weedon (2019):

$$p* = \frac{p(n-1)\ +\ \frac{1}{2}}{n}$$

with p being the observed proportions of disease severity, $p*$ the transformed proportions and n the total number of observations.

As an additional analysis of the late blight epidemic, we calculated the average severity over the measurement period by dividing the area under the disease progress curve (AUDPC) by the duration of the observation period in each year. This metric is also called the standardized AUDPC (sAUDPC; Campbell and Madden, 1990). The period from the first assessment date to the last (in 2022 until the epidemic halted) was taken, resulting in an observation period of 9 days in 2021, 11 days in 2022, and 18 days in 2024. Similar to the analysis of disease severity, a GLMM with beta distribution (with logit link), and a nested random effect was applied to the sAUDPC data (model 3, Table 3.1).

Green leaf area cover

Final green leaf cover was classified into five classes of cover (see above). The resulting categorical data were analysed using a multinomial mixed-effect logit model.

This analysis shows whether a specific green-cover class was more often scored in one treatment compared to another. For this purpose, the function multinom in the R package nnet was used (Ripley and Venables, 2022). The four site-year combinations were analysed in one model, with the interaction of site-year and treatment as predictor (model 4, Table 3.1). Plot and strip were defined as random effects, with strip nested in plot. Additionally, we tested whether a shift in the distribution of green cover classes between treatments could be detected by assigning each class a representative value, which was the midpoint of the corresponding percentage range (resulting in class 1 = 5%, class 2 = 30%, class 3 = 70%, class 4 = 94.5%, and class 5 = 99.5%). These midpoint values were analysed using a beta regression, including plot as random effect (model 5, Table 3.1). To account for heteroscedasticity, '*Treatment*' and '*Site_Year*' were added in the *dispformula* argument of the glmmTMB function (Brooks et al., 2017).

Yield

Yield data were analysed with ordinary regression using normal error distribution (models 6, 7, 8, Table 3.1). Similar to the analysis of disease severity, a nested random effect was added. The normal error assumption was checked by plotting the distribution of residuals. In 2022, the potatoes were harvested at the same location as where the disease assessments were made. For this year, we determined the correlation between proportion disease severity at the last assessment date before haulm killing and yield (model 9, Table 3.1).

The goodness of the fit of the GLMM to the disease severity assessments (model 1, Table 3.1) was checked visually. To assess the goodness of the fitted error model, data were generated based on the estimated model parameters (including the θ of the beta distribution), and these generated data were compared to the observations (see Supplementary information Method S3.4 for more information). Using a Gompertz distribution for fitting the GLMM did not improve the model fit in terms of AIC, nor did it affect the conclusions about the significant differences between treatments in their estimates. Hence the model with the beta distribution was chosen.

Table 3.1 Summary of the fitted models to the data. Model 3 is a multinomial mixed effect model, all others are generalized linear mixed models. + means additive effects are assumed, while * means main effects and interactions are estimated. A slash / before a random effect means that it is nested in the preceding random effect to the left of it.

Model #	Response variable	Distribution	Link function	Predictors	Random effects	Dispersion parameter
1	Disease severity	Beta	logit	Treatment * Year * DAFA	Site-year/ plot/strip/ transect	
2	Disease severity in each strip-crop	Beta	logit	Row * Year * DAFA	Site-year/ plot/strip/ transect	
3	sAUDPC	Beta	logit	Treatment + Year	Site-year/ plot/strip/ transect	
4	Green leaf area cover scores	Multinomial	Multinomial logit	Treatment * Site_Year	Plot/strip	
5	Midpoint green leaf classes	Beta	logit	Treatment + Site_Year	Plot	Treatment + Site_Year
6	Yield	Gaussian	-	Treatment * Year	Site-year/ plot/strip/ transect	
7	Yield in the strip-crop with grass	Gaussian	-	Row + Year	Site-year/ plot/strip/ transect	
8	Yield in the strip-crop with maize or faba bean	Gaussian	-	Row * Year	Site-year/ plot/strip/ transect	
9	Yield	Gaussian	-	Disease severity * Treatment	Site-year/ plot/strip/ transect	

Note: *Treatment* in models 1, 3, 4, 5 and 9 is a categorical variable with four levels; monoculture, strip-crop with grass, strip-crop with maize, and strip-crop with faba bean. *Row* represents the position of the rows within the strip, and has two levels, inner and outer (i.e. those in direct contact only with other potato plants, or with both potato and the companion crop). *DAFA* is the time at which disease assessments were made, in days after the first assessment. *Year* is a categorical variable with three levels, 2021, 2022, and 2024.

3.3 Results

3.3.1 Disease severity

2021

The wet conditions in the Netherlands in the summer of 2021 were ideal for the spread of *P. infestans*. Therefore the epidemic during this year spread fast in the potato monoculture, from not diseased on 8 July to on average 50% disease severity on 17 July, i.e. in less than 10 days (Fig. 3.3A). On the last assessment day, average disease severity was the lowest in the potatoes that were strip-cropped with grass (23%, 95% confidence interval (CI) [10, 45]), and highest in the potato monoculture (50%, 95% CI [24, 76]). While the difference was not significant in 2021, it was similar in magnitude and direction to the significant difference found in 2022 and 2024 (see below). Strip cropping potato with maize resulted in a disease severity of 35% (95% CI [16, 60]) that was intermediate between the potato-grass and potato monoculture and not significantly different from either. There was substantial variation in disease severity between the two replicates of the grass strip-crop treatment in 2021. One plot had on average only 8% disease severity whereas the other had 48% severity on the last measuring day (Fig. 3.3A).

2022

In the dry and warm summer of 2022, *P. infestans* did not spread as fast as in the wetter summer of 2021. The epidemic progress was halted around 19 July, when the weather was very hot with maximum temperatures reaching up to 36.6 °C, effectively killing all foliar lesions. After that, the disease did not develop much further, and we therefore present data until this point. The full time series is provided in Supplementary information Fig. S3.6. Similar to 2021, average disease severity was lowest in the potatoes strip-cropped with grass before the epidemic halted (13% (95% CI [10, 17]) at site A and 15% (95% CI [12, 18]) at site B), which was significantly lower than potato monoculture (23% (95% CI [17, 30]) at site A and 44% (95% CI [38, 49]) at site B) (Fig. 3.3B and C). Maize as a companion crop suppressed potato late blight to a similar extent as grass at both sites (Fig. 3.3).

At site A, the faba bean did not establish well, presumably due to a soil-borne disease. There was no significant difference in disease severity between the potato strip-cropped with faba bean and sole potato at this site (Fig. 3.3B). At the other site, faba bean grew normally, and strip cropping with faba bean at site B suppressed potato late blight to a similar extent as maize did (disease severity of 19% (95% CI [16, 23]) at the last assessment day) (Fig. 3.3C).

2024

In 2024, the first symptoms of *P. infestans* occurred very early; only 28 days after planting the first symptoms were observed in the field. Similar to the previous two years, average disease severity was lowest in the potatoes strip-cropped with grass (Fig 3.3D). On the last assessment day, average disease severity in the potatoes strip-cropped with grass was 5% (95% CI [3, 7]), which was significantly lower than the potato monoculture (12%, 95% CI [8, 16]). The potatoes strip-cropped with maize and faba bean had similar disease severities as the monoculture (12%, 95% CI [8, 17] and 15% (95% CI [11, 20], respectively).

No significant difference in disease severity was found between the inner and outer rows of the strip (i.e. those in direct contact only with other potato plants, or with the companion crop species). This applied to all strip-crop treatments in all years.

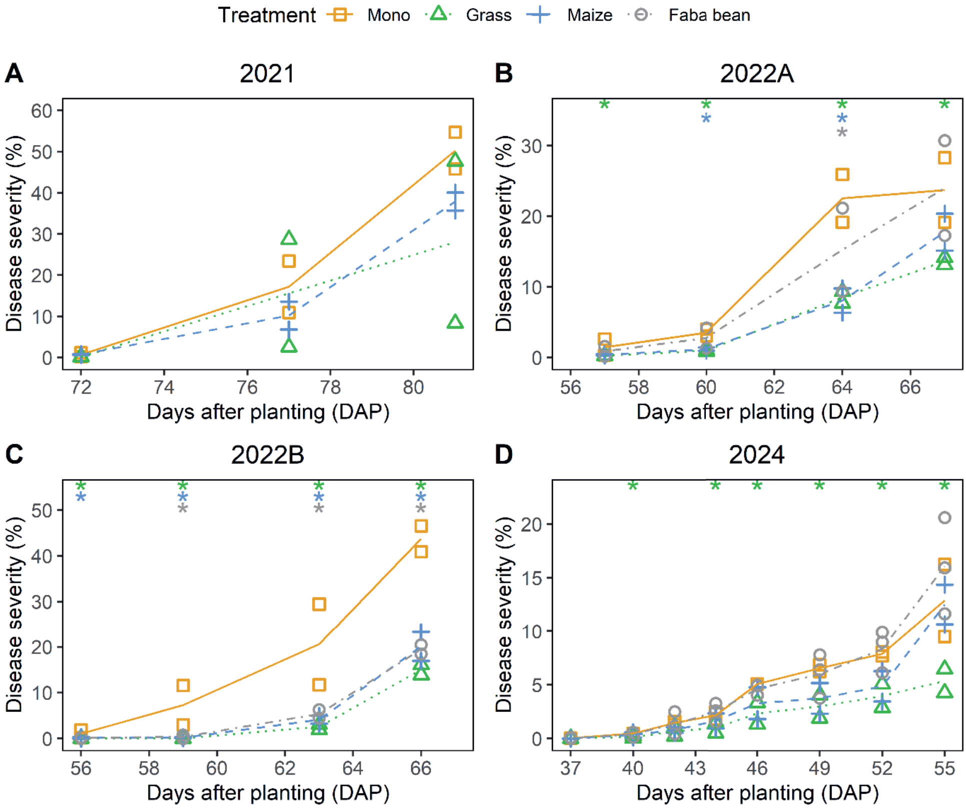

Fig. 3.3 Disease progress curves for potato late blight on potato in 2021 (A), 2022 at site A (B) and site B (C), and 2024 (D). The points (symbols) represent the mean disease severity per plot based on visual observations on 36 (A), or 24 (B, C and D) plants per plot. The lines are drawn between the midpoints of the two plots for each treatment. ☐ = potato monoculture; △ = potato strip-cropped with grass; + = potato strip-cropped with maize; ○ = potato strip-cropped with faba bean. Stars indicate a significant difference between the strip-crop and the monoculture on a given day; top asterisk (green) for the strip-crop with grass, middle asterisk (blue) for the strip-crop with maize, and lowest asterisk (gray) for the strip-crop with faba bean.

Disease progress

In 2021, the apparent infection rate (measured as the relative rate of increase in disease severity, *r* in Table 3.2) was significantly lower in potatoes grown with grass or maize than in the monoculture ((P=0.02 and P<0.0001, respectively), Table 3.2, Fig. 3.4). In 2022, the apparent infection rates in the three strip-crop treatments were not significantly different from that in the monoculture. Nevertheless, because of a lower initial disease severity, the severity remained lower in the strip-crops compared with the monoculture over the growing season (Fig. 3.4B). As in 2021, in 2024 the apparent infection rate was significantly lower in the potatoes strip-cropped with grass than in the monoculture ($P<0.001$). The apparent infection rate was not significantly different between the strip-crop with maize and the monoculture, while potatoes strip-cropped with faba bean had a significantly higher apparent infection rate than the monoculture ($P=0.002$).

The average proportion severity over the observation period (sAUDPC) was highest in the potato monoculture (0.105), followed by bean (0.072), maize (0.053) and grass (0.040). The sAUDPC of the strip-crop with grass or the strip-crop with maize was significantly lower than the monoculture ($P<0.001$ for both cases) across the three years (Table 3.2), but the faba-bean strip crop was not significantly different from the monoculture ($P=0.067$). There was no significant difference in sAUDPC between the strip-crop with grass and maize, or between the strip-crop with maize and faba bean. The strip-crop with grass had a significantly lower sAUDPC than the strip-crop with faba bean ($P=0.006$).

Table 3.2. Summary of estimated parameters for logistic fits[a] with beta regression to disease progress curves for the proportion disease severity of potato late blight of potatoes grown in monoculture (Mono), or strip-cropped with grass, maize or faba bean for the 2021, 2022 and 2024 growing season. And the estimated sAUDPC for each treatment across the three years.

Treatment	2021		2022		2024		
	x_0	r	x_0	r	x_0	r	sAUDPC
Mono potato	0.008± 0.28ab	0.543± 0.011a	0.011± 0.21b	0.371± 0.007c	0.007± 0.29ab	0.171± 0.006d	0.105 ± 0.16a
Strip-crop potato-grass	0.004± 0.28ab	.506± 0.012b	0.003± 0.22a	0.372± 0.010c	0.005± 0.29ab	0.143± 0.007f	0.040 ± 0.15c
Strip-crop potato-maize	0.007± 0.28ab	0.476± 0.012b	0.004± 0.22a	0.392± 0.010c	0.005± 0.29ab	0.182± 0.006de	0.053 ± 0.15bc
Strip-crop potato-faba bean	-	-	0.005± 0.21ab	0.377± 0.009c	0.006± 0.24ab	0.194± 0.005e	0.072 ± 0.17ab

[a] Logistic function $x(t) = \frac{1}{1+\left(\frac{1}{x_0}-1\right)*exp(-r*t)}$, with x_0 the proportion of disease severity at the first assessment day, and *r* the apparent infection rate (day^{-1}). Letters indicate significant differences for each parameter at $P < 0.05$.

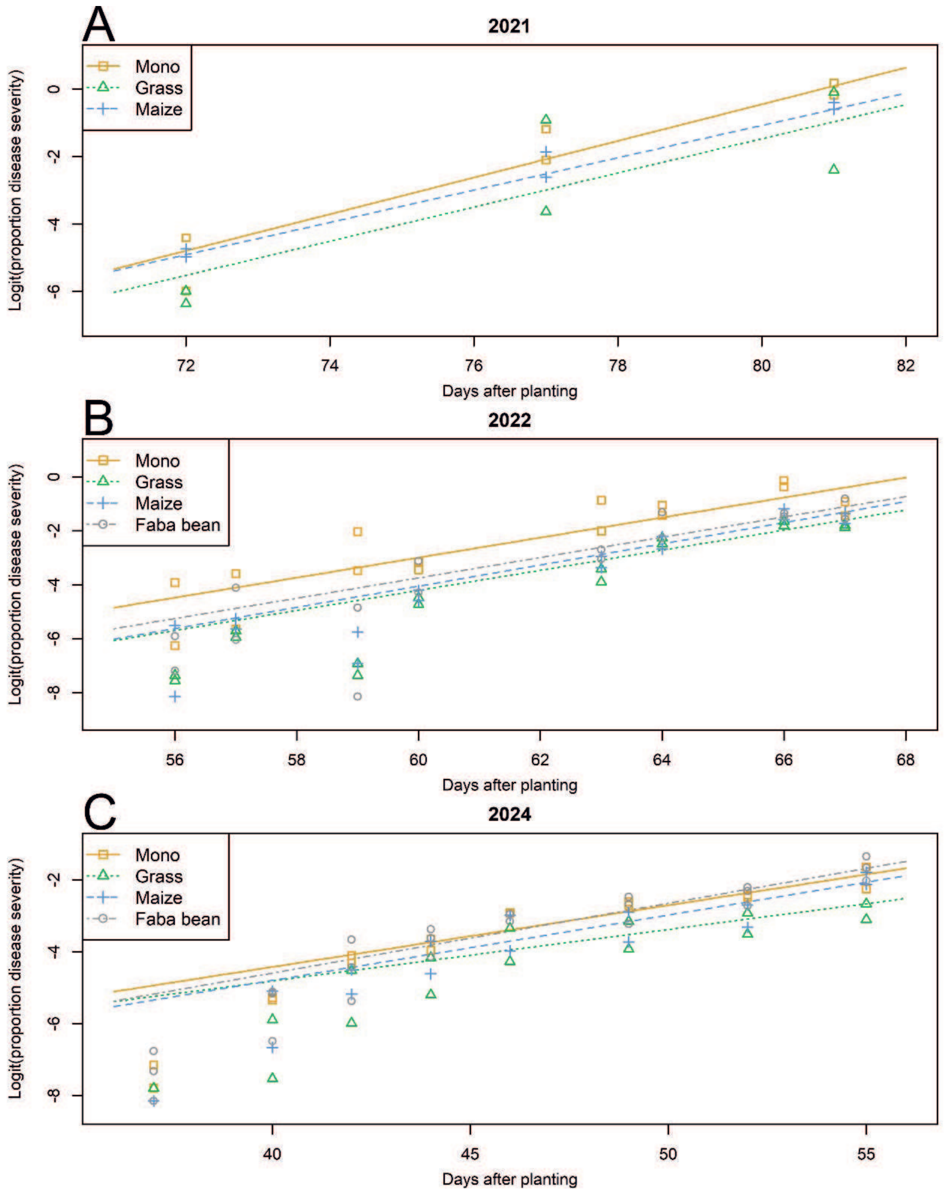

Fig. 3.4 Estimated logistic disease progress curves for proportion disease severity (plotted on logit scale) during the 2021 (A), 2022 (B) and 2024 (C) growing season for potatoes grown as monoculture (Mono), or as strip-crops with grass, maize, or faba bean. The points (symbols) represent the mean observed proportion leaf area diseased per experimental plot.

Delay in disease progress

From the logistic fits, we calculated the difference in time (in days) that potatoes in strip crops or monoculture reached given proportions of disease severity (Fig. 3.5). In 2021, the grass strip-crop system reached a severity of 10% approximately 1.8 days later than the monoculture (Fig. 3.5A). For this disease level, the strip-crop with maize had a delay of approximately 0.9 days compared with the monoculture. In 2022, the delays were longer; potatoes strip-cropped with grass, maize or faba bean reached 10% severity approximately 3.2, 2.6 and 1.9 days later, respectively, than the monoculture (Fig. 3.5B). In 2024, the delay was even longer for potato strip cropped with grass (5.3 days to reach 10% severity), but the strip-crop with maize or faba bean were less effective (1.2 days delay and 0.6 day advance, respectively) (Fig. 3.5C).

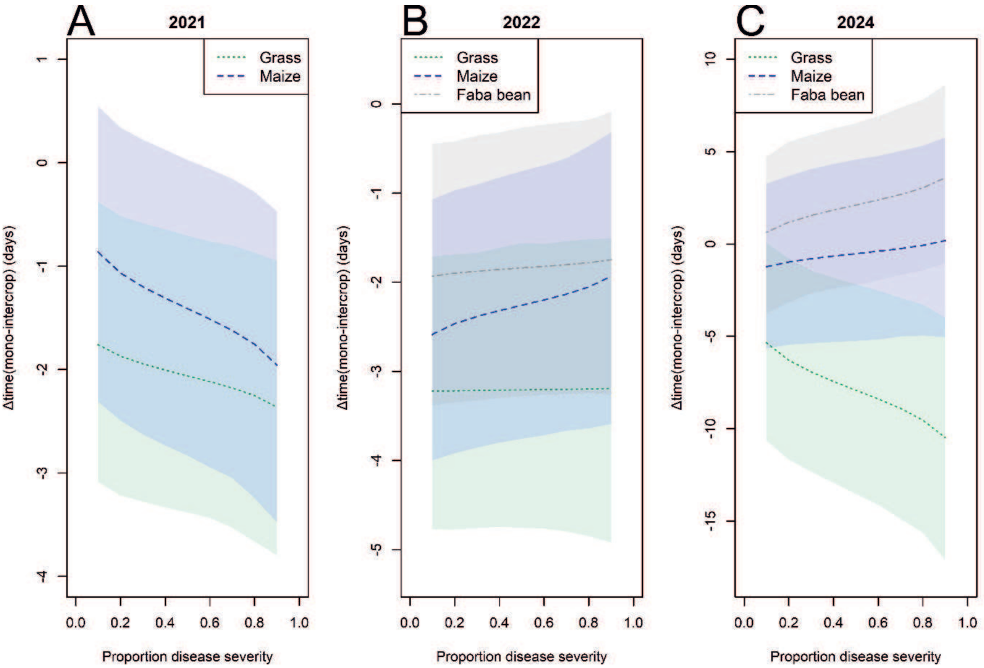

Fig. 3.5 Estimation of the time difference (in days) between the strip-crop system with grass or maize and the monoculture to reach a proportion disease severity, for the 2021 (A), 2022 (B) and 2024 (C) growing season. Estimation was done using the fitted disease progress curves of potato late blight (Fig. 3.4). The coloured bands around the dotted lines represent the 2.5% and 97.5% quantiles, which represent the uncertainty in the delay due to uncertainty in the estimates of x_0 and r (Table 3.2) (see Supplementary information Method S3.5 for more information).

3.3.2 Green leaf cover before crop termination

We made an assessment of the green leaf cover over the whole plot area at the time of haulm killing, and assessed differences between treatments within each scoring class. The results are in line with the results from the analysis of disease severity. In 2021, lower greenness classes, 1 (0-10% green) and 2 (10-50% green), were significantly more frequently observed in the potato monoculture than in the potatoes strip-cropped with grass or maize (Fig. 3.6A) (P < 0.001 for all class comparisons). This indicates that the monoculture canopy was the least green out of the three treatments. Potatoes that were strip-cropped with grass on the other hand had mostly scores in class 3, 4 and 5, indicating that potatoes strip-cropped with grass had more green leaf cover than potato monocultures.

Likewise, in 2022, potatoes grown in monoculture were mostly scored in the lower greenness classes. The monoculture had a significantly greater proportion of scorings in class 1 than the other treatments at site B, and in class 2 at both sites (Fig. 3.6B and C) (P < 0.01 for all comparisons). Potatoes strip-cropped with grass were significantly more frequently scored in class 4 (90-99% green) than the other treatments at site A (Fig. 3.6B) and class 4 and 5 at site B (Fig. 3.6C).

In 2024, potatoes strip-cropped with either grass or maize had a significantly higher frequency of scores in class 3 and 4 than the monoculture (P < 0.001 for all comparisons). The monoculture and strip crop with faba bean were more often scored in class 1 or 2 (Fig. 3.6D). Potatoes strip-cropped with faba bean had a similar green leaf cover as the monoculture indicating this treatment had not controlled late blight.

Analysis of the shift in the distribution of all five greenness classes between treatments confirmed that strip cropping with grass significantly shifted towards the higher greenness classes compared with the monoculture across the three years (P < 0.001). In the strip-crop with maize, the distribution was marginally shifted towards the greener classes compared with the monoculture (P = 0.06) The strip-crop with faba bean did not significant shift the distribution (P =0.34).

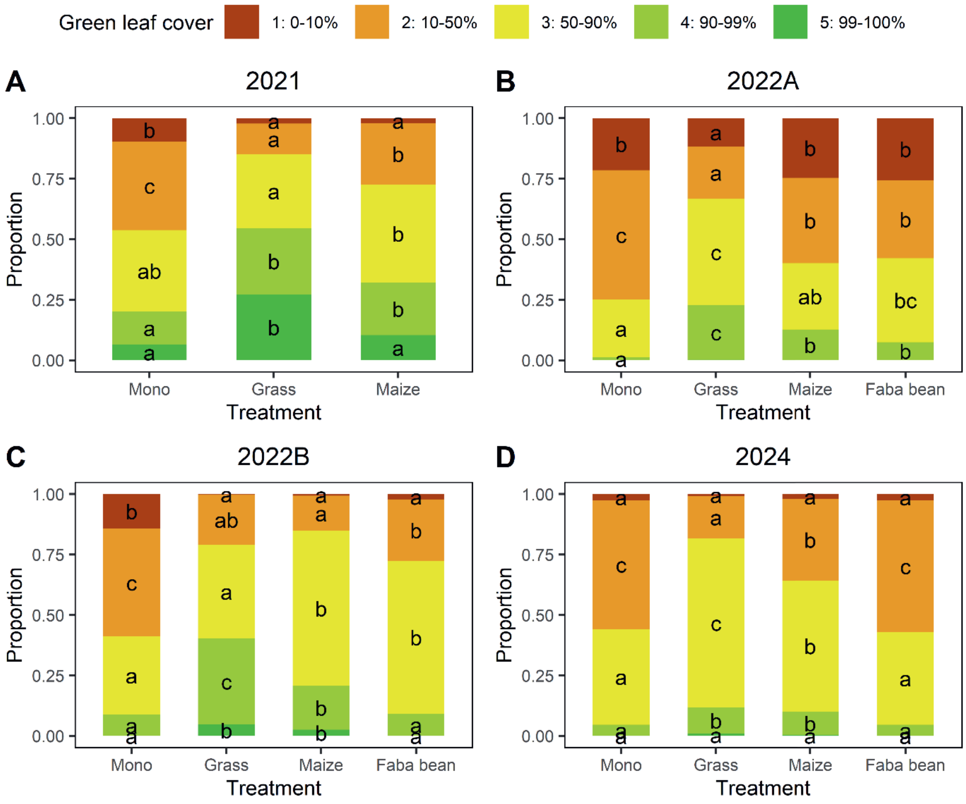

Fig. 3.6 Green leaf cover scorings of potatoes infected with potato late blight in 2021 (A), 2022 site A (B), and B (C), and 2024 (D). Potatoes were either grown in monoculture (Mono), strip-cropped with grass (Grass), strip-cropped with maize (Maize), or strip-cropped with faba bean (Faba bean). Every one meter in each potato row was given a score from 1 to 5, whereby 1 = 0-10% green leaf cover, 2 = 10-50 % green, 3 = 50-90 % green, 4 = 90-99 % green, and 5 = between 99-100% green leaf cover. Letters indicate significant differences between treatments within each scoring class for each year at P < 0.05. These letters can be used to interpret the shift in green leaf cover between treatments.

3.3.3 Tuber yield

The rapid progression of late blight in 2021, and the early onset of late blight in 2024, shortened the growth duration of potato substantially, which is apparent in the lower yields in these years as compared with 2022 (Fig. 3.7A). In 2021 and 2022 potatoes strip-cropped with grass had significantly higher yields per unit potato area (25.9 t ha^{-1} potato area in 2021 and 38.9 t ha^{-1} potato area in 2022) than potatoes grown in monoculture (19.8 and 29.2 t ha^{-1}) (P=0.039 in 2021, and P<0.001 in 2022). In 2024, no significant difference between treatments was found. The maize strip-crop treatment had a similar yield as the monoculture across the three years (Fig. 3.7A). In 2022, potatoes strip-cropped with faba bean (34.3 t ha^{-1}) had a significantly higher yield than potatoes grown in monoculture (P=0.014), but in 2024 no differences were found.

The outer rows of the potato strips strip-cropped with grass had on average 1.8 t ha^{-1} higher yield (P=0.02) than the inner rows across the three years (Fig. 3.7B). For the strip-crop with maize an interaction with year was found. The outer rows had on average 3.4 t ha^{-1} higher yield than the inner rows (P=0.02) in 2021. However, in 2022 and 2024 this was reversed, and the inner rows produced on average 2.9 and 2.4 t ha^{-1} higher yield than the outer rows, respectively (P<0.001 in both cases). The outer rows of the potato strips strip-cropped with faba bean tended to yield slightly higher than the inner rows in 2022 (p=0.06), and tended to yield lower in 2024 (P=0.053) (Fig. 3.7B).

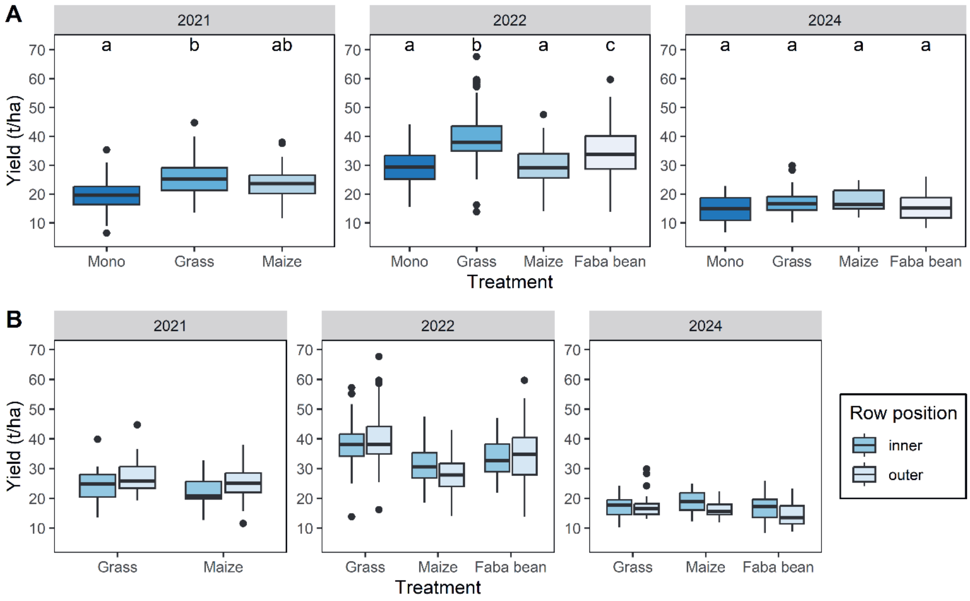

Fig. 3.7 (A) Tuber yield (t ha^{-1}) per area of the potato crop either grown in monoculture (Mono), or strip-cropped with grass, maize or faba bean, for the 2021, 2022 and 2024 growing season. Letters indicate significant differences between treatments for each year at P < 0.05. (B) Differences in potato yield between inner and outer rows of potato strips in strip cropping treatments.

The yield loss relationship between proportion disease severity and total tuber yield was analysed for the 2022 growing season (Fig. 3.8). Slopes of the relationship for monoculture and potato/maize strip cropping were both negative, -17.0 and -35.8 t ha^{-1} yield per unit disease severity, respectively, both significantly different from zero, but not significantly different from each other. No significant relationship was found between disease and yield for the strip-crop with grass or the strip-crop with faba bean.

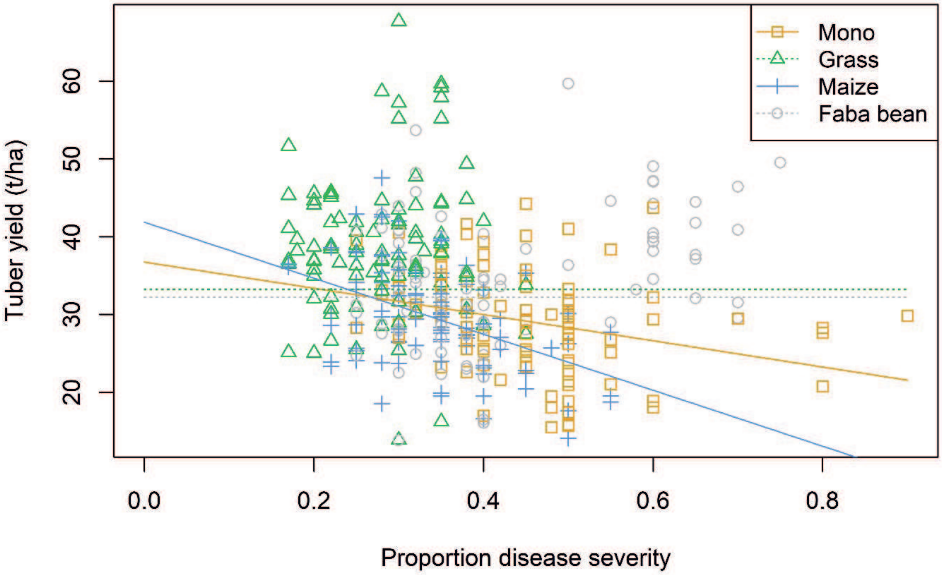

Fig. 3.8 Regression of proportion disease severity of potato late blight at the last assessment date and tuber yield (t ha^{-1}) in potatoes planted in monoculture (Mono, regression slope p-value = 0.03), or strip-cropped with either grass (regression slope p-value = 0.19) or maize (p-value = 0.001) or faba bean (p-value = 0.64) during the 2022 growing season. Points represent each assessment (24 locations per plot). □ = potato monoculture; △ = potato strip-cropped with grass; + = potato strip-cropped with maize; ○ = potato strip-cropped with faba bean.

3.4 Discussion

3.4.1 Epidemic progress

The main objective of this study was to investigate the effect of strip cropping potato with different companion crop species on epidemic development of *P. infestans*. Three companion crop species, contrasting in stature, were strip-cropped with potato: grass, faba bean or maize. Disease intensity was measured in various ways, and although there was some variation across the three years, together these metrics confirm the disease-suppressive effect of strip cropping with either grass or maize (Table 3.3). Overall, strip cropping with grass or maize lowered the average severity during the observation period (sAUDPC) across three years, slowed down the epidemic progress (for both grass and maize in 2021, and for grass in 2024) and lowered disease severity at the last assessment day (for both grass and maize in 2022, and for grass in 2024) compared with potatoes grown in monoculture. Furthermore, in each of the three years, the potatoes strip-cropped with grass or maize had more green leaf cover remaining at haulm killing than the monoculture. Out of the three companion crop species, grass was the most effective at suppressing potato late blight (Table 3.3). Although potatoes strip-cropped with maize had similarly low disease severity as those strip-cropped with grass, the strip-crop with maize had less green leaf cover remaining at haulm killing than the strip-crop with grass in 2021 and 2022.

Table 3.3 Summary of the performance of the strip-crop with either grass or maize, compared with the potato monoculture, using different metrics for determining disease intensity. All comparisons are significant, if the comparison was not significant in a specific year, this is indicated by *ns*.

Metric	Reference in text	Strip-crop potato-grass	Strip-crop potato-maize	Strip-crop potato-faba bean
sAUDPC	Table 3.2	Lower (0.040) than the monoculture (0.105), across three years	Lower (0.053) than the monoculture (0.105), across three years	Not significantly different
Apparent infection rate (*r*)	Table 3.2, Fig. 3.4	2021: Lower (0.506 day^{-1}) than the monoculture (0.543 day^{-1}) (7% reduction) 2022: *ns* 2024: Lower (0.143 day^{-1}) than the monoculture (0.171 day^{-1}) (16% reduction)	2021: lower (0.476 day^{-1}) than the monoculture (0.543 day^{-1}) (12% reduction) 2022: *ns* 2024: *ns*	2022: *ns* 2024: Higher than the monoculture
Initial disease severity (x_0)	Table 3.2, Fig. 3.4	2021 and 2024: *ns* 2022: lower	2021 and 2024: *ns* 2022: lower	2022 and 2024: *ns*

Final disease severity	Fig. 3.3	2021: *ns* 2022: lower at both locations (severity of 13-15%), compared with the monoculture (23-44%) (reduction of 42-66%) 2024: lower (5%) compared with monoculture (12%) (reduction of 58%)	2021 and 2024: *ns* 2022: lower at both locations (18-20%), compared with the monoculture (23-44%) (reduction of 25-54%)	2022: lower at one location 2024: *ns*
Green leaf cover	Fig. 3.6	2021, 2022 and 2024: significantly more green leaf cover remaining at haulm killing than the monoculture	2021, 2022 and 2024: intermediate levels of green leaf cover; marginally more green than monoculture	2022: intermediate levels of green leaf cover, more green than monoculture 2024: comparable green leaf cover as monoculture

Strip-cropping with faba bean was not consistent at suppressing late blight compared with strip-cropping with the other companion crops. In 2022 at site A and in 2024, this strip cropping treatment had comparable levels of disease severity as the potato monoculture. Faba bean reaches tall stature relatively early in the season especially compared to maize. This could lead to an increased humidity in the potato strips next to faba bean. At the same time, the faba bean canopy might not be tall enough to form a barrier for spore influx into the canopy from outside or spore dispersal between potato strips. This suggests that both final stature and the temporal height growth dynamic of a companion may influence its effectiveness in suppressing late blight. Since the strip-crop treatments with grass or maize reduced late blight severity to a similar extent (i.e., being not significantly different from each other), a reduced density of potatoes, increased spatial distance between potato strips leading to a loss of spores to the companion crop canopy seems like an important mechanisms behind this reduction.

The weather and disease conditions during the three years were very contrasting; in 2021 the epidemic started at the usual time in the Netherlands, but progressed fast due to the humid conditions (74% relative humidity and 191 mm of rain during June and July). In 2022 the epidemic started at the same time as in 2021, but went fairly slow because of lower humidity (66% relative humidity and 129 mm of rain during June and July). In 2024, weather conditions were intermediate (77% relative humidity and 157 mm of rain during June and July), but there was a very early onset of late blight. The experiments were conducted across four site-years with limited replicates of each treatment in each site-year due to the large plot size (21x24m). While this could be seen as a concern, under the mentioned contrasting conditions, the findings were consistent. Strip cropping with grass or maize consistently suppressed potato late blight, with grass as a companion crop species showing slightly higher efficacy in all years, as seen in the strip-crop with grass maintaining more green leaf cover at the time of haulm killing than the strip-crop with maize or bean. Additionally, the relatively large experimental plots likely played a role in mitigating interplot interference and increased independence between plots. Our strip-crops hence significantly reduced potato late blight compared with the monoculture, underscoring the sufficient statistical power of the experimental design, despite the limited number of replicates.

The relative contribution of different mechanism behind the observed disease suppression of strip-crops likely varied given the differences in weather conditions. During the favourable conditions of 2021 (prevalence of humid weather conditions), strip cropping significantly lowered the apparent infection rate (Table 3.2). This could indicate that under conducive weather conditions (such as those in 2021), the suppressive effect of strip cropping is mostly mediated by its modification of the microclimate, i.e., making it less conducive to disease spread. Conversely, in 2022, when the weather was much drier, strip cropping appeared to have a more pronounced effect on reducing the initial inoculum load. In all years the dilution effect will have additionally contributed. Thus, strip cropping appears to be able to lower disease severity under varying weather conditions.

In a previous study, Ditzler *et al.* (2021) also found that *P. infestans* severity was significantly lower in potato-grass strip-crops than in potato monoculture. They also showed that narrower strips of potato (from 48m width down to 3m width) tended to have lower apparent infection rates compared with wider strips. Bouws & Finckh (2008) strip-cropped potato with either spring wheat or a grass-clover mix. They found 4 –

20% reductions in foliar late blight severity in the strip-crop compared with pure stands of potato, i.e. lower reductions than in our experiments (between 52 and 62%). One explanation for this difference in disease suppression could be the width of the strips; in our experiment, we used strips of three meters, whereas Bouws & Finckh (2008) used strips of six meters. This is in accordance with the results from Ditzler *et al.* (2021), who showed that narrower strips reduce disease more than wider ones. The disease-suppressive effect of strip cropping might thus be even larger with strips smaller than 3 meter width.

Not only is there variation in the efficacy of strip cropping in reducing potato late blight between experiments, but there are also substantial differences between experimental plots of the same treatment within a site. For instance, in 2021, one of the grass strip-crop experimental plots had an extremely low disease severity (8%) at the end of the epidemic, whereas the other experimental plot reached similar levels as the monoculture (48%) (Fig. 3.2A). Potato late blight epidemics usually start focal (resulting from an initial spot infection, e.g. volunteer tubers or incoming spores from outside the trial e.g. from waste piles or volunteer potatoes) (Dong and Zhou, 2022). There is randomness in where the first spores land, and the location of this focal point can greatly influence the disease severity; if a focal point is in an assessment location within an experimental plot, this plot will have a higher disease severity than when the focal point is not in an assessment location. Due to this focal characteristic of the disease, the efficacy of strip cropping in reducing late blight might be variable, even with the same companion crop species or strip width, although it is expected that when strip cropping is employed on large fields, these patch effects will even out.

3.4.2 Yield

In practice, it is not realistic to consider epidemics up to 100% disease severity; crops are terminated when severity reaches a certain threshold. In the case of potato late blight, this is done especially to reduce the risk of tuber blight (Cooke et al., 2011), to protect surrounding potato fields from infection, and to limit prolonged production of inoculum on the foliage, which stimulates pathogen adaptation (Fry et al., 2015). It could therefore be of great importance for tuber yield if strip cropping could delay the start of the epidemic or slow down the disease progress. No clear delay in the first observation of late blight symptoms was observed in the strip-crop treatments in the field, but strip cropping with either grass or maize lowered the apparent infection rate compared with the monoculture in 2021, and lowered the initial severity in 2022. As a result, the strip-cropped potatoes reached a disease severity of 10% on average between 1 and 3 days later than potatoes grown in monoculture. In 2024, the delay was even more pronounced for potatoes strip-cropped with grass, estimated to reach 10% severity 5.3 days later than the potato monoculture. Although this number of days is a rough estimate, with some uncertainty, it indicates that farmers can potentially slightly delay the termination of their potato crop when strip-cropped. These extra days of growth could enhance the total tuber yield, since a potato canopy can produce 700 to 900 kg/ha fresh weight per day (Möller et al., 2006). A larger yield advantage might be attainable if strips can be terminated separately based on their individual disease severity. In the Netherlands, each strip is officially seen as a separate field (Rijksdienst voor Ondernemend Nederland, 2021), therefore, it is allowed to terminate each strip separately. The legal threshold for compulsory crop desiccation due to excessive late blight in the Netherlands is however quite low, around 1% severity (De Minister van Landbouw, Natuur en Voedselkwaliteit, 2021).

Nevertheless, late blight epidemics can, and often will, progress very rapidly. Despite the reduction in the apparent infection rate in the strip-crop treatments, the rate remained relatively high. The estimated few days delay in crop termination might give incentive for organic growers to adopt strip cropping practices, since they cannot use fungicides to prevent the disease. However, for conventional farmers, fungicides provide more certainty for crop protection, with longer delays in the start of the epidemic (Wiik, 2014) and thus crop termination than what can be achieved solely by strip cropping. The practice of strip cropping would need to be integrated with other control measures, which can be challenging because strip cropping can make crop management more complex (Himanen et al., 2016; Huss et al., 2022). In short, even though strip cropping can lower the apparent infection rate and disease severity, to effectively employ this practice, more work is needed to integrate this practice with other control measures.

Potatoes strip-cropped with grass yielded significantly more than both the monoculture and the maize strip-crop treatment, even though in this experiment, all treatments were terminated at the same time. Lower disease severity was observed in the grass strip-crop treatment, however, this might not be the only explanation for the higher tuber yield. Other strip crop studies showed that the more dominant crop in the mixture often overyields, especially in the border rows, whereas the less dominant crop has lower yields in border rows than outer rows (Gou et al., 2016; Li et al., 2001; Wang et al., 2020). This effect of competition probably played a major role in the observed yield increase of potato strip-cropped with grass, because grass does not strongly compete for light with potato. Additionally, it was observed that potato plants in the outer rows often took up space over the neighbouring grass, and those outer plants also yielded the most. Although maize was also able to suppress late blight severity in the neighbouring potatoes, potatoes strip-cropped with maize had approximately the same yield as the potato monoculture. Competition with maize for light likely led to no additional yield. This competition effect is visible in the different performance of the inner and outer rows of the potatoes strip strip-cropped with maize. Due to a cold spring in 2021, the maize plants grew slowly, and started to surpass the potatoes in height only around the beginning of July. The outer rows, potentially experiencing little competition from the shorter maize plants, relative to competition from potatoes in the inner rows, had higher yields than the inner rows. By contrast, during 2022, when maize surpassed the height of the potato canopy for the majority of the growing season (starting from around 20 June), the outer rows of the potato strip had lower yields than the inner rows.

To evaluate the performance of the strip-crop treatments, not only the performance of the potato crop should be evaluated, but an assessment of the productivity and profitability of the companion crop species is also required. This includes the yield (and other ecosystem service) of the companion crop species, its market value, and the costs associated with establishing and maintaining the strip of the companion crop species (e.g. nutrient input, water, labour). Since the strip of the companion crop species occupies land within the farming system, it should offer a return on the investment made. By conducting a more inclusive analysis of these aspects, a more informed choice for the companion crop species can be made.

3.4.3 Practical considerations when choosing a companion crop species

Farmers experience barriers when considering the adoption of crop diversification practices, such as strip cropping. Such barriers include the lack of practical knowledge and the lack of resources for investing in new machinery (Meynard et al., 2018; Mortensen and Smith, 2020; Revoyron et al., 2022). Farmers who grow potatoes in the Netherlands rarely grow maize as potato is an arable crop grown by arable farmers while maize is grown mostly on pig farms or cattle farms. Grass-clover, on the other hand, is often used as a break crop in arable crop rotations (Toorop et al., 2017), and can be exchanged with dairy farmers for manure (de Wit et al., 2006). Potato growers are more likely to have the knowledge and machinery for growing grass strips in between potato than maize strips. Furthermore, harvesting potatoes involves a harvester operating side-by-side with a trailer into which the harvested potatoes are deposited (Juventia et al., 2022). This means that at present the neighbouring strip needs to be driven on at the time of harvest. Since maize is not ready to be harvested before potato, due to the longer growing season of maize, having a maize strip next to potato will interfere with harvesting. However, with the development of a single row potato harvesters (Johnson and Auat Cheein, 2023), this constraint on the companion crop species would be overcome. Thus, besides the effect companion crop species can have on potato late bight, their productivity and profitability, farmers' knowledge and their available tools, as well as practical considerations need to be taken into account in the selection of a companion crop species.

3.5 Conclusion

We compared the effects of strip cropping potato with grass, maize or faba bean on natural epidemics of *P. infestans*. Strip cropping with grass or maize suppressed foliar potato late blight severity. Furthermore, strip cropping with grass led to a significantly higher tuber yield per unit potato area than achieved in monoculture, due to the low severity and low (aboveground) competition from grass. While our data is specifically about grass, these results could be transferrable to other companion crop species with similar characteristics, because underlying disease-suppressive mechanisms might work similarly with other short crops, and placing potato next to other non-competitive crops could likely lead to higher tuber yield. The outcomes of these experiments suggest that growers might want to choose a short, non-competitive companion crop species that fits into their system, to ensure both effective reduction in late blight, while enhancing yields compared with potato monoculture. However, as only half the plot area was used for growing potato, it is important to consider also the production or non-production value of the companion crop and the agronomic feasibility of strip cropping it with potato. While strip cropping can suppress epidemic development and late blight severity, it is important to recognize that it will not provide complete control of the disease. Therefore, it needs to be integrated with other effective control measures. Strip-cropping could thus be an addition to the existing disease management practices to move towards more sustainable disease management.

Acknowledgements

We would like to thank Peter van der Putten and the Unifarm staff for managing the field experiments. We also thank Zoltán Csengő, Paola Cassiano, Mary Chege and Viacheslav Shevchuk for their help with harvesting potatoes.

Supplementary material

Method S3.1 management practices

The fields were managed according to standard Dutch organic practices. We did not use any pesticides or fungicides. Weeds were controlled by tillage and hand weeding. We did not apply irrigation. Nutrients were applied as animal manure. For quantity and composition of manure, see Table S3.1. This table gives detailed information about the management practices.

Table S3.1 Details about the management of the field experiments.

	2021	**2022**	**2024**
Pre-crop	Spring wheat	Grass clover (loc A), spring barley (loc B)	Winter triticale
Application of manure	potato strips and potato monoculture: 40m^3/ha maize strips: 35m^3/ha grass strips: 25m^3/ha	potato strips and potato monoculture: 35m^3/ha maize strips: 25m^3/ha grass strips: 10m^3/ha faba bean strips: no fertilisation	potato strips and potato monoculture: 35m^3/ha maize strips: 25m^3/ha grass strips: 10m^3/ha faba bean strips: no fertilisation
Manure composition	2.6 kg N, 1.4 kg P, 2.9 kg K per ton	8 kg N, 1.7 kg P, 9.1 kg K per ton	3 kg N, 1.7 kg P per ton (amount of K not analysed)
Weed management	Potato ridges were re-hilled. Mechanical weed control was applied to the maize and faba bean strips, along with hand weeding within the row. Grass strips were mowed.		
Planting of potatoes	28 April	17 May	13 May
Haulm killing	19 July	11 August	9 July

Fig. S3.1 The arrangement of experimental plots in the field, for the three site-years. Blue strips and squares represent potato strips and monocultures, respectively. Grass strips are represented in green, maize in orange, and faba bean in pink. Plots were 21 x 24 m large and were separated by grass.

Method S3.2 wind direction

Although the prevailing wind direction in the Netherlands is from the southwest, the average wind direction during the month of June and July was variable in all three years (Fig. S3.2).

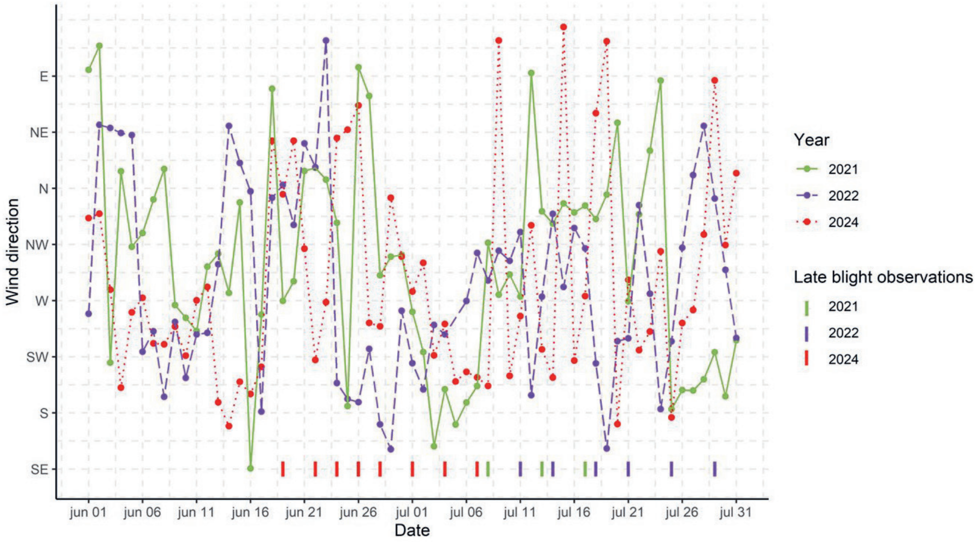

Fig. S3.2 Average daily wind direction during the month of June and July for the 2021 (green, solid), 2022 (purple, dashed) and 2024 (red, dotted) growing season. Ticks on the x-axis mark late blight observations dates (green for 2021, purple for 2022, and red for 2024). Data obtained from weather station De Veenkampen operated by Wageningen University.

Methods S3.3 relationship between the number of leaflets with lesion and percentage diseased leaf area

Late blight severity was assessed by both counting the number of leaflets with lesions per plant, and as a percentage diseased leaf area per plant, following the scheme of James (1971). When counting the number of diseased leaflets was not possible anymore due to high disease severity, only percentage diseased leaf area was recorded. Assessments based on the number of diseased leaflets were converted to percentage diseased leaf area using regression equations. These regressions were based on observations with information on both the number of diseased leaflets and percentage diseased leaf area. This appendix details the method for the conversion of the number of diseased leaflets to the percentage diseased leaf area.

Severity scorings based on the number of diseased leaflets was converted to percentage diseased leaf area using regression equation 1 for 2021, equation 2 for 2022 and equation 3 for 2024. These equations were based on scorings that had information on both the number of diseased leaflets and the percentage diseased leaf area of an assessed plant (Figure S3.3, S3.4, S3.5).

2021: percentage diseased leaf area = 0.63 * number of diseased leaflets (1)
2022: percentage diseased leaf area = 0.28 * number of diseased leaflets (2)
2024: percentage diseased leaf area = 0.30 * number of diseased leaflets (3)

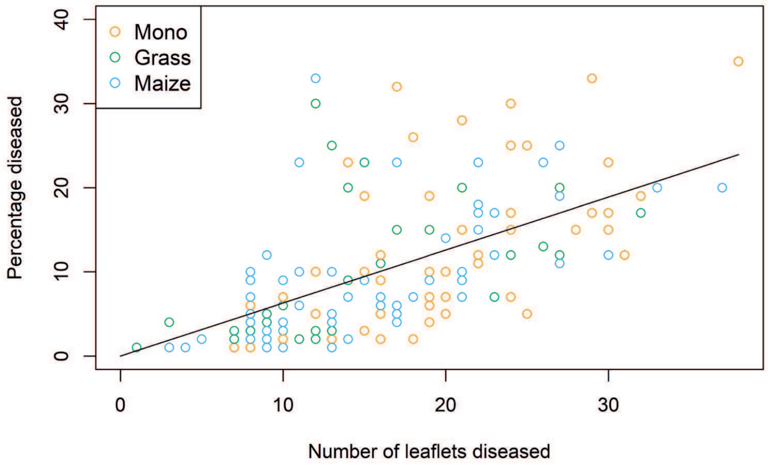

Fig. S3.3 Relationship and regression equation between the number of diseased leaflets per plant and the percentage diseased leaf area during the 2021 growing season.

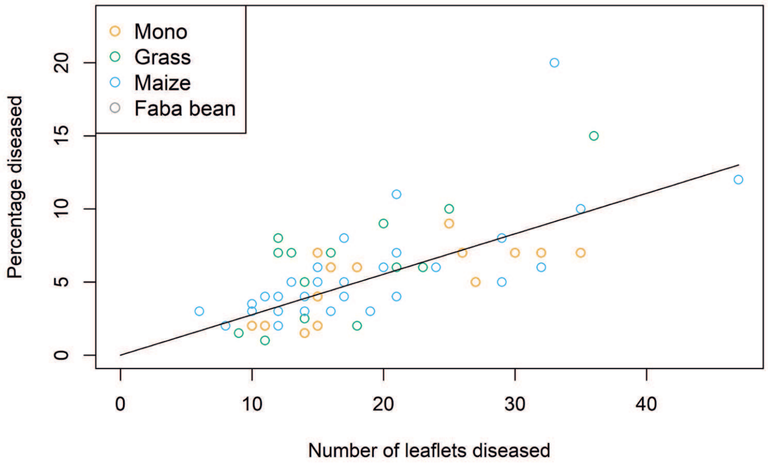

Fig. S3.4 Relationship and regression equation between the number of diseased leaflets per plant and the percentage diseased leaf area during the 2022 growing season.

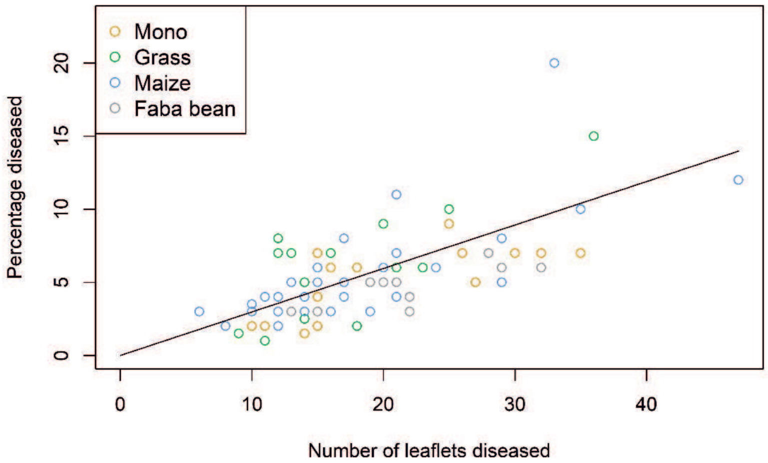

Fig. S3.5 Relationship and regression equation between the number of diseased leaflets per plant and the percentage diseased leaf area during the 2024 growing season.

Methods S3.4 validation of beta regression model

After fitting a generalized linear mixed model to the disease assessment data, the fit of the model was visually checked. The dispersion parameter (for this model 25.8) was used to calculate the shape parameters of the beta distribution (Bolker, 2008):

shape1 = $\alpha = \theta p$

shape2 = $\beta = \theta(1-p)$

with *p* being the proportion of severity based on the fitted model and θ the dispersion parameter. These shape parameters were used in the beta random number generating function (rbeta), to generate random data points based on the model. Subsequently, these generated data were visually compared to the observed field data (see Fig. S3.6 for examples).

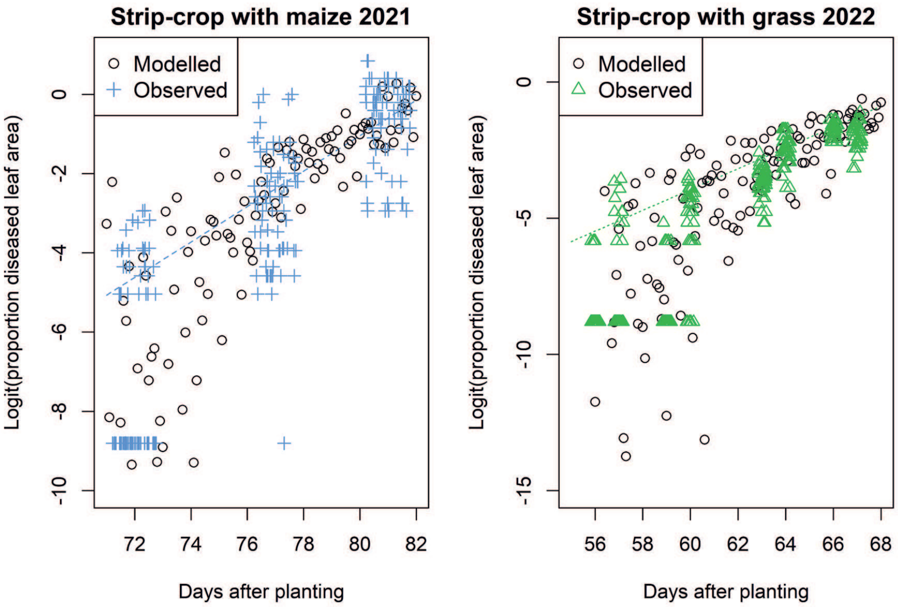

Fig. S3.6. Two examples of visual model comparison with the observed data; data from the strip-crop with maize in 2021 (left) and from the strip-crop with grass in 2022 (right). The coloured symbols are the observed proportion leaf area diseased per plant. Black circles are the modelled data based on the fitted model. Dashed lines are the estimated logistic disease progress curves for potato late blight.

Results S3.1 disease progress in 2022

The summer of 2022 was dry and warm in the Netherlands, and *P. infestans* did not spread as much as in 2021. Around 19 July (64 DAP), the epidemic progress was halted due to maximum temperatures reaching up to 36.6 °C. This appendix contains the complete assessment data over the measurement period for the two sites (Fig. S3.7).

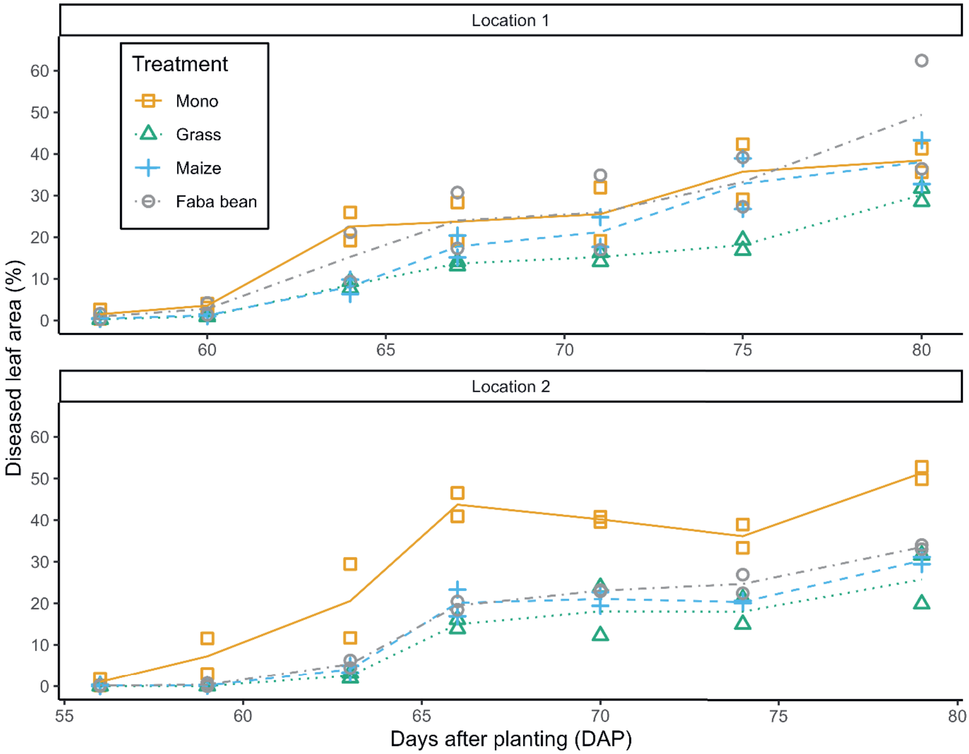

Fig. S3.7 Disease progress curves for potato late blight on potato in 2022 at site A (top) and site B (bottom). The points (symbols) represent the mean percentage diseased leaf area per plot based on 24 visual observation per plot. The lines are drawn between the mid points of the two plots for each treatment. ☐ = potato monoculture; △ = potato strip-cropped with grass; + = potato strip-cropped with maize; ○ = potato strip-cropped with faba bean.

Methods S3.5 calculating the 2 .5% and 97.5% quantiles for the delay in crop termination

We calculated the difference in the time that potatoes in strip crops or monoculture reached given levels of severity. We also calculated the 2.5% and 97.5% quantiles of this delay, based on the uncertainty in the estimates of the logistic fit (Table 3.2, main text). The model coefficients along with the variance-covariance matrix of the coefficients was used to generate plausible combinations of parameter values of x_0 and r for each treatment and year. Plausible combinations (1000) were drawn randomly from a multivariate normal distribution with the means equal to the model estimates and the variance-covariance matrix of the model coefficients (Bolker, 2008). Next, quantiles were calculated representing the uncertainty in the difference in time when a given severity level is reached.

Chapter 4

Disease-suppressive mechanisms in contrasting potato-based strip-cropping systems

Zohralyn Homulle[1], Paola Cassiano[1], Slava Shevchuk[1], Niels P.R. Anten[1], Tjeerd Jan Stomph[1], Wopke van der Werf[1], Jacob C. Douma[1]

[1]Centre for Crop Systems Analysis, Wageningen University, 6700 AK, Wageningen, the Netherlands

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Abstract

Intercropping has been shown to suppress diseases in many crop-pathogen combinations and could be a component of more sustainable integrated crop protection. While various disease-suppressive mechanisms have been proposed, how different companion species influence these mechanisms, and whether trade-offs or synergies exist between them, remains unclear. Field experiments were conducted in the Netherlands to study various disease-suppressive mechanisms affecting late blight epidemics in potato strip-cropped with contrasting companion crops (grass, faba bean, or maize). Strip cropping significantly altered the microclimate in the potato strip; relative humidity was lower in potato-grass than in the potato monoculture, whereas the humidity was increased in potato-maize, especially later in the season. Strip cropping with faba bean did not significantly change the microclimate. Furthermore, potato-maize received the lowest number of particles over the growing season (a proxy for incoming spores). Strip cropping had little to no effect on potato plant morphology or canopy structure. Grass as a companion created drier conditions in the neighbouring potato canopy making it less conducive for disease development, while maize formed a barrier for spore dispersal though it increased humidity later in the season. But the barrier strategy appears to be a less certain approach across growing seasons, as it relies on the companion crop reaching sufficient height before the epidemic begins, but the timing of the epidemic is unpredictable and may be very early. This study offers insights into how companion species with specific traits can assist disease control in strip cropping.

Keywords: strip cropping, intercropping, potato late blight, disease suppression, disease-suppressive mechanisms

4.1 Introduction

Crops are frequently exposed to biotic and abiotic stresses, which may damage them. Biotic stresses may be caused by weeds, arthropod herbivores (insects, mites), nematodes, bacteria, fungi and oomycetes. For the past sixty years, chemical biocides have been a mainstay in pest control, but these substances have negative environmental side effects (Mahmood et al., 2016; Sánchez-Bayo, 2011; Tilman et al., 2001). Biocides also pose health risks due to occupational exposure or spillover of pesticides to residential areas (European Environment Agency, 2023; Navarro et al., 2023; Ottenbros et al., 2023). Additionally, development of resistance to biocides negatively affects their efficiency over time (Fones et al., 2020; Gould et al., 2018). Future cropping systems need to be more resilient against pests and diseases while using fewer, or at least different and less environmentally harmful, pesticides than is currently allowed (Bryson, 2022; European Commission, 2020). Therefore, there is a need to explore ecologically-based control options that are sustainable in the long run. Intercropping (the practice of growing multiple crop species in the same field at the same time) could be an interesting component of integrated crop protection, as numerous studies have confirmed its disease-suppressive potential (Boudreau, 2013; Stomph et al., 2020; van der Werf & Bianchi, 2022).

Mechanisms contributing to disease suppression in intercrop systems include the companion species acting as a barrier for the dispersal of disease propagules (hereafter referred to as the barrier effect), an altered microclimate in the host canopy (microclimate effect), a resistance response in the host elicited by the presence of the companion crop (induced host resistance or host susceptibility), and altered plant morphology and canopy structure of the host due to interactions with the companion crop (morphological effect) (Boudreau, 2013). These mechanisms will be further introduced in the following sections. Additionally, in replacement-type intercrop systems, i.e. mixtures created by replacing plants of one crop species with those of another such that the relative plant density total stays constant (van der Werf et al., 2021), the density of the host crop is reduced, which may, in turn, reduce the chance that a given pathogenic propagule reaches a host crop (dilution effect) (Boudreau, 2013; Hiddink et al., 2010). Although these mechanisms have been hypothesised and studied individually, it is largely unknown whether and how the mechanisms can be influenced by the identity and traits of the companion species, and how the effects of different mechanisms work out in combination (i.e., there being trade-offs or synergies). Such knowledge, though, could help our understanding of why certain crop combinations are more effective at disease suppression than others, and could thus improve intercrop designs to enhance disease management.

The companion crop's structure can influence the above-mentioned mechanisms. For example, Shtaya et al. (2021) found a negative correlation between faba bean rust severity and the height and fresh biomass of the accompanying cereal crop (oat, barley, wheat or triticale), indicating that the barrier's effectiveness depends on the height and likely the canopy density of the companion crop. Furthermore, the traits of companion crop species can affect the microclimate in the host canopy. A tall companion crop species will shade and reduce incoming radiation, resulting in a cooler canopy during the day, but potentially a warmer canopy during the night (Castro et al., 1991; Zhang et al., 2008). A tall and dense companion crop species can also influence the humidity in the host canopy by reducing wind speed and air movement, which decreases evaporation and increases relative humidity (Boudreau, 1993; Ong et al., 1991). In contrast, intercropping with a short companion crop creates a more open canopy with greater incoming radiation, and greater air movement, thereby often reducing relative humidity (Gómez-Rodríguez et al., 2003).

The presence of a companion crop can also induce morphological and physiological changes in the host plant, which could impact disease dynamics. For example, shading of a taller companion could cause the neighbouring host plants to elongate (Roig-Villanova & Martínez-García, 2016; Smith & Whitelam, 1997), which in turn can increase the host canopy porosity, affecting the microclimate inside the host canopy, generating favourable or unfavourable conditions for pathogen development (Calonnec et al., 2013; Tivoli et al., 2013). Plants also respond to changing light conditions by adjusting leaf size, leaf angle, leaf thickness and leaf mass (Chitwood et al., 2012; Dong et al., 2024; Ratjen & Kage, 2013; Wu et al., 2017). These anatomical features of leaves can affect the susceptibility of plants to disease (Ahn et al., 2020; Alonso-Villaverde et al., 2011; Smith et al., 2018). Furthermore, a low ratio of red to far-red light has been reported to decrease plants' defence responses against pathogens, thereby increasing plant susceptibility (Cerrudo et al., 2012; de Wit et al., 2013). Lastly, incompatible pathogens or pollen dispersing from a companion species could elicit a resistance response in the host plant, protecting it against infection by virulent pathotypes (Finckh et al., 2000; Mundt, 2002).

The overall disease-suppressive effect of a certain companion crop species thus depends on the strength and direction of its influence on these mechanisms and the potential interactions among them. Indeed, strip cropping potato with grass, faba bean, or maize, resulted in varying levels of late blight suppression among the three companion crops (Homulle et al., 2024). On average over multiple years, strip cropping potato with different companion species reduced late blight by different percentages, e.g. 51% reduction with grass, 41% with maize %, and 22% with faba bean, when compared with potatoes grown in monoculture (Homulle et al., 2024). Since late blight (*Phytophthora infestans*) sporangia are mainly dispersed by wind (Aylor et al., 2001; Harrison & Lowe, 1989), a tall companion crop species was expected to act as a barrier for incoming spores, thereby reducing the incoming inoculum (He et al., 2010). A short companion crop species, on the other hand, could increase wind speed and solar radiation in the potato canopy, which would make the microclimate dryer, and less conducive for late blight development, thereby slowing down the progression of the epidemic (Bouws & Finckh, 2008; Ditzler et al., 2021). Furthermore, the different companion crop species could influence the morphology and susceptibility of the neighbouring potato plant and the structure of the potato canopy in various ways. Lastly, regardless of which companion crop species is used, each companion crop species occupies the space that would otherwise be occupied by potatoes, consequently lowering the number of hosts and the likelihood of a spore landing on a host.

The objective of this study was to investigate how these different companion crop species (grass, faba bean, maize) mediate disease-suppressive mechanisms. Potato was strip-cropped with either grass (shorter than potato), faba bean (slightly taller than potato at the time when late blight was present) or maize (considerably taller than potato at that time). We use potato and potato late blight as a focal crop-pathogen combination because *P. infestans* is considered to be the most devastating pathogen in potato (Campos & Ortiz, 2020; Majeed et al., 2017), and conventional growers rely heavily on fungicides to prevent and control potato late blight (Goffart et al., 2022;

Yuen, 2021). Hence there is a great need to develop control options that are ecology-based and sustainable in the long run.

4.2 Methods

In Chapter 3, we described disease suppression in the strip-crops using data from three experimental years (2021, 2022 and 2024), but we did not investigate the underlying mechanisms responsible for these results. We did in-depth measurements on disease-suppressive mechanisms in one of the years (2022) and present the results here. Some of the measurements were also conducted during the other experimental year(s), details of these additional data, where available, are provided in Supplementary material B.

4.2.1 Field experiments

A field trial was conducted in 2022 at the organic experimental farm of Wageningen University & Research, located in Wageningen, The Netherlands. The trial was conducted at two experimental sites, located at approximately 850 meter distance from each other (51°59'36"N 5°39'30"E (hereafter referred to as site A) and 51°59'32"N 5°40'16"E (site B), Fig. SA4.1). Four experimental treatments were tested at each site: potato (*Solanum tuberosum* cv. Agria) grown in monoculture, potato strip-cropped with English ryegrass (*Lolium perenne*) (hereafter referred to as potato-grass), potato strip-cropped with faba bean (*Vicia faba* cv. Cartouche) (potato-faba bean), and potato strip-cropped with maize (*Zea mays*) (potato-maize). Two replicates of each treatment were at each site. As noted in “Data Analysis” section the data from this setup have a nested structure with plot nested within site (two sites with two treatment replicates per site). The potato cultivar used (Agria) is moderately susceptible in the foliage and fairly resistant in the tuber to potato late blight (The European Cultivated Potato Database, 2005). Potatoes were planted on 17 May 2022, faba bean was sown on 3 May, and grass and maize on 29 April 2022.

Each plot measured 21 m in width x 24 m in length and comprised either only potato (monoculture plots) or alternating strips of potato and companion crops (strip-cropping plots). In strip-cropping plots, three 3 m wide potato strips were alternated with four 3 m wide strips of a companion species, such that the borders of the plots were strips of the companion species (Fig. 4.1). Each strip consisted of either four rows of potato (row width of 75 cm), four rows of maize, six rows of faba bean, or 20 rows of grass. The monoculture plots comprised 28 rows of potato at a 75 cm distance. In potato strips in strip-crops, a distinction was made between the inner rows that have only potato rows as direct neighbours and the outer rows that border on the companion species. Plots were separated by a 6 meter strip of grass. Strips were planted in an east-west direction, corresponding to the prevailing wind direction in the Netherlands. The fields were managed organically; organic fertilizer was used and no pesticides or irrigation. For detailed information on crop management, see Chapter 3.

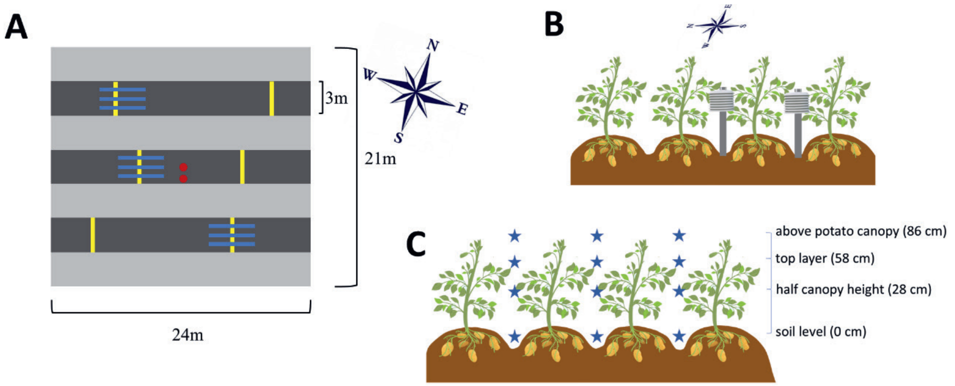


Fig. 4.1 (A) Schematic arrangement of one experimental strip-cropping plot. Strips of each crop species were 3 meter wide, and all plots were oriented from east to west. The plots had a size of 21 m × 24 m. The dark grey strips in the schematic arrangement represent potato, and the light grey strips either maize, grass or faba bean grown as a companion species. The yellow lines perpendicular to the strips represent transects for making disease assessments and measurements of crop height. Each transect consists of four plants, one per row. Transects were placed at random locations in each strip. Red dots indicate the position of the microclimate sensors. Blue lines parallel to the strip indicate where measurements of light interception were made with the SunScan (a 1-m long probe). (B) Side view of the placement of the microclimate sensors. Sensors were placed in the furrow between the potato rows. They were positioned roughly at the midpoint of the height of the canopy and the position was adjusted upwards throughout the growing season as the potato canopy grew in height. (C) Cross-sectional view of the positions of the light interception measurements (the SunScan probe was directed parallel to the rows). Measurements with the Sunscan were made in three strips in each plot and per strip in three furrows and in each of these locations at four heights. The heights were: above the potato canopy (86 cm from the top of the soil), within the top layer of the potato canopy (58 cm), at half the potato canopy height (28 cm), and at soil level (0 cm).

The summer of 2022 was warm and dry in comparison to the climatic mean for the area, with average daily temperatures around 18 °C during July, a relative air humidity level of 64%, and a total rainfall of 25 mm during July (Fig. SA4.2).

4.2.2 Disease assessment

During the growing season, foliar late blight severity caused by natural infections was assessed in all plots. We used two assessment methods: (1) counting the number of leaflets with lesions per plant, and (2) estimating the percentage diseased leaf area per plant. In the early stages of the epidemic, it was more accurate to count the number of leaflets with lesions per plant, rather than to estimate a very low percentage of diseased leaf area. As the epidemic progressed, counting the number of diseased leaflets was not possible anymore due to high disease severity, and only the percentage diseased leaf area per plant was recorded, following the classification scheme of James (1971). At some dates we conducted both measurements to enable calibration. We then used these data to perform a regression to convert the number of diseased leaflets into a percentage diseased leaf area (see Chapter 3 for details). This allowed for the combination of the two assessment methods into a single metric, hereafter referred to as disease severity.

To quantify disease severity, we randomly selected in each of the three potato strips in a plot two transects perpendicular to the strip, with each transect comprising four plants (Fig. 4.1A), resulting in a total sample of 24 plants per plot. In 2022, first symptoms were observed on 8 July, and assessments were made four times during the epidemic (on 12, 15, 19, 22 July at site A, and on 11, 14, 18, 21 July at site B). The plants were desiccated on 11 August 2022. The epidemic progress was halted around 19 July, when the weather was very hot with maximum temperatures reaching up to 36.6 °C, effectively killing all foliar lesions. After that, the epidemic did not progress much.

Overview of the investigated mechanisms and their related measurements

Within the treatments, various measurements were taken to investigate the relative role of different disease-suppressive mechanisms. See Fig. 4.2 for an overview of the hypothesised effects of strip cropping with different companion species.

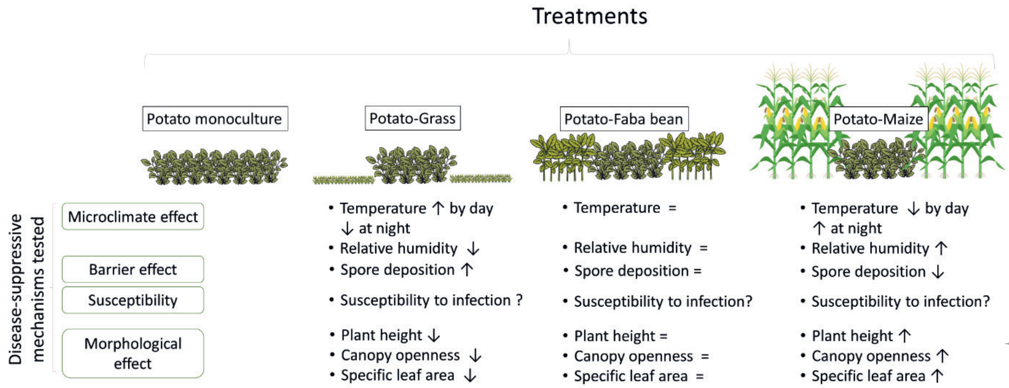


Fig. 4.2 Overview of the treatments, the investigated disease-suppressive mechanisms, their related measurements and the hypothesised effects of the strip-cropping treatments compared to potato monoculture. The symbol ↑ indicates that the variable was hypothesised to be higher than in the monoculture, while ↓ signifies that it was expected to be lower. The symbol = is used when the variable was not anticipated to deviate significantly from the monoculture, and ? indicates uncertainty in forming a hypothesis. The canopy illustrations are for illustration only and do not accurately represent the actual height-to-width ratios.

4.2.3 Microclimate measurements

Temperature and relative humidity inside the potato canopy were measured continuously over time in each of the four treatments, using MicroLite III Temperature/RH data loggers (LITE5032L-RH, Fourtec, Israel), which record both parameters. These data loggers were placed inside a radiation shield (model 7714, Davis Instruments, USA). The measurements were made in two plots per treatment at site A and in one plot at site B (hence in three out of the four replicates). In the strip-crops this was done in one strip per plot, placing one sensor in the furrow between the inner rows of the strip and the other one in the furrow between the third and fourth row, counted from the north side of the strip (Fig. 4.1A). In the monocultures, a single sensor was placed in a furrow in the middle of the plot. Sensors were positioned roughly at the midpoint of the canopy's height and were adjusted throughout the growing season as the potato canopy grew. All sensors were set to continuously record data every 10 minutes, starting from 16 June 2022 (early vegetative stage) until the end of the potato growing season (8 August 2022).

Wind speed and wind direction were measured continuously at the western (windward) edge of one experimental field with a single cup anemometer (6410 Davis

Anemometer, Davis Instruments, USA). The anemometer was regularly adjusted to keep its measuring height level with the top of the potato canopy.

4.2.4 Particle counts

To measure the role of the companion crop as a barrier for the dispersal of disease propagules, passive spore traps were used to catch particles slightly above the potato canopy. This was done over the whole growing season because the onset of late blight epidemics varies substantially and we wanted to assess the barrier effect irrespective of the timing of the epidemic in our experiment. The assessment considered all particles in the size range of *P. infestans* sporangia. Additionally, the number of sporangia depends on the progression of the epidemic, which might differ between treatments because of the effect of the companion crop on microclimate and induced resistance. Thus measuring particles provides insight into what the barrier effect might be at any starting time of an epidemic, and independent of the epidemic.

To catch particles, we placed a passive spore trap in the middle of each replicate of each treatment. Passive spore traps were built using the design of Blackall et al. (2020) and Atkinson et al. (2019), see Supplementary method S1 for more details about the design of the passive spore traps. Three microscope slides, covered with a thin layer of Vaseline, were placed in each passive spore trap daily around 4 pm and collected the next day before 9 am for processing. To determine the density of particles deposited on the slide we took four pictures at 100× magnification of each microscope slide using a microscope camera (ODC832, Kern and Sohn GMBH, Germany) in combination with the software Microscope VIS pro. Each photo represented an area of 12.57 mm^2. We used ImageJ software to count particles within the size range of 314-1257μm^2, i.e. approximately the size of *P. infestans* sporangia. This range was calculated based on the documented length and width of *P. infestans* sporangia (Mariette et al., 2018), and taking their elliptical shape into account.

4.2.5 Detached leaf assays to measure susceptibility to infection

Companion species can affect the susceptibility of focal crops to pathogens, either due to induced resistance triggered by pollen or spores originating from companion plants, or due to other potential mechanisms such as nutrient competition, or volatile organic compounds. To measure the net effect of these influences on the susceptibility of potato, we performed a detached leaf assay (Lapwood, 1961; Vleeshouwers et al., 1999). We collected leaflets for this assay in the field, five weeks after potato planting (vegetative growth stage). We collected seven lateral leaflets from seven monocropped potato plants (one leaflet per plant), as well as seven leaflets from the inner rows and seven from both outer rows of strip-cropped potato plants. The youngest fully expanded leaflets were collected. The time of collection, five weeks after planting, was a compromise between allowing sufficient time for potato plants to interact with companion species and avoiding infection of the collected leaflets by naturally occurring sporangia. Each leaflet was consequently placed upside-down on a water agar layer in a 100 mm Petri dish. The abaxial surface of each leaflet was inoculated with 10 droplets of 10 µL each, containing *P. infestans* sporangia (5000 sporangia/ml, strain EU_36). Five droplets were placed on each side of the midrib. Four leaflets per plot (two from the inner rows and two from the outer rows of the strip-crops, and two random leaflets of the monoculture plots) were inoculated with distilled water only and used as a control. All the samples were kept in a climate cell at 15°C with 16 hours of daylight. After five days, the number of lesions developed out of the 10 droplets was counted.

4.2.6 Plant height

The height of the potato plants and each companion crop species was measured at four separate times during the growing season. At site A, measurements were taken at 32, 43, 49, and 67 days after planting (DAP), and at site B at 35, 42, 50, and 67 DAP. The measurements were made on 24 plants per plot, arranged in six transects of 4 plants each (same transects as for disease assessment, Fig. 4.1A). Height was measured from the potato ridge until the highest point of the potato plant. The height of 12 companion plants per plot (either grass, faba bean or maize) directly neighbouring the potatoes was measured as the distance between the soil surface and the highest point of the plant.

4.2.7 Light interception

The openness of the potato canopy was characterised by measuring light interception at different heights of the potato canopy. The openness of the canopy determines the probability of a spore to be intercepted by the foliage. Measurements were taken once at eight weeks after planting. Again, this sampling date was a compromise between allowing sufficient time for the crop species to interact while avoiding a sampling date too late in the season, as late blight could reduce the canopy cover and thus influence the canopy openness. Photosynthetically active radiation (PAR) was measured in the potato canopies using a SunScan (SS1-STD3 by Delta T) (a 1-m long probe equipped with 64 individual sensors). Measurements were conducted from two hours before to two hours after solar noon. Light interception was measured at three locations in each potato monoculture plot and strip-plot (once per strip) (Fig. 4.1A). At each location, three positions were assessed: the probe was positioned parallel to the strip between the first and the second row counted from the north side of the strip, then between the second and the third row, i.e. in the middle of the strip, and finally between the third and fourth row of the strip. In the monoculture plots, per location, three positions in adjacent rows were assessed. Measurements were taken at four heights: above the potato canopy (86 cm from the top of the soil), within the top layer of the potato canopy (58 cm), at half the potato canopy height (28 cm), and soil level (0 cm) (Fig. 1C). Light interception was expressed as the ratio of PAR measured by the probe and PAR measured at the same time by a sensor placed at one-meter height in an unshaded point in the border of the field.

4.2.8 Specific leaf area (SLA)

At 60 DAP, three lateral leaflets from separate leaves were collected per plant from 12 randomly selected plants per plot. The youngest fully expanded leaflets were collected. Leaf area was measured using a leaf area meter calibrated to mm^2 (LI-3100C by LI-COR Biosciences, Lincoln USA). Subsequently, the leaflets were dried in an oven at 105°C for 24 hours, and the dry weight was measured. Finally, SLA was calculated as the ratio of leaf area to leaf dry mass (cm^2/g) and expressed as the average SLA of the three leaflets per plant.

4.2.9 Data analysis

Differences in microclimate, particle count, susceptibility, and morphology aspects (plant height, canopy porosity and SLA) between treatments as well as differences between inner and outer rows of the strips within the strip-crops were analysed using (generalized) linear mixed models ((G)LMM). Mixed models were used to account for the nested structure of the data, with plot nested within site (two sites with two treatment replicates per site). In case measurements were done in different strips, strip was added as a third nested random effect, with strip nested in plot, and plot nested in site (models 5, 6, and 7, Table 4.1). For the variables measured over time (e.g. microclimate, particle count and plant height), day was included as a crossed random effect (models 1, 2, 3 and 5, Table 4.1). Models were fitted in R (R Core Team, 2022) using the package glmmTMB (Bolker, 2016; Magnusson et al., 2017).

Models for different response variables were tailored to fit the characteristics of the data (Table 4.1). If variables followed a normal distribution (e.g. temperature and plant height), we used LMMs; otherwise, we used GLMMs. Susceptibility (i.e. the 10 inoculation spots per leaflet of the detached leaf assay) was analysed using a binomial distribution (model 4, Table 4.1). Given the excess of zeros in the data set, the binomial distribution was enhanced to a zero-inflated binomial (ziformula = ~1). The analysis of light interception used a beta distribution, since PAR captured was a proportion of total light (model 6a, 6b, Table 4.1). Since PAR was measured at multiple canopy levels, an interaction between treatment and height (categorical; 4 levels) was included in these models. Also, we accounted for heteroscedasticity across canopy height, using the *dispformula* argument of the glmmTMB function (Brooks et al., 2017).

The analysis of the particle counts used a negative binomial GLMM. Furthermore, initial exploration of the particle data showed that the top slides in the spore traps (Fig. SA4.4) caught on average more particles than the middle ones, while the ones at the bottom captured the least. Therefore, slide position in the trap was added as a fixed factor within the models for particle data (models 3, Table 4.1).

In addition to comparing treatments, we also investigated the effect of companion crop height on incoming particle counts (model 3b, Table 4.1). A smooth curve was plotted through the weekly height measurements of the companion crops, from which the average daily height was obtained (Fig. SA4.6). Lastly, wind speed and wind direction were tested as explanatory variables for particle count (model 3c Table 4.1, and models 1,2, 6 and 12 Table SA4.1). As the microscope slides were present in the spore traps from approximately 16:00 until 9:00 the following day (when they were collected), the average wind speed during this time frame was considered. Wind direction was recalculated to a number between 0 and 1, to represent the perpendicularity of the wind direction in relation to the East-West orientation of the strip (see Supplementary methods SA4.2). A value of one indicates that the wind was completely perpendicular to the direction of the strips (from the north or south), while a value of zero indicates that the wind was parallel to the strips (from the west or east). When wind speeds were zero, the anemometer would record 0° wind direction; these zeros were removed from the dataset.

Table 4.1 Summary of the fitted models to the data. The symbol + means additive effects are assumed, while * means main effects and their interactions are estimated. The notation A/B means B is nested in A.

Model ID	Response variable	Distribution	Link function	Predictors	Random effects	Disp-formula
1a	Mean daily temperature	Gaussian	-	Treatment	Day + Site/Plot	
1b	Temperature in either one of the strip-crops	Gaussian	-	Row position	Day + Plot	
2a	Daily duration (in min) relative humidity >90%	Gaussian	-	Treatment	Day + Site/Plot	
2b	Daily duration (in min) relative humidity >95%	Gaussian	-	Treatment	Day + Site/Plot	
2c	Daily duration relative humidity >90% in either one of the strip-crops	Gaussian	-	Row position	Day + Plot	
3a	Particle count	Negative binomial [a]	Logistic	Treatment + Slide	Day + Site/Trap/Slide	Treatment + Slide
3b	Particle count	Negative binomial [a]	Logistic	Height companion crop + Slide	Day + Site/Trap/Slide	Height companion crop + Slide
3c	Particle count	Negative binomial [a]	Logistic	Treatment * Wind Speed + Slide	Day + Site/Trap/Slide	Treatment + Slide
3d	Particle count	Negative binomial [a]	Logistic	Treatment * Day + Slide	Site/Trap/Slide	Treatment + Slide
4	In vitro infections	Binomial with zero inflation	Logit	Treatment	Site/Plot	-
5a	Potato plant height	Gaussian	-	Treatment	Day + Site/Plot/Strip	-
5b	Potato plant height in either one of the strip-crops	Gaussian	-	Row position	Day + Site/Plot/Strip	-
6a	Proportion of PAR captured	Beta	Logit	Treatment * Canopy level	Site/Plot/Strip	Treatment * Canopy level
6b	Proportion of PAR captured in either one of the strip-crops	Beta	Logit	Row position * Canopy level	Site/Plot/Strip	Canopy level
7a	Specific leaf area	Gaussian	-	Treatment	Site/Plot/Strip	-
7b	Specific leaf area in either one of the strip-crops	Gaussian	-	Row position	Site/Plot/Strip	-

Note: *Treatment* is a categorical variable with four levels: monoculture, potato-grass, potato-maize or potato-faba. *Row position* represents the position of the rows within the strip, it has two levels: inner and outer (i.e. those in direct contact only with other potato plants, or with both potato and the companion crop). *Slide* represents the three microscope slides within one spore trap. *Canopy level* represents the height at which PAR was measured, and has four levels: above the canopy, in the top layer, in the middle layer and the bottom layer.

[a] The negative binomial can be specified in two ways (NB-1 and NB-2). NB-2 performed better on the data than NB-1 (model 10 vs. model 11 in Table SA4.1), therefore this distribution was used.

4.3 Results

4.3.1 Disease severity

Average disease severity over the measurement period during the 2022 growing season was lowest in the potatoes strip-cropped with grass (5% (95% CI [4, 6]) at site A and 3% (95% CI [2, 4]) at site B), which was significantly lower than potato monoculture (11% (95% CI [8, 14]) at site A and 13% (95% CI [11, 17]) at site B) (Fig. 4.3A and B). Maize as a companion crop also significantly suppressed potato late blight compared with potato monoculture, with an average disease severity of 5% (95% CI [4, 7]) at site A and 4% (95% CI [3, 5]) at site B, estimates not significantly different from those of potato-grass, but significantly lower than sole potato. There was no significant difference in disease severity between the potato strip-cropped with faba bean and sole potato at site A (Fig. 4.3A). However, strip cropping with faba bean at site B suppressed potato late blight to a similar extent as maize did (average disease severity of 4% (95% CI [3, 6])) (Fig. 3B) and not significantly different from potato-grass.

Both the 2021 and 2024 growing seasons confirmed a consistent disease-suppressive effect of strip cropping potato with grass (Fig. 3.3 (Chapter 3)). The results for maize were more variable between years, and faba bean did not significantly suppress late blight in 2024.

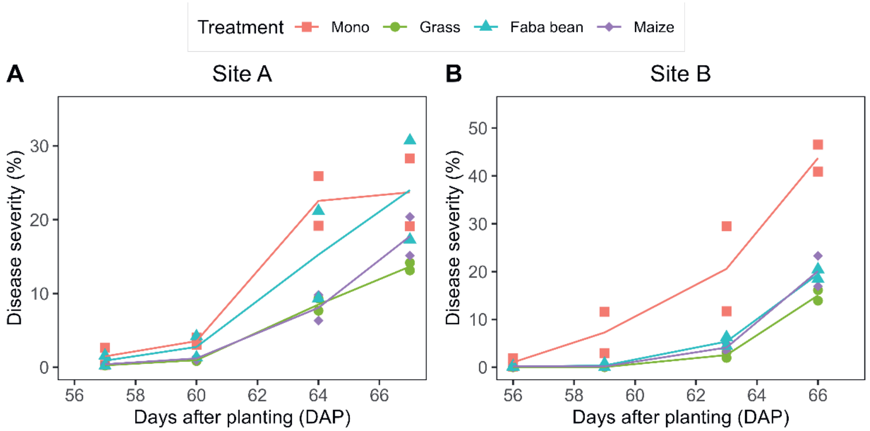


Fig. 4.3 Disease progress curves for potato late blight on potato during the 2022 growing season at site A (A) and site B (B), modified from Homulle et al. (2024). The points (symbols) represent the mean disease severity per plot based on visual observations on 24 plants per plot. The lines are drawn between the midpoints of the two plots for each treatment.

4.3.2 Microclimate in the potato canopy

We found no significant differences in temperature within the potato canopy between mono- and strip-cropped potatoes at any time during the growing season (Fig. SA4.7). Both the average daily temperature and temperature variations during the day were similar and not significantly different ($p > 0.9$ in all comparisons). Furthermore, within the strip-crops, the temperature was similar in the inner and outer rows of the potato strip for all strip-cropping treatments.

We used the observed relative humidity within the potato canopy to assess whether and how many hours per day the microclimate in different treatments had been suitable for infection (RH ≥ 90% required) or sporulation (RH ≥ 95% required). We quantified the average number of hours per day with suitable conditions according to these two thresholds (Table 4.2) and found no significant differences between the treatments over the whole season. However, we observed significant differences when examining different periods in the growing season. From 1 to 10 July (the period surrounding the first finding of late blight in the field on July 8), the daily duration of relative humidity above 90% was similar in potato monoculture (11.5 ± 1.7 hours), potato-maize (11.4 ± 2.0 hours) and potato-faba bean (11.0 ± 2.4 hours), but substantially and significantly lower in potato-grass (9.7 ± 1.9 hours). Similar results were obtained for the duration of RH > 95%. Interestingly, towards the end of the growing season (25 July to 4 Augustus), the daily duration of relative humidity above 90% was significantly longer in the potatoes-maize (11.3 ± 3.8 hours) than in potato monoculture (9.4 ± 3.6 hours) ($p = 0.03$). Thus, the microclimate effects of strip cropping varied over the season, probably as the stature of the plants changed.

Microclimate in the potato strip was also measured during the 2021 and 2024 growing season (Supplementary material B). During these years, temperature within the strip-crop potato canopy was also not influenced by the companion crop species (Fig. SB4.3). In 2021, around the period surrounding the first finding of late blight in the field, the daily duration of relative humidity above 90% was substantially lower in potato-grass than in the potato monoculture (Fig. SB4.4). This difference was not observed during the 2024 growing season. During this year, late blight arrived early when the potato plants were still young, and the growing season was considerably shorter than in 2021 and 2022, with potato plants desiccated on 9 July. These conditions could explain why no effects were observed.

Table 4.2 Average daily hours with relative humidity equal to or exceeding 90% or 95%, and their respective standard deviations, throughout the full measurement period (from 16 June until August 7), around the time that late blight was first observed in the field (1 – 10 July)), and during the end of the growing season (25 July – 4 August, a period where maize was distinctly taller than potato). Letters indicate significant differences at $P < 0.05$ between treatments within each column.

	16 June – 7 August		1 – 10 July		25 July – 4 August	
Treatment	RH ≥ 90%	RH ≥ 95%	RH ≥ 90%	RH ≥ 95%	RH ≥ 90%	RH ≥ 95%
Mono	9.8 ± 5.0a	7.2 ± 4.8a	11.5 ± 1.7a	8.8 ± 2.0a	9.4 ± 3.6a	6.5 ± 3.6ab
Potato-grass	9.1 ± 4.5a	6.5 ± 4.4a	9.7 ± 1.9b	7.0 ± 2.5b	9.1 ± 3.9a	6.3 ± 3.8a
Potato-faba bean	9.6 ± 5.0a	6.6 ± 4.8a	11.0 ± 2.4ab	7.4 ± 2.9ab	9.6 ± 4.3a	6.6 ± 4.2ab
Potato-maize	10.4 ± 4.7a	7.7 ± 4.7a	11.4 ± 2.0a	8.3 ± 2.7ab	11.3 ± 3.8b	8.6 ± 4.0b

Furthermore, when considering the whole measurement period from 1 July to 4 August, in potato-maize and potato-faba bean, we found that the inner rows of the potato strip had a significantly longer duration with a high relative humidity than the outer rows (Fig. 4.4C). In potato-maize, the inner potato rows had an average duration of relative humidity above 90% of 10.9 ± 4.8 (SD) hours while the outer rows had a duration of 9.9 ± 4.6 (SD) hours ($p < 0.01$). In potato-faba bean, the inner potato rows had an average daily duration of relative humidity above 90% of 9.8 ± 4.8 hours whereas the outer rows had a duration of 9.3 ± 5.1 hours ($p < 0.01$). In potato-grass, there was no significant difference in relative humidity between the inner and outer potato rows ($p = 0.55$).

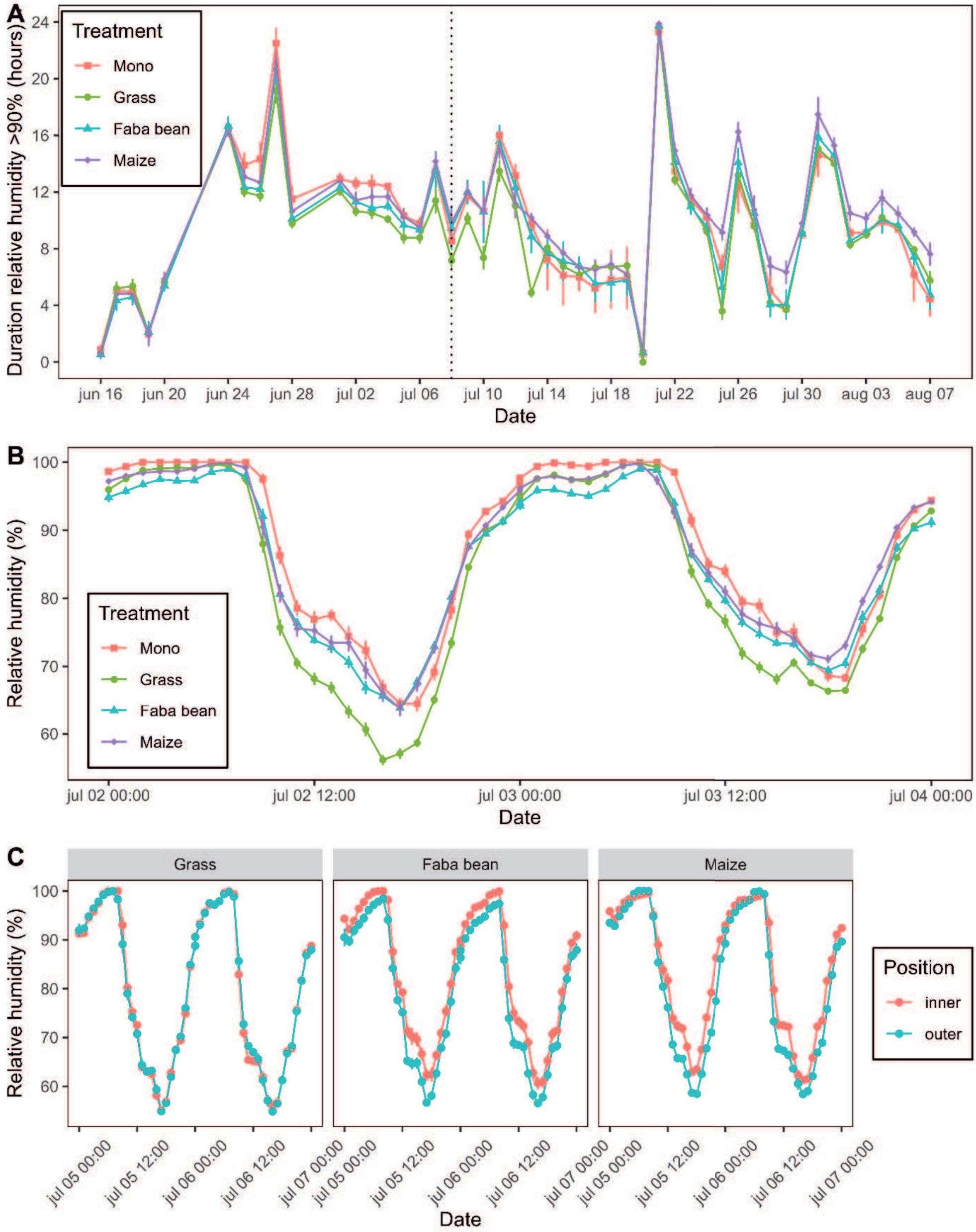


Fig. 4.4 Relative humidity in the potato canopy for potatoes either grown in monoculture (Mono), or strip-cropped with grass, faba bean, or maize. (A) Daily hours with relative humidity equal to or exceeding 90% for each treatment across a part of the growing season. The vertical dotted line marks the first detection of late blight. (B) Hourly relative humidity for each treatment between 2 and 4 July; the time around which the first infections took place. (c) Hourly relative humidity of the inner and outer rows of potato strips in the strip-cropping treatments between 5 and 7 July.

4.3.3 Particle counts

Potato-maize generally had the lowest number of particles in the size range of *P. infestans* sporangia out of all treatments, in line with the hypothesis that a tall companion species would act as a barrier against particle dispersal (Fig. 4.5A). On several individual days, and across the growing season, this difference was significant. Summing the daily particle counts over the measurement period (30 June – August 1) showed an even clearer difference between the treatments (Fig. 4.5B). On average, across the growing season, potatoes strip-cropped with maize received in total 36% fewer particles than potatoes grown in monoculture ($p < 0.001$). The number of particles was not significantly lowered in potato-grass or potato-faba bean compared to potato.

There was weak support for a negative exponential relationship between the height of the companion crop and the number of intercepted particles ($exp^{2.86-0.0013x}$, $p = 0.063$) (Fig. 4.5C). The height of the companion crop could, however, not predict particle count as effectively as the companion crop identity; the model using companion crop species as an explanatory variable (Table SA4.1 Model 3) had a better fit to the data ($\Delta AIC = -48.4$) than a model using the height of the companion crop (Table SA4.1 Model 9).

A significant interaction effect was found between treatment and wind speed just above the potato canopy (Chi-square test, $\chi^2 = 28.86$, df = 3, $p < 0.001$). Increasing wind speeds were associated with significantly lower particle counts in potato-maize or potato-faba bean than the monoculture ($p < 0.001$ for both comparisons) or potato-grass (grass-maize: $p = 0.006$; grass-bean: $p = 0.09$) (Fig. SA4.8).

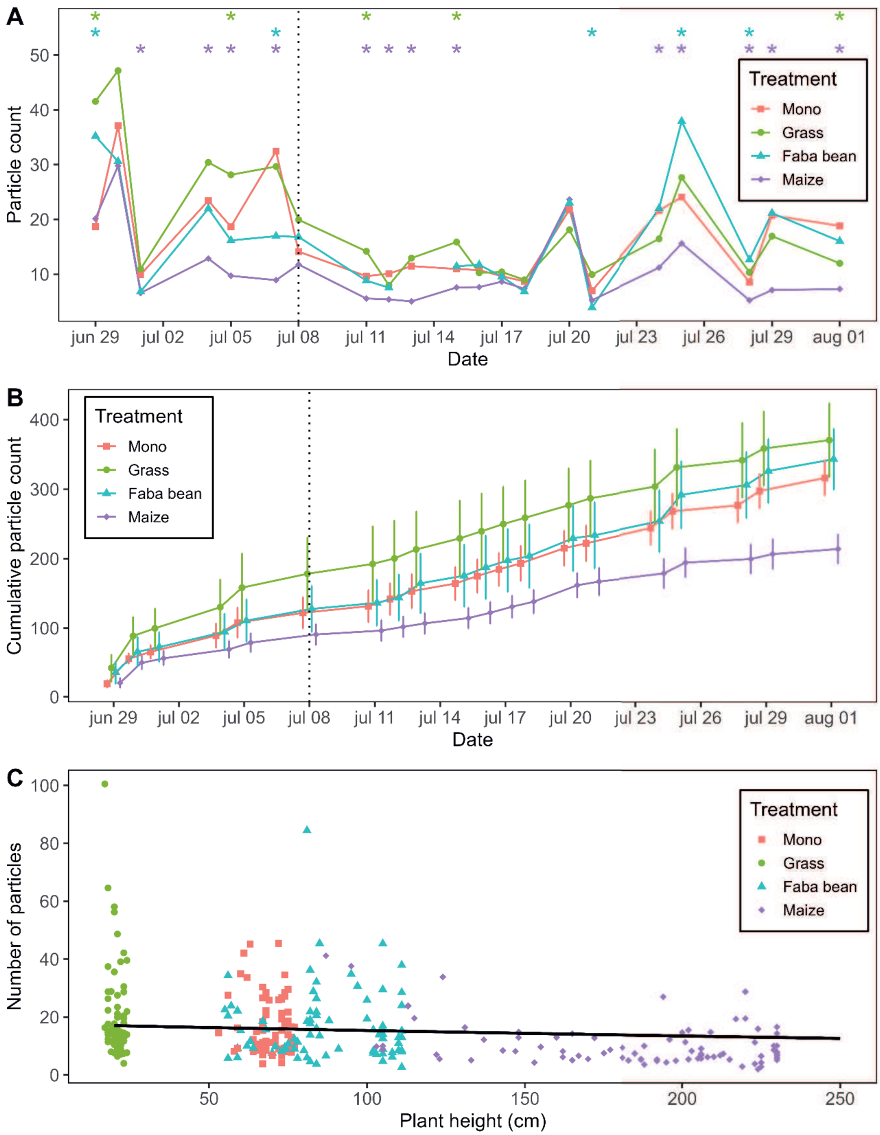


Fig. 4.5 Particle counts in the potato canopy in potato mono (Mono), potato-grass, potato-faba, or potato-maize over the growing season, as an index for the barrier effect of the companion crop. Particles were sampled using Vaseline-covered glass slides in passive spore traps placed in each plot. The vertical dotted line in A marks the first detection of late blight. (A) Particle counts on measurement days over the growing season. Stars indicate a significant difference between the strip-crop and the monoculture on a given day; top asterisk (green) for potato-grass, middle asterisk (blue) for potato-faba, and bottom asterisk (purple) for potato-maize. (B) Cumulative counts of measurement days across the season and their standard error. (C) Particle count in the potato canopy in relation to the height of the companion crop. Dots represent average particle counts per spore trap per day. The line represents the estimated regression: $exp^{2.86-0.0013x}$, where the slope is not significant (p = 0.063).

4.3.4 Particle counts

Potato leaflets taken from the field and inoculated with *P. infestans* spores developed lesions (Fig. 4.6) while control samples (leaflets inoculated with water) did not develop any lesions, indicating that at the time of the detached leaf assay, 23 June, late blight was not present in the field, and all the lesions developed on the non-control samples resulted from the inoculation.

The average number of lesions that developed per treatment (out of 10 droplets) was 2.6 ± 0.5 in the monoculture, 2.8 ± 0.4 in potato-maize, 3.9 ± 0.4 in potato-grass and 4.8 ± 0.4 in potato-faba bean. There were significantly fewer lesions on leaflets from the monoculture than on those from potato-faba bean or potato-grass (p = 0.005 and 0.006, respectively), while no difference with potato-maize was observed (p = 0.6). In potato-grass or potato-faba bean, there was no significant difference in number of lesions between leaflets taken from the inner and outer rows. However, leaflets from the inner rows of potato-maize tended to develop more lesions than those from the outer rows (3.2 versus 2.3, p = 0.091).

A repeat of the detached leaf assay in a similar setup in 2024 showed no significant differences between treatments (Fig. SB4.5).

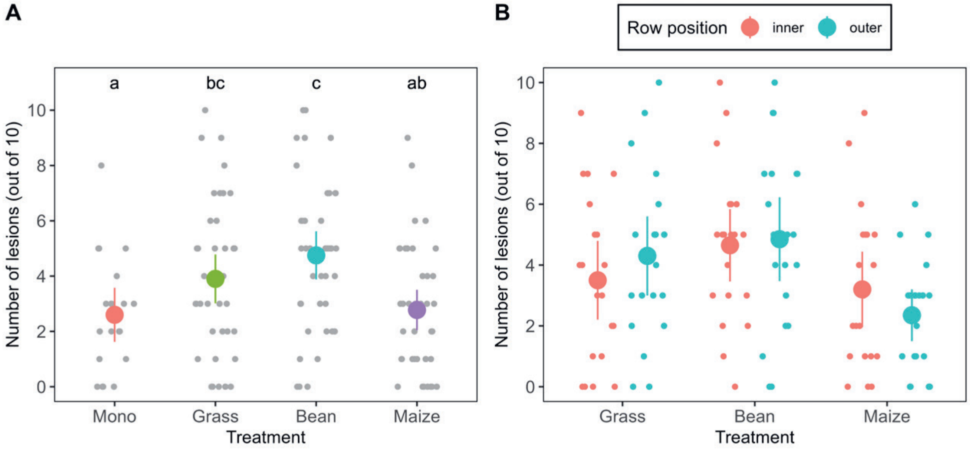


Fig. 4.6 (A) Number of lesions out of 10 inoculations in detached leaf assays with leaflets from field-grown potato plants grown in monoculture (mono) or strip-cropped with grass, faba bean, or maize. Large circles represent the means and error bars indicate the confidence interval. The smaller points represent measurements on

individual leaflets. Letters indicate significant differences between treatments at P < 0.05. (B) Number of lesions separately for inner and outer rows of potato strips in the strip-cropping treatments.

4.3.4 Structure of the potato canopy

We found no significant difference in the height of the potato canopy between the strip-crops and the potato monoculture (Fig. SA4.9). During the 2021 and 2024 growing season, also no height difference was observed between treatments (Fig. SB4.7). However, within the potato strip, there were small differences in height between the inner rows of the strip and the outer rows (Fig. 4.7). These differences became only significant at the end of the growing season, at 67 DAP. Potatoes strip-cropped with grass were on average 3.5 cm taller in inner as compared to outer rows (p = 0.012) while potatoes strip-cropped with maize were on average 5.7 cm taller in outer as compared to inner rows (p = 0.014). These effects on plant height can be interpreted as shade avoidance responses, with plants growing taller when they have taller neighbours.

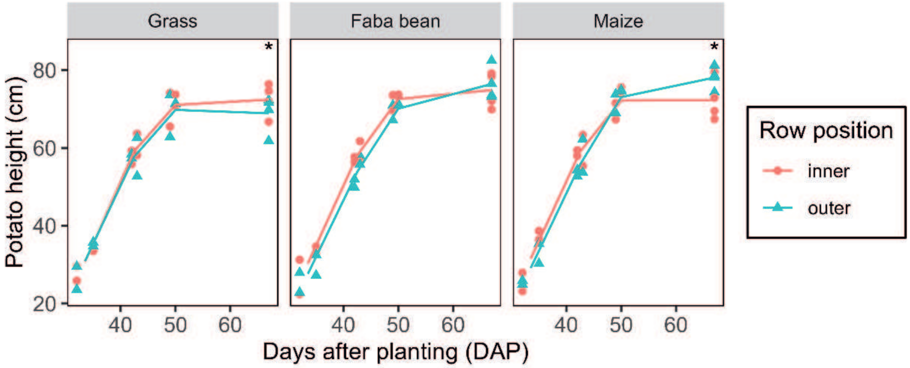


Fig. 4.7 Height of potato plants in the inner and outer rows of potato-grass, potato-faba bean, and potato-maize across the growing season. Points represent the mean height of the potato plants in a plot, and lines represent the mean heights per row position. The grey line represents the average potato height in the monoculture for reference. Asterisks indicate significant differences between inner and outer rows (p <0.05).

As expected, the proportion of total PAR captured decreased from the top to the bottom of the canopy (Table SA4.3). At each canopy level, there were no significant differences among treatments indicating LAI and canopy porosity were not significantly affected by the treatments.

Specific leaf area (SLA) of potato leaflets was significantly higher in potato-maize (271 ± 4.4 cm^2/g) than in monoculture (243 ± 4.3 cm^2/g), or potato-grass (238 ± 3.8 cm^2/g) ($p = 0.013$ and $p = 0.002$, respectively) (Fig. 4.8A). Also, potato plants strip-cropped with maize had a significantly higher SLA in the outer rows compared with the inner rows (280 ± 6.2 cm^2/g versus 263 ± 5.9 cm^2/g, $p = 0.018$). The contrary was observed in potato-grass; here leaflets from the inner rows had a significantly higher SLA compared with the outer rows (246 ± 5.7 cm^2/g versus 230 ± 4.6 cm^2/g, $p = 0.002$) (Fig. 4.8B). As for plant height, these responses can be interpreted as shade adaptation as leaves that are well lit tend to be thicker, having a lower SLA, than leaves that are shaded.

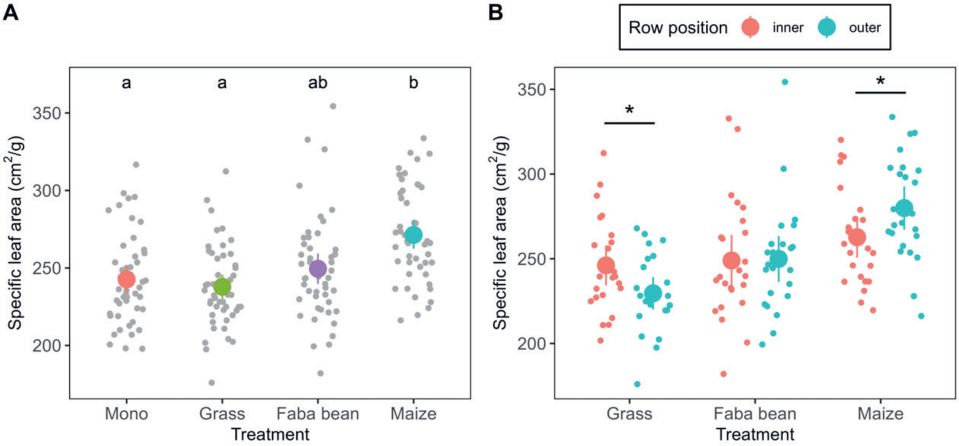


Fig. 4.8 (A) Specific leaf area (cm^2/g) from potato plants grown in monoculture (mono) or from potatoes strip-cropped with grass, faba bean, or maize. Large circles represent the means and error bars the confidence interval. The smaller points represent the average SLA per plant. Letters indicate significant differences between treatments at $P < 0.05$. (B) Specific leaf area of potatoes from inner and outer rows of the potato strips in the strip-cropping treatments. Asterisks indicate significant differences between inner and outer rows within a treatment at $P < 0.05$.

4.4 Discussion

In this study, we investigated how different identities and traits of companion crop species affect disease-suppressive mechanisms in potato-based strip-cropping systems. Disease suppression observed with each companion crop (Fig. 4.3) is achieved through different mechanisms. These mechanisms can either strengthen or counteract one another, resulting in potential synergies and trade-offs (see Table 4.3 for an overview of the outcome of the multiple mechanisms investigated in this paper).

Table 4.3 Summary of the investigated disease-suppressive mechanisms in the strip-crops.

Mechanism	Key findings on each mechanism	Reference in text
Microclimate change	Measurements on microclimate in the potato canopy showed that a short companion crop (e.g. grass) decreases the duration of humid conditions that are conducive to infection and disease progress in the potato strip. A tall companion crop (e.g. maize) increased the relative humidity later in the growing season. We found no significant effect of strip cropping on temperature in the potato strip.	Table 4.2, Fig. 4.4
Barrier effect on spore dispersal	Measurements on particle deposition showed that a tall companion species (e.g. maize) decreased deposition of particles, indicating that taller companion species would interfere with spore dispersal between potato strips.	Fig. 4.5
Change in susceptibility	Leaflets taken from potato-grass and potato-faba bean were slightly more susceptible to in vitro *P. infestans* inoculations than those from the monoculture.	Fig. 4.6
Change in morphology	Strip cropping with maize increased specific leaf area (SLA), particularly in the outer rows of the strip. In contrast, in potato-grass, the leaflets from the inner rows had a significantly higher SLA than the outer rows. Potato canopy height and canopy openness showed no significant difference between strip-cropping and monoculture.	Fig. 4.8

Strip cropping with grass lowered the relative humidity in the potato canopy during the early epidemic, reducing the duration of favourable conditions for infection by almost two hours per day around the time of the first late blight detection. Changes in the duration of moist conditions are considered highly relevant for the epidemiology of potato late blight because daily patterns of humidity and leaf wetness duration (relative humidity >90%, (Sentelhas et al., 2008)) impact several components of the pathogen's lifecycle and relatively small differences in wetness duration can greatly affect disease progress. For instance, *P. infestans* sporangia are sensitive to drying (Minogue & Fry, 1981), so if the relative humidity decreases earlier during the day, their survival chance will be affected negatively. Likewise, sporangia are formed only if the humidity is at or very close to saturation (Harrison & Lowe, 1989), and infection requires a minimum of 2 to 3 hours of leaf wetness to infect, but usually more, (Crosier, 1934), and a break in leaf wetness markedly reduces disease severity (Hartill et al., 1990). Humidity and wetness requirements were less often met in the potato-grass strip-crop than in the other systems and could thus have reduced the survival of sporangia and limited spore germination, thereby slowing down the onset and progress of the epidemic. Together this indicates that a short companion crop can make the conditions in the neighbouring host potato canopy less favourable for the late blight, though more testing with shorter companion crops other than grass is needed to verify the generality of this mechanism.

The positive drying effect of using a shorter companion crop (grass) was not associated with a significant increase in the number of particles arriving in the potato strip. However, using grass as a companion species influenced the susceptibility of the potato plants; leaflets taken from potato-grass were more susceptible to in vitro *P. infestans* inoculations than those from the monoculture. The short grass creates a more open canopy for the neighbouring potato strip, possibly exposing these potatoes to more mechanical stress from wind than those in monoculture. This stress can affect leaf traits, and has been reported to, among others, reduce leaf mass and leaf area (Anten et al., 2010). Interestingly, we observed that the outer potato rows of potato-grass had a significantly lower SLA than the inner rows, and the leaflets from these outer rows also tended to develop more lesions than the inner rows. In potato-maize a similar association between SLA and susceptibility was found; the outer rows had a significantly higher SLA compared with the inner rows, and leaflets from those outer rows tended to develop fewer lesions in vitro inoculation than leaflets from the inner rows. However, previous work on other species showed that leaves with low SLA are more resistant against fungal pathogens (O'Hara et al., 2016; Toome et al., 2010), possibly because these leaves are not infected as easily as thinner leaves (with high SLA). The response of detached leaves is, however, not always representative of attached leaves (Liu et al., 2007); and the detached leaf assay was only performed once during the season. A repetition of the detached leaf assay in 2024 did not confirm the current findings, stressing the need to investigate the reproducibility of these trends within and across seasons more closely.

Maize as a companion crop acted as a barrier for incoming particles to the neighbouring potato strip. Over the growing season, potatoes strip-cropped with maize received the lowest number of particles; we found an average reduction of 36% compared with potato monoculture. Such a reduction would logically translate to a proportional decrease in the incidence of primary infections caused by spores originating from outside the strip. Similarly, in an intercrop of pepper (*Capsicum annuum*) and maize, maize functioned as a physical barrier, lowering spore density within the pepper canopy, resulting in reduced anthracnose incidence (Gao et al., 2021). The height of the companion crop species likely influences how effective it will be as a barrier for spore dispersal. However, other aspects of the companion species, such as the leaf area density, are likely also important (Shtaya et al., 2021). This reasoning is supported by a model comparison that showed that the identity of the companion crop had greater explanatory power than the height of the companion crop alone. Although faba bean was slightly taller than potato, it did not provide an effective barrier, possibly due to its lower leaf area density (m^2 leaf per m^3 canopy volume) and earlier senescence (in late July) as compared to maize. In another intercrop experiment, while similar in height, barley, which produced more biomass than wheat, was more effective than wheat in reducing powdery mildew on pea (Villegas-Fernández et al., 2021).

Interestingly, within the potato-maize system, there was a trade-off between the barrier effect and the microclimate effect, and both effects varied over time but in opposite directions. The humidity increased in the potato strips next to maize, especially later in the season when maize was taller than potato and when late blight already had established. Dense crop canopies increase relative humidity and consequently the leaf wetness duration, due to reduced air circulation and slower leaf drying (Monteiro et al., 2006; Rowlandson et al., 2015; Vidal et al., 2017). While maize functions as a barrier, it may have thus in addition have created more conducive conditions to infection and epidemic progress.

Furthermore, the presence of maize also affected the morphology of the potatoes. We observed that the plants in the outer rows of the potato strip were taller than those in the inner rows; likely due to shading by the maize. Shading-induced elongation can influence plant and crop porosity, potentially affecting pathogen development (Calonnec et al., 2013; Tivoli et al., 2013). However, crop porosity (measured by light interception at different layers in the potato canopy) was not affected by strip cropping with maize, compared with the monoculture. It is therefore unlikely that strip-cropping induced changes in porosity, which subsequently could affect disease development.

Strip cropping with faba bean (slightly taller than potato) only slightly and not significantly lowered the duration of periods with high relative humidity in the potato canopy compared with potato monoculture (Table 4.2). Additionally, potatoes strip-cropped with faba bean received a similar number of particles as those in potato monoculture, and the morphology of potato plants was not significantly affected by faba bean. These findings suggest that the reduction in disease that was obtained by strip cropping with faba bean may have been due to a reduction in the area of potato, thereby resulting in spores landing on non-hosts which would tend to interfere with the rate of secondary spread. Similarly, simulation studies of spatially heterogeneous mixtures of susceptible and resistant potato plants show that as the number of susceptible units decreases, the probability of pathogen inoculum reaching another susceptible genotype also declines, as more inoculum is lost to non-hosts (Skelsey et al., 2005). In potato-grass, both the reduced potato area and the less conducive microclimate work together to enhance disease suppression, thereby leading to a higher disease suppression than in potato-faba bean. In potato-maize, while the barrier effect on spore dispersal is beneficial, the more humid microclimate may counteract these advantages, thus leading to a slightly lower disease suppression than in potato-grass.

4.4.1 Practical implications

We measured various disease-suppressive mechanisms throughout one growing season. The strength of the various mechanisms will likely vary from year to year, depending on, for instance, the timing of the arrival of the first *P. infestans* spores in the field and the prevailing weather conditions during a certain year. For example, if the epidemic had started earlier in the season, maize would have been smaller in stature, which could have led to a reduced barrier effect against spore introduction. This was the case for the growing season of 2024 when late blight arrived early in the season, and maize was less effective in suppressing late blight than in the season reported here (Homulle et al., 2024). Hence, we speculate that strip-cropping potato with maize is a riskier disease-suppressive strategy compared to strip-cropping potato with a shorter companion crop, although the latter system might also fail in years with exceptionally high relative humidity. Indeed, grass-clover as a companion crop was more consistently effective than wheat in suppressing late blight (Bouws & Finckh, 2008). Although the strength of each mechanism may vary from year to year according to the prevailing weather and the time of onset of late blight epidemics, we expect the effect obtained by host dilution will always be present. Multi-year experiments would be required to test the consistency of mechanisms across growing seasons. Additionally, modelling might be an option to explore the relative effects of different factors, helping to simulate and predict outcomes of strip cropping under varying conditions.

Research is needed to explore how the disease-suppressive effect varies with strip width. When strip cropping is done with wider strips, the conditions in the inner rows become more similar to monoculture (van Oort et al., 2020). For instance, in wider strips, the advantage of the less favourable microclimate in potato-grass could be diminished. Strip cropping potato with 6 meter wide strips has indeed been found less effective in suppressing late blight than strip cropping with strips of 3 meter (Ditzler et al., 2021). This observation aligns with the concept of Genotypic Unit Area (GUA), where increasing the area occupied by a single host genotype (increasing strip size) decreases interaction between species, leading to easier disease spread (Garrett & Mundt, 1999). In theory, strip widths smaller than 3 meter would lead to stronger disease suppression. From the perspective of spores dispersing from within the potato canopy, it might be beneficial to have more intimate mixing of hosts and non-hosts, but turbulence and wind speed patterns will also change, making it hard to predict actual disease suppression. Strip width is thus an important factor affecting the disease-suppressive effect of strip cropping and requires careful consideration when designing strip-cropping systems. In such designs also labour costs related to management complexity and machine use will have to be considered.

4.5 Conclusion

Various disease-suppressive mechanisms play a role in intercrop systems, and different companion crop species suppress disease through different (combinations of) mechanisms. Grass as a companion crop reduced the duration of humid conditions in the potato canopy, and it reduced late blight severity most out of the three different companion crops, suggesting that an unsuitable microclimate might be more important for suppressing late blight development than a reduction in incoming spores as the latter is partly countered by an increased humidity. A significant barrier effect was observed in the potato-maize, but the tall maize strips resulted in enhanced humidity in the strip-cropped potatoes, which counteracted the disease-reducing barrier effect. Additionally, even if a companion crop species reduces the number of incoming spores, the few spores that manage to reach the potato canopy can start a late blight epidemic which can then spread quickly within the strips. Humidity, on the other hand, plays a major role at various stages in the disease cycle of potato late blight, and unsuitable conditions can thus slow down the progress of the epidemic. Moreover, since the barrier strategy depends on the companion crop reaching sufficient height before the epidemic begins and the time of arrival of the pathogen is hard to predict, it is presumably a less reliable disease-suppressive strategy across different growing seasons. The findings in this paper provide useful clues on how the choice of companion species with specific traits can best assist in disease control by strip cropping.

Acknowledgements

We would like to thank Peter van der Putten and the Unifarm staff for managing the field experiments.

Supplementary material A

Fig. SA4.1 Map of the location of the experimental sites (red rectangles). The two experimental sites were located at approximately 850 meter distance from each other.

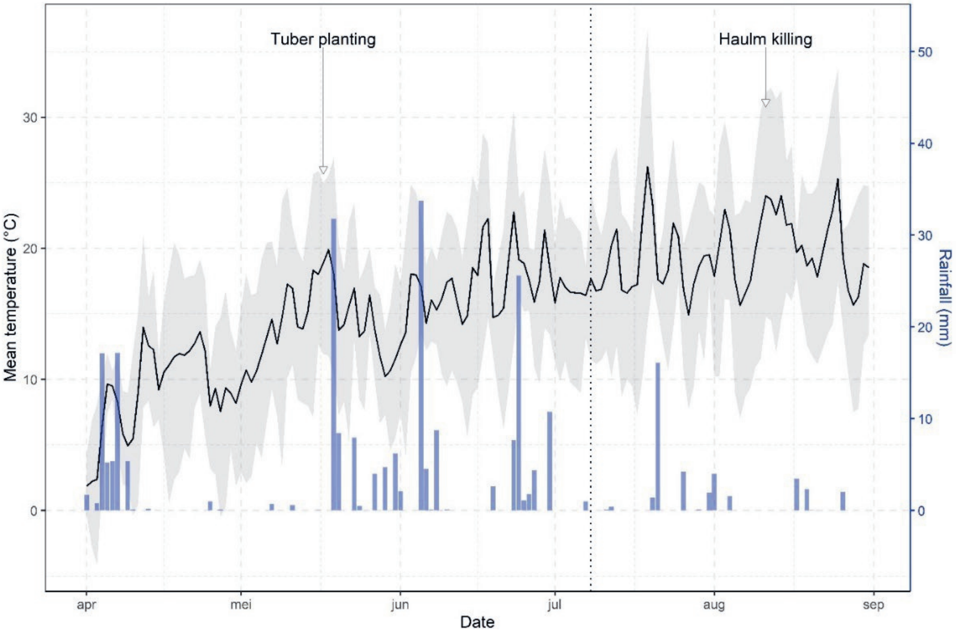


Fig. SA4.2 Weather conditions during the 2022 growing seasons. The vertical dotted line mark the first detection of late blight. Black lines show mean temperature (degrees Celsius), grey ribbons span daily minimum and maximum temperatures, and blue bars are the total daily precipitation (mm). The dashes on the x-axis indicate the first of each month. Data was obtained from weather station De Veenkampen operated by Wageningen University, located approximately 3 km west of the experimental site.

Method SA4.1 Passive spore traps

Passive spore traps were designed to catch particles from the air onto greased microscope slides. The spore trap consists of a 33 cm long cylinder, with a 12.5 cm diameter, through which wind can pass. Attached to the cylinder is a trapezoid shaped fin, which ensures the movement of the cylinder to face into the prevailing wind (Fig SA4.3). Both cylinder and fin were made of PVC. The cylinder was placed on a wooden pole of 150 cm, connected with a 20 cm long stud screw running throughout the cylinder. The stud screw was secured by a bolt and metal spacers at the top and the bottom of the cylinder, to ensure the cylinder was able to spin freely in the wind.

For within the cylinder, a microscope slide holder was made, which holds three microscope slides at a 45 degree angle (Fig SA4.4). As wind passes across the surface of the greased slides, fine particles are captured on their sticky surfaces.

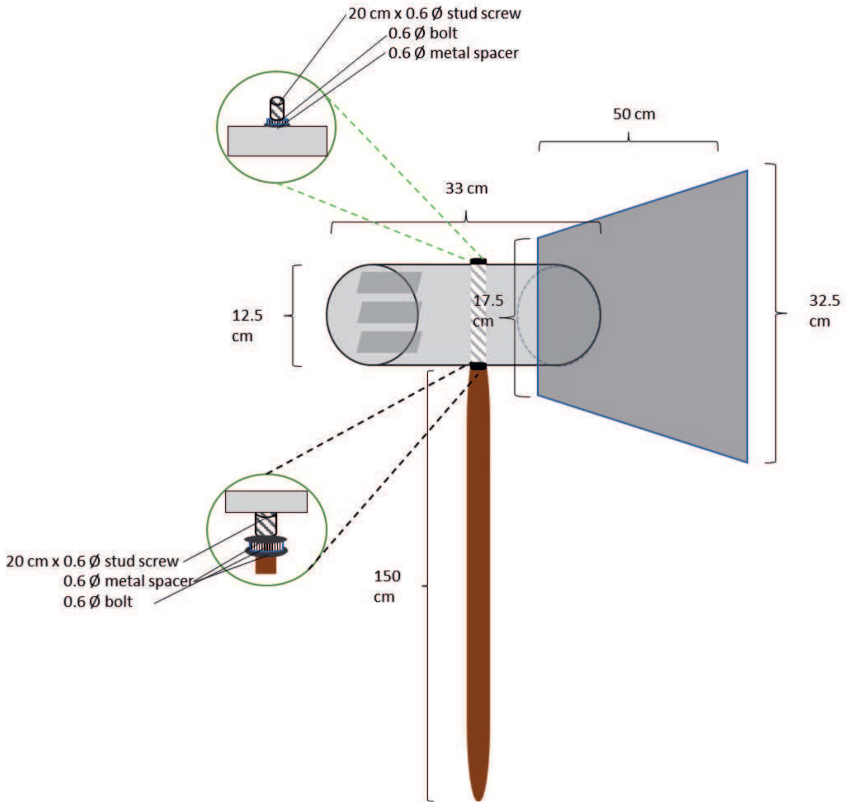


Fig. SA4.3 Schematic drawing of a passive spore trap, with the dimensions of the different parts. Inside the cylinder, three microscope slides are depicted.

Fig. SA4.4 Picture of the microscope slide holder inside the cylinder of the spore trap. The holder can hold three microscope slides at a 45 degree angle.

Method SA4.2 From wind direction to a measure of perpendicularity

Wind direction at the periphery of the field was measured every 10 minutes, returning a value between 0 and 360 degrees. This value was recalculated to a value between 0 and 1 to represent the perpendicularity of the wind in relation to the direction of the strips, using equation 1. The +20 in the equations accounts for the positioning of the strips in the 70-250 degree direction. (Fig SA4.5). For example, if the wind came from a 250° direction, which is parallel to the strips, the perpendicularity would be 0. In contrast, if the wind came from a 160° direction, which is completely perpendicular to the strips, the perpendicularity would be 1. With this recalculation, wind with similar perpendicularity in relation to the strips, but coming from a different direction in degrees, would be classified similar. For example, wind coming from either a 200° or 20° direction, both has a perpendicularity of 0.77.

$$Perpendicularity = | \, cos \, \frac{(Wind\ direction\ degrees + 20) * \pi}{180} \, |$$

Eq. 4.1

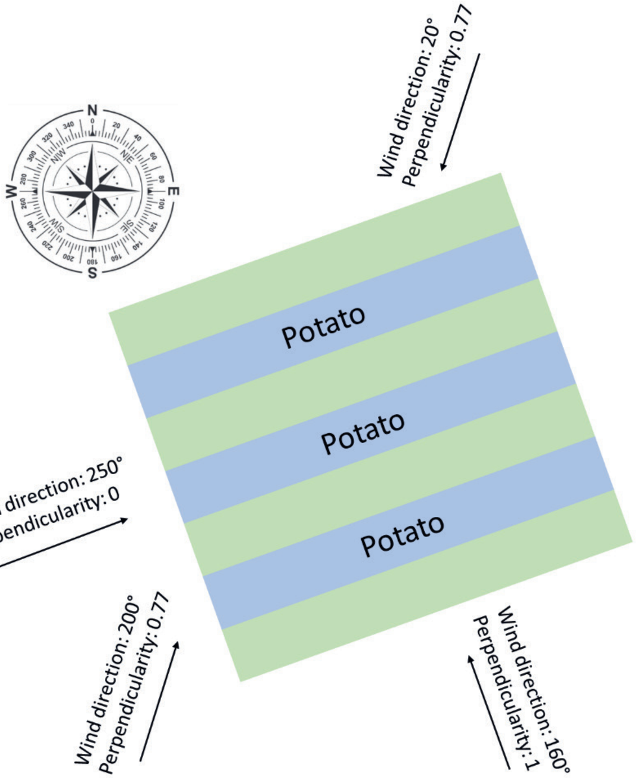


Fig. SA4.5 Schematic overview of the orientation of the strips, and examples of different wind directions and their level of perpendicularity in relation to the orientation of the strips. Perpendicularity was calculated using Equation 4.1.

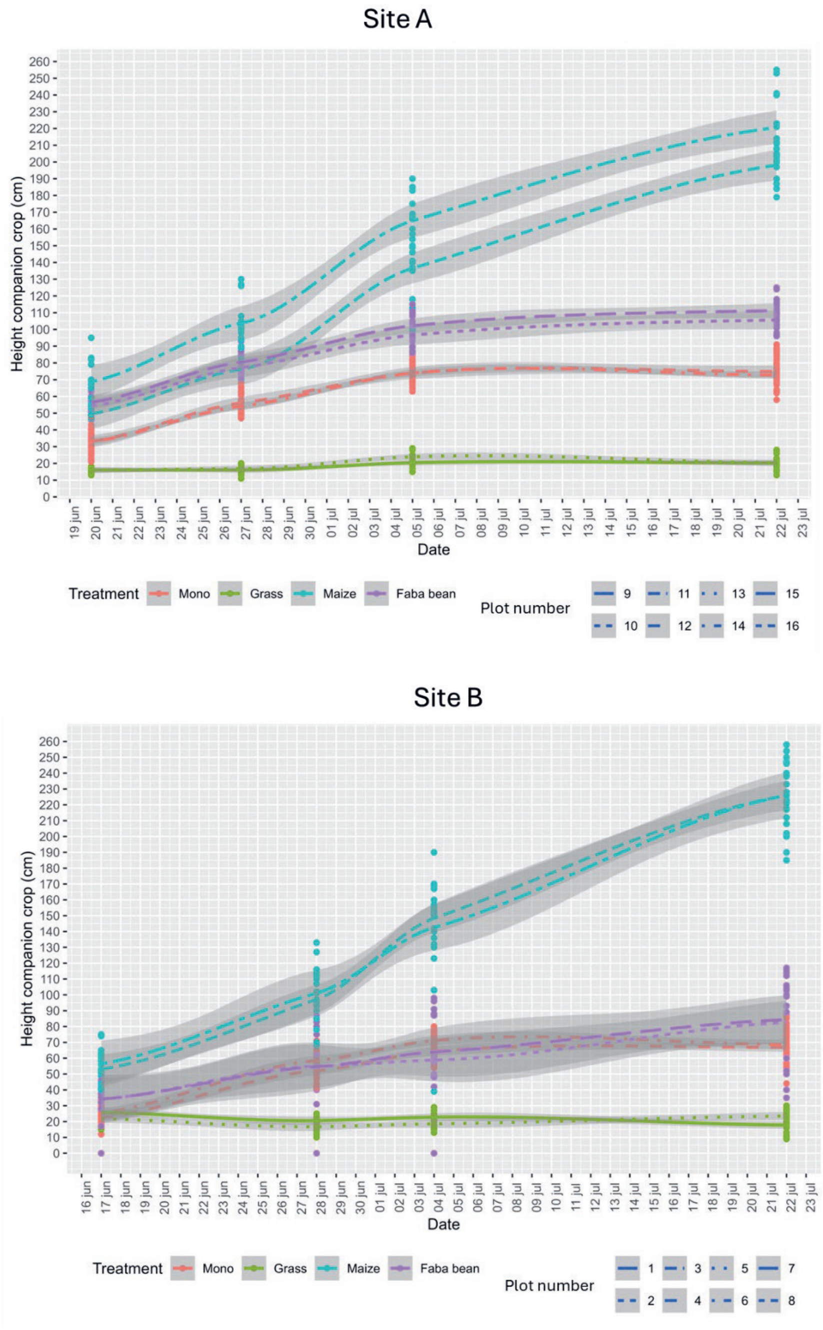


Fig. SA4.6 Height of the companion crops of the strip-crop treatments with grass, maize or faba bean, at site A and B. For Potato plants grown in monoculture (mono), height of the neighbouring potato plants are presented. Points represent the measured heights, the dotted line represents the interpolation, which was used to estimate the daily height.

Table SA4.1 Summary of the fitted models to the particle count data. + means additive effects are assumed, while * means main effects and interactions are estimated. A slash / before a random effect means that it is nested in the preceding random effect to the left of it.

#	Fixed effect	Random effect	Distri-bution	dispformula	Log-likelihood	AIC
1	Treatment * Wind Speed + Slide	Day ; Site/Trap/Slide	NB-2	Treatment + Slide	-13323.1	26686.2
2	Treatment * Wind Direction + Slide	Day ; Site/Trap/Slide	NB-2	Treatment + Slide	-13326.7	26693.4
3	Treatment + Slide	Day ; Site/Trap/Slide	NB-2	Treatment + Slide	-13337.5	26707.0
4	Treatment + Slide	Day ; Site/Trap/Slide	NB-2	Treatment	-13341.6	26711.2
5	Treatment + Slide	Day ; Site/Trap/Slide	NB-2	Slide	-13356.1	26738.2
6	Height companion * Wind Speed + Slide	Day ; Site/Trap/Slide	NB-2	Height companion + Slide	-13356.0	26740.1
7	Treatment + Slide	Day ; Site/Trap/Slide	NB-2	-	-13360.2	26742.3
8	Treatment + Slide	Day ; Site/Trap/Slide	NB-2	Location	-13359.4	26742.8
9	Height companion + Slide	Day ; Site/Trap/Slide	NB-2	Height companion + Slide	-13365.7	26755.4
10	Treatment	Day ; Site/Trap/Slide	NB-2	-	-13381.6	26781.2
11	Treatment	Day ; Site/Trap/Slide	NB-1	-	-13603.2	27224.4
12	Treatment * Wind Speed * Wind Direction + Slide	Day ; Site/Trap/Slide	NB-2	Treatment + Slide	-13310.6	26677.1

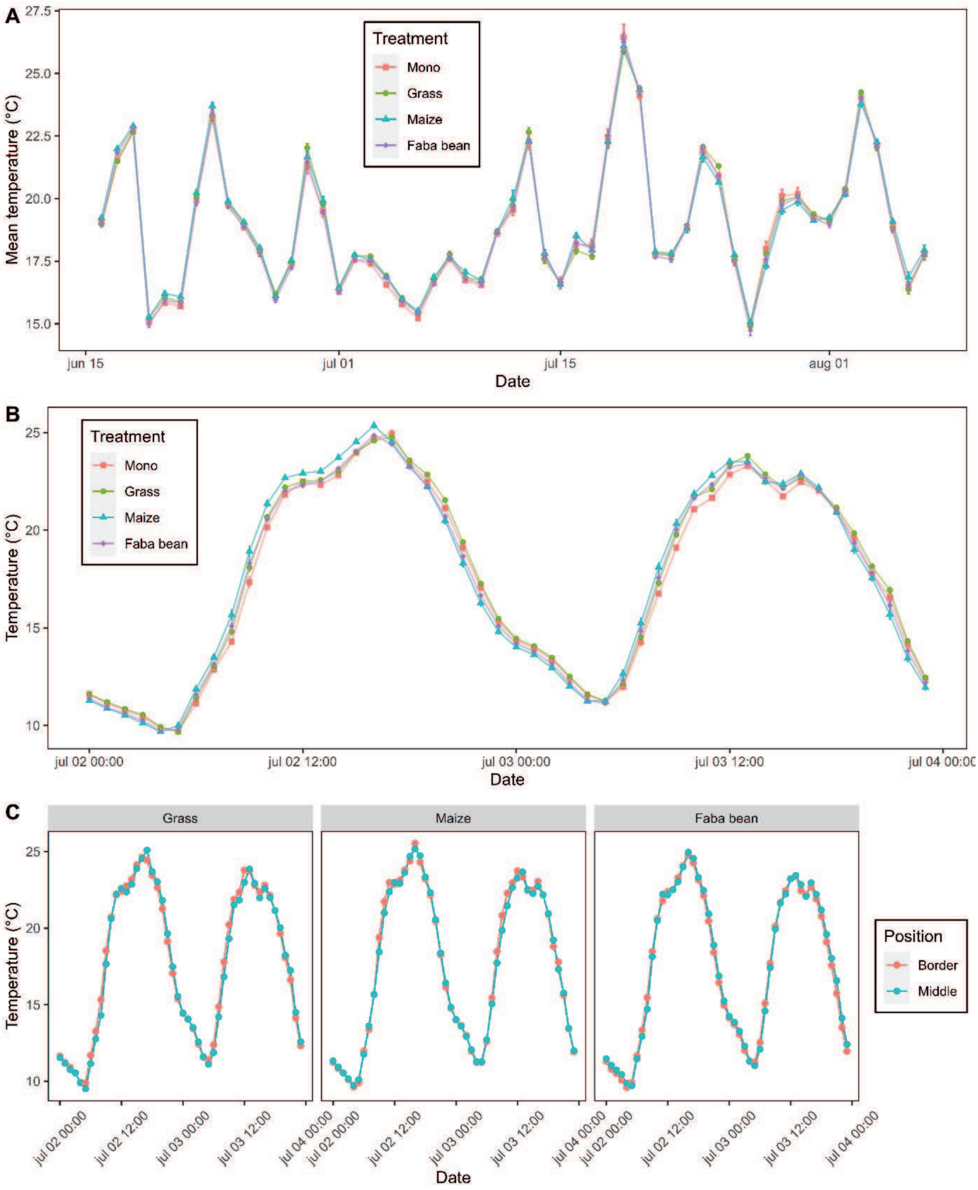


Fig. SA4.7 Temperature in the potato canopy for potatoes either grown in monoculture (Mono), or strip-cropped with grass, maize or faba bean. (A) Mean daily temperature for each treatment across the growing season. (B) Hourly temperatures for each treatment between 2 and 4 July. (C) Hourly temperatures of the inner and outer rows of potato strips in the strip cropping treatments between 2 and 4 July.

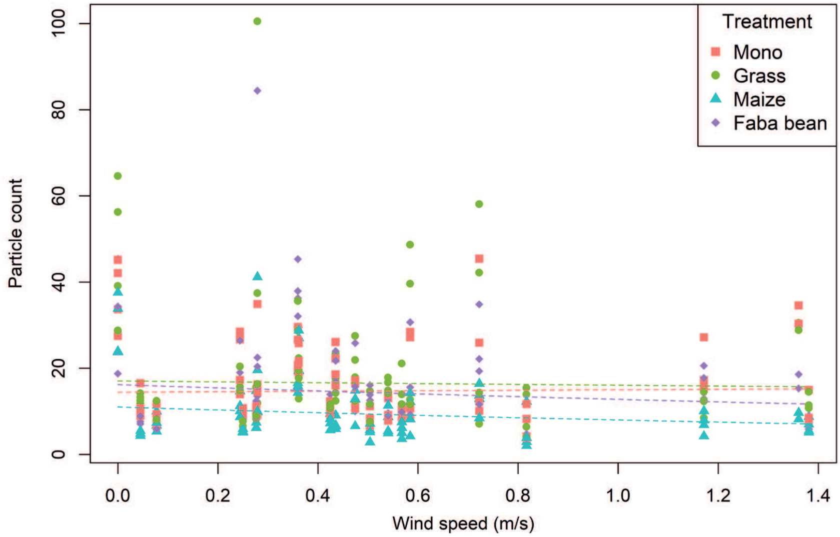


Fig. SA4.8 Particle count in the potato canopy in relation to the wind speed in the 17 hours preceding collection of the microscope slides. Particles with a size between 314-1257µm2 were considered in the potato canopy for potatoes either grown in monoculture (Mono), or strip-cropped with grass, maize or faba bean. Particles were counted on 4 areas per microscope slide, each covering 19.63mm^2. Dots represent average particle counts per spore trap per day. Increasing wind speeds were associated with significantly lower particle counts in potato-maize or potato-faba bean than the monoculture ($p < 0.001$ for both comparisons) or potato-grass (grass-maize: $p = 0.006$; grass-bean: $p = 0.09$).

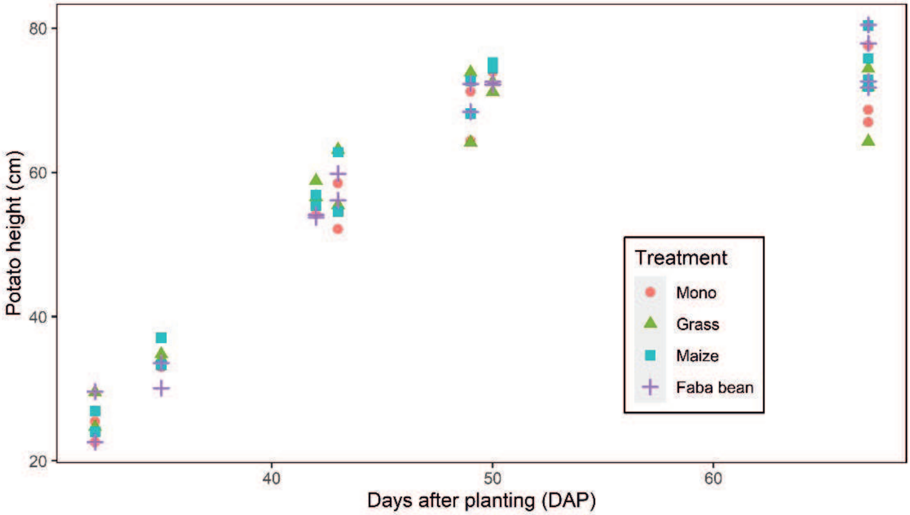


Fig. SA4.9 Height of potato plants grown in monoculture (mono), or strip-cropped with either grass, maize, or faba bean across the growing season. Points represent the mean potato height per plot.

Table SA4.3 Proportion of total PAR captured at four levels in the canopy of potatoes grown in monoculture or strip-cropped with grass, maize, or faba bean and its standard deviation.

Treatment	Canopy level			
	Above canopy (86cm)	High canopy (58 cm)	Middle canopy (28 cm)	Low canopy (0 cm)
Monoculture	0.93 ± 0.05	0.61 ± 0.20	0.19 ± 0.16	0.07 ± 0.05
Grass	0.90 ± 0.06	0.58 ± 0.22	0.18 ± 0.16	0.06 ± 0.05
Maize	0.90 ± 0.06	0.49 ± 0.20	0.12 ± 0.08	0.05 ± 0.04
Faba bean	0.91 ± 0.05	0.53 ± 0.18	0.14 ± 0.09	0.06 ± 0.05

Supplementary material B Data collected in other experimental years

The strip-crop experiment presented in the main text was replicated in 2021 and 2024 using a similar setup (see Chapter 3 for details of these experiments).

Below, we present the data from these additional growing seasons, including microclimate measurements, plant height, and detached leaf assay. These data allow for a broader understanding of year-to-year variability.

Microclimate

In 2021, three sensors were employed per treatment. In 2024, two sensors were used in each strip-crop plot, while one sensor was used per sole potato plot.

Across the three years, temperature within the potato canopy was not systematically influenced by strip cropping, and we also found no differences among different companion crop species (Fig SB4.3).

The daily duration of relative humidity above 90% was substantially lower in potato-grass than in the potato monoculture around the time of the first late blight finding in the field in both 2021 and 2022 (dotted line in Fig SB4.4). This difference between potato-grass and potato mono was not observed in 2024. The 2024 potato growing season was substantially shorter than 2021 and 2022 as potato plants had to be desiccated on 9 July, which could explain why no effects were observed.

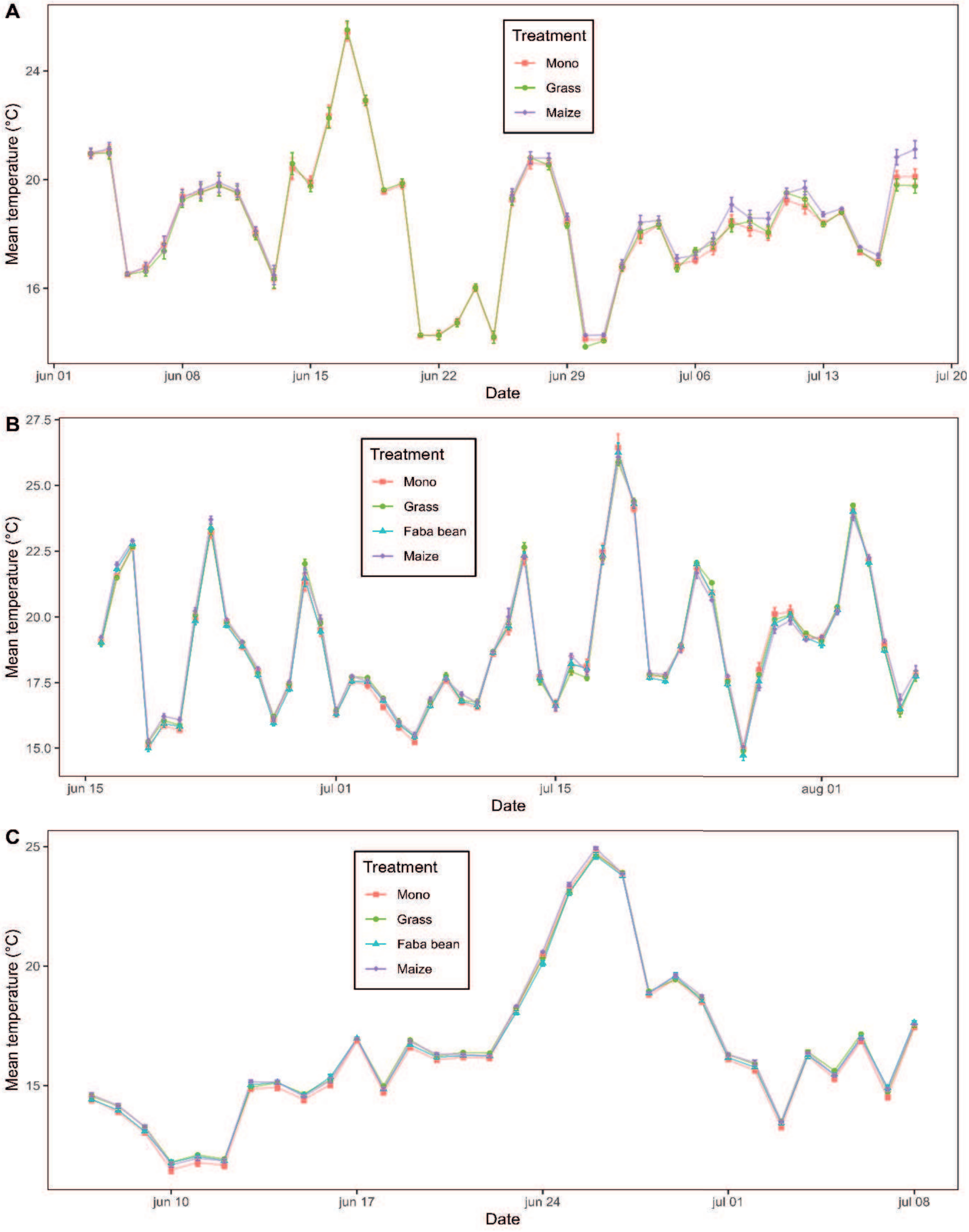


Fig. SB4.3 Temperature in the potato canopy for potatoes either grown in monoculture (Mono), or strip-cropped with grass, maize or faba bean, during the 2021 (top), 2022 (middle) and 2024 (bottom) growing season.

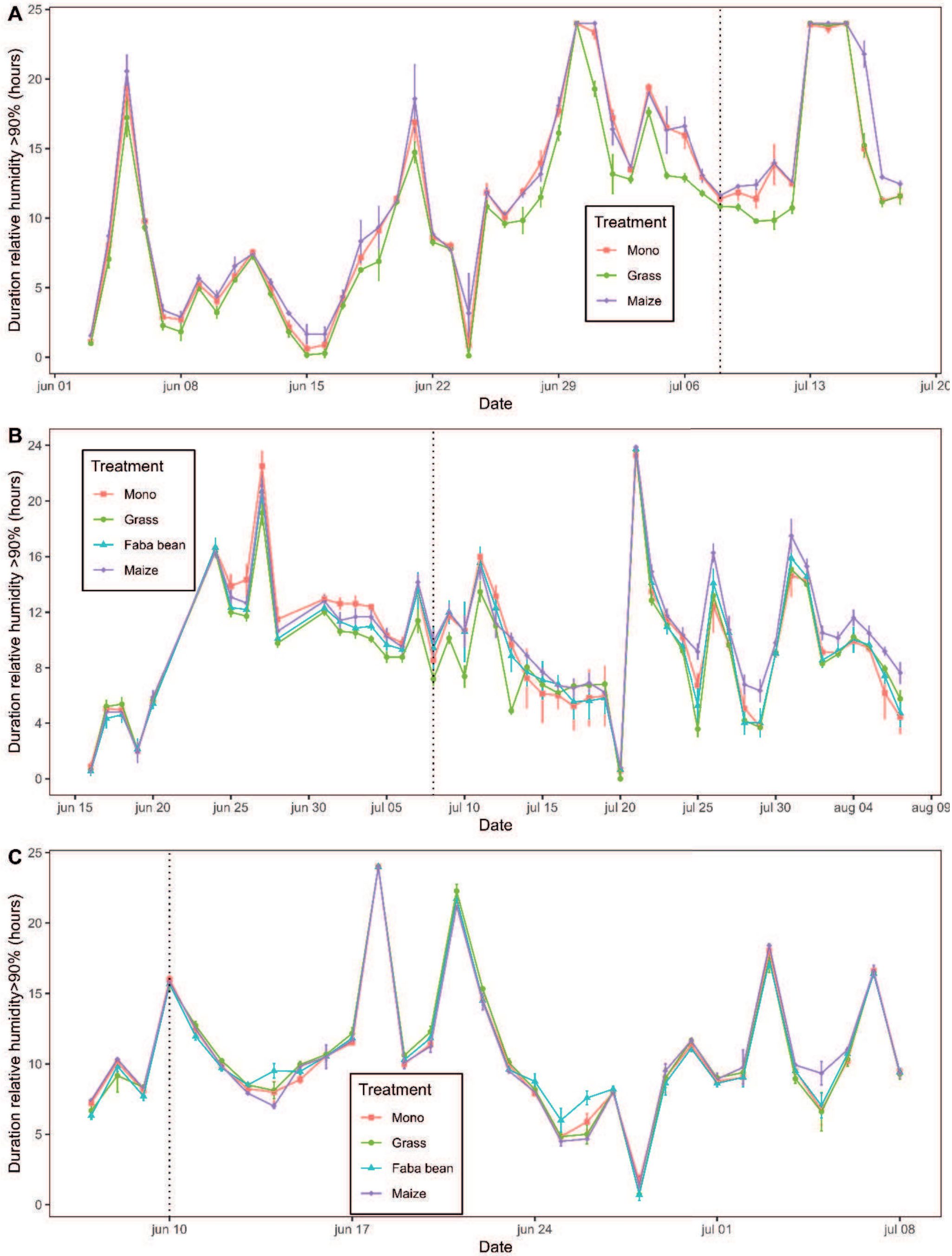


Fig. SB4.4 Daily duration (hours) with relative humidity equal to or exceeding 90% in the potato canopy during the 2021 (top), 2022 (middle) and 2024 (bottom) growing season. Vertical dotted line marks the first detection of late blight. Please note: x-axis are not aligned across graphs.

Detached leaf assays

Detached leaf assays were performed in 2021 and 2024.

Leaflets were collected from monocropped and strip-cropped plants at 11 weeks after potato planting in 2021. From each strip-cropping plot, ten leaflets from the inner rows and ten from both outer rows of strip-cropped potato plants were collected. Per monoculture plots, 20 leaflets were collected. Ten leaflets per strip-cropping treatment (five from the inner rows and five from the outer rows) and ten random leaflets from the monoculture plots were inoculated with distilled water only and used as a control. In 2024, leaflets were collected from monocropped and strip-cropped plants at 5 weeks after potato planting. In each strip-cropping plot, eight leaflets were collected from the inner rows and eight from both outer potato rows. In the monoculture plots, ten leaflets were collected. Four leaflets per strip-cropping plot (two from the inner rows and two from the outer rows) and three random leaflets from the monoculture plots were inoculated with distilled water only and used as a control.

In both years, the inoculations followed the same protocol as described in the main text, using the same *P. infestans* strain and dose of sporangia.

In 2021, the leaf assay was performed when late blight was already present in the field. While the collected leaflets were symptom-free, latent infections must have been present on the leaves, as infection were found in the negative control (Fig. SB4.5A). These infections interfere with the infections from the inoculations, making it challenging to assign differences between treatment. The repeat of the detached leaf assay in 2024 showed no significant differences between treatments (Fig. SB4.5B).

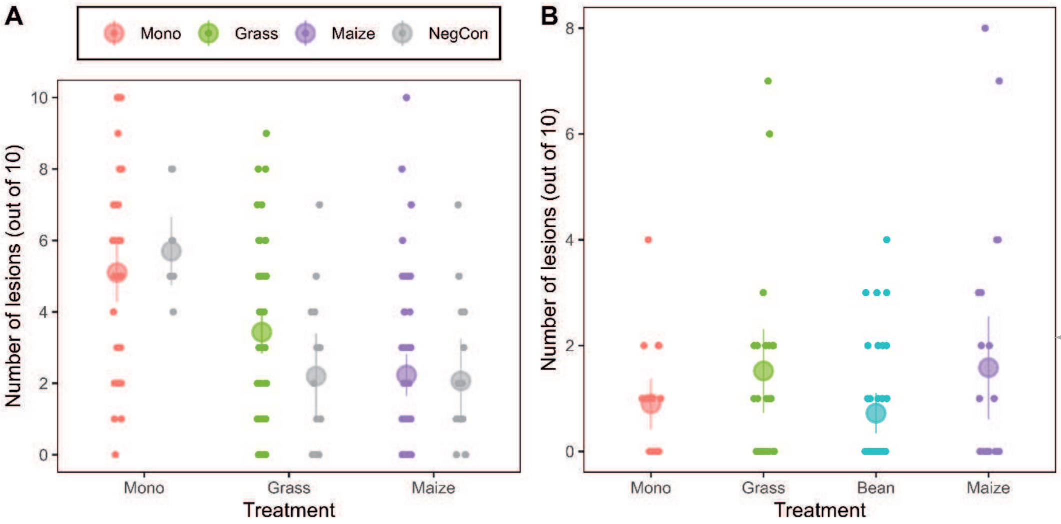


Fig. SB4.5 Detached leaf assay of the 2021 (A) and 2024 (B) growing season. Number of lesions developed out of 10 droplets in detached leaf assay from potato plants grown in monoculture (mono) or strip-cropped with grass, maize, or faba bean. Grey points represent the negative control (inoculation with water). Large circles represent the means and error bars the confidence interval. The smaller points represent individual measurements.

Plant height

The plant height of the potato and each companion crop species was measured in each year. We randomly selected in each plot in each of the three potato strips two transects perpendicular to the strip, with each transect comprising four plants, resulting in a total sample of 24 plants per plot. Per plot, 24 potato plants were selected from both the inner and outer rows of the strips, and their height was measured from the potato ridge until the highest point of the potato plant. The height of 12 companion plants per plot (either grass, faba bean or maize) directly neighbouring the potatoes, was also measured as the distance between the soil surface and the highest point of the plant.

heights dynamics of the companion crops differed from year to year due to differences in planting dates and weather. In 2021, maize started to surpass the potato in height around the beginning of July (Fig SB4.6A). In 2022, maize was already taller than potato in mid-June, whereas faba bean was only slightly taller than potato (Fig SB4.6B). In 2024, faba bean was the tallest of all the crop species for most of the growing season (Fig SB4.6C). These height dynamics across time may influence the spore deposition.

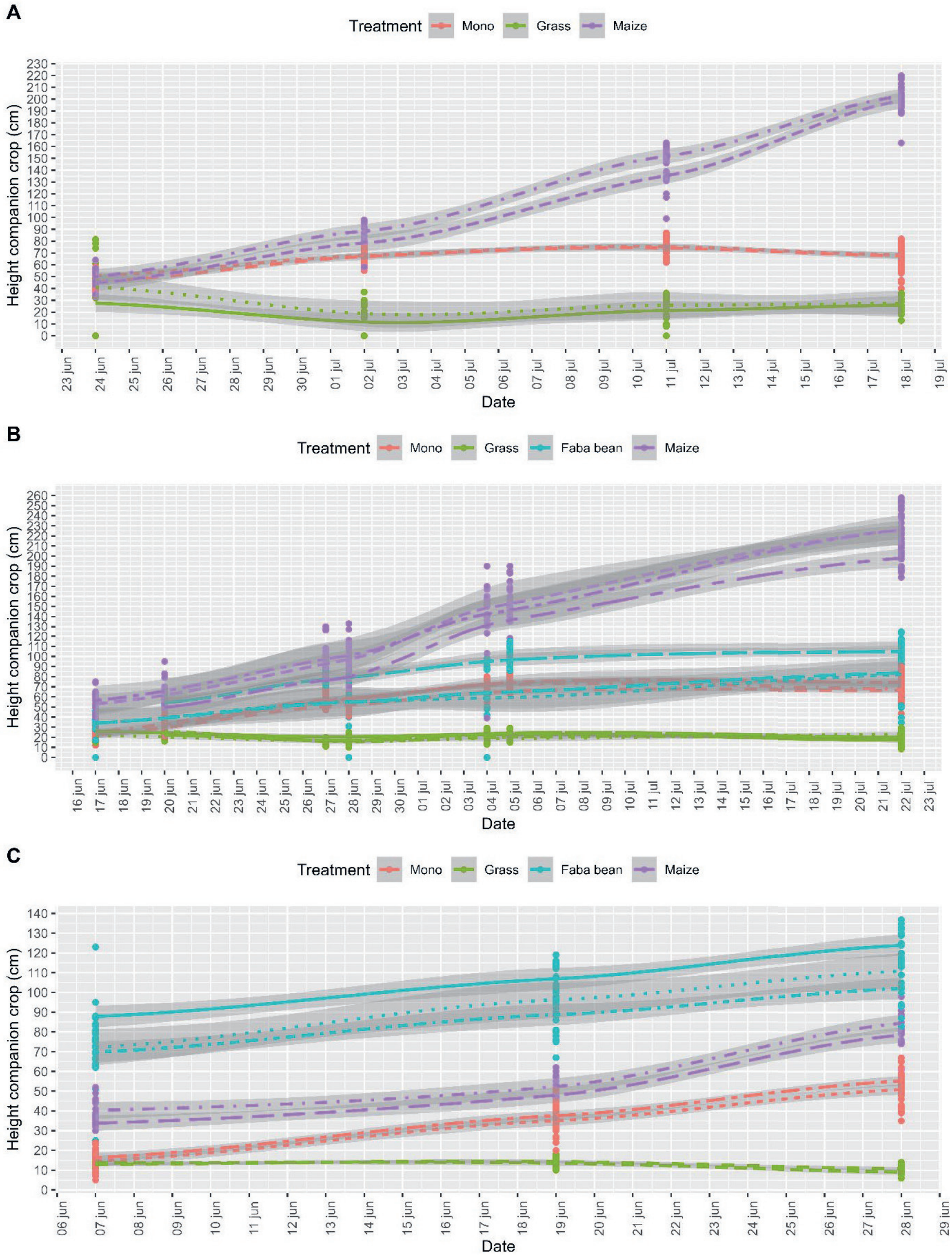


Fig. SB4.6 Height of the companion crops of the strip-crop treatments with grass, maize or faba bean, in 2021 (top), 2022 (middle) and 2024 (bottom). Height of sole potato is given for comparison. For Potato plants grown in monoculture (mono), height of the neighbouring potato plants are presented. Points represent the measured heights, the dotted line is a smoothed curve through the points. Please note: x-axes differ between years.

Across the three years, the different companion crop species did not substantially influence the height of the potato plants (Fig SB4.7).

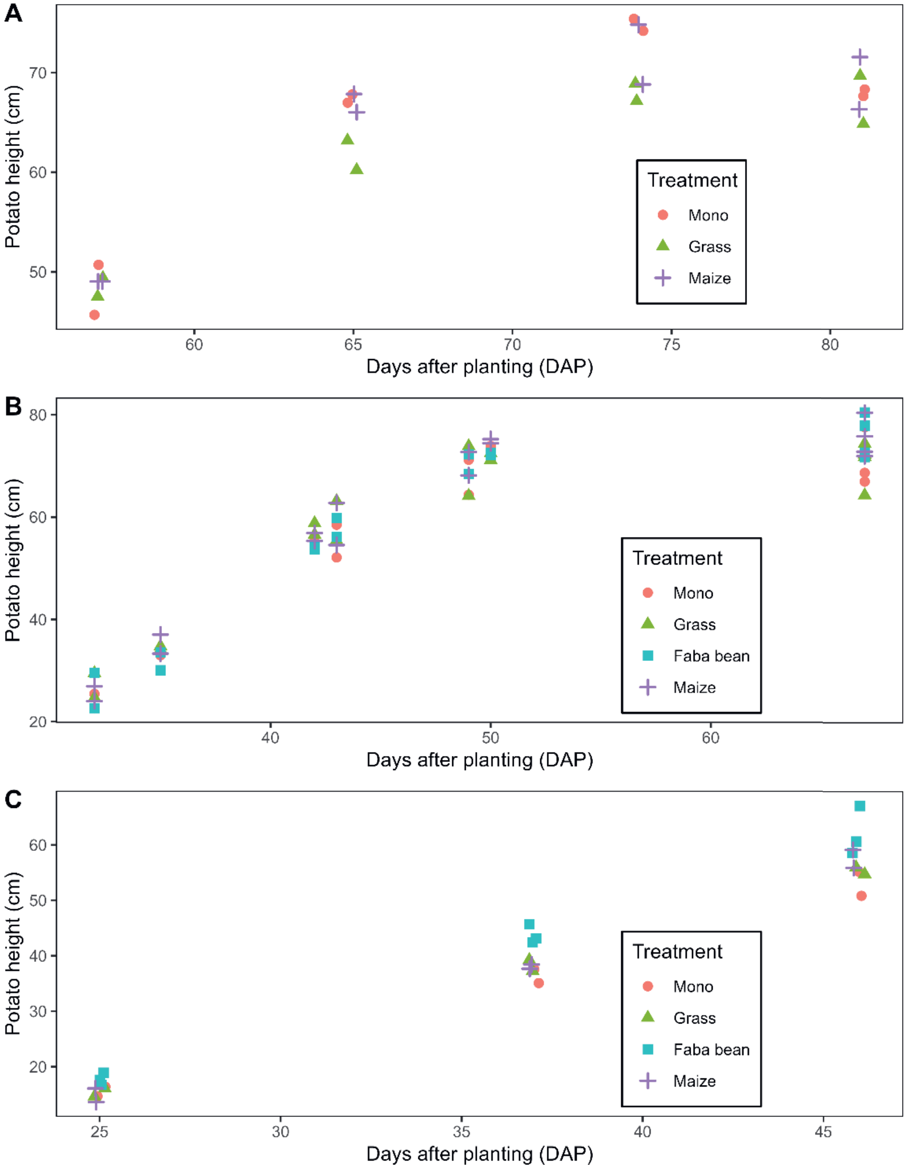


Fig. SB4.7 Height of potato plants grown in monoculture (mono), or strip-cropped with either grass, maize, or faba bean during the 2021 (top), 2022 (middle) and 2024 (bottom) growing season. Points represent the mean potato height per plot. Please note: x-axis are not aligned across graphs.

Chapter 5

Quantifying the relative importance of disease-suppressive mechanisms in species mixtures: a case study of late blight in strip-intercropped potato

Matthew Brandon[1], Zohralyn Homulle[1], Jacob C. Douma[1]

[1]Centre for Crop Systems Analysis, Wageningen University, 6700 AK,
Wageningen, the Netherlands

Abstract

Numerous studies have reported disease suppression in intercropping systems, attributing it to mechanisms such as host dilution, microclimate modification, barrier effect, and induced resistance. However, the relative contribution of these mechanisms to altered disease dynamics remains unclear. We used a combination of field data and modelling to quantify the importance of these mechanisms for the case of *Phytophthora infestans* in intercropped potato. Data from field experiments in which potato was strip-intercropped with faba bean, ryegrass, or maize, were used to estimate effects of disease-suppressive mechanisms. These estimates were integrated into a microclimate-dependent late blight simulation model to predict effects on disease severity. Small differences in relative humidity, due to companion crops, significantly impacted disease dynamics. The model most accurately predicted disease suppression when combining host dilution, microclimate modification and barrier effect, suggesting similar importance of these mechanisms. For each companion crop, mechanisms suppressed disease at different strengths, or counteracted (particularly microclimate modification and barrier effect), but their combined effect remained disease suppressive. This study provides a methodological framework to quantify the contribution of different disease-suppressive mechanisms in intercropping systems, enhancing our understanding of disease suppression in species mixtures, to help design cropping systems less reliant on chemical protection.

Keywords: disease-suppressive mechanisms, dispersal, epidemiology, microclimate, *Phytophthora infestans*, simulation model, *Solanum tuberosum,* strip intercropping

5.1 Introduction

Modern agriculture hinges on the intensive use of pesticides, but there is a demand for more natural pest control in the growing push to transition towards ecological intensification (Kremen, 2020; Tittonell, 2014). Diversification of farming systems at the field and landscape level offers alternative strategies for pest and disease management (van der Werf & Bianchi, 2022). Intercropping, the simultaneous cultivation of multiple crops in the same field for at least part of their growing season (Stomph et al., 2020; Vandermeer, 1992), is recognised for its potential to improve crop yield (Li et al., 2020b; Li et al., 2023), enhance crop stability (Raseduzzaman & Jensen, 2017), improve resource use efficiency (Glaze-Corcoran et al., 2020), and reduce disease pressure (Boudreau, 2013; Chadfield et al., 2022). Notably, disease is suppressed across numerous unique intercrop-disease combinations (Boudreau, 2013; Mundt, 2002; Stomph et al., 2020).

Despite its promising potential, disease reduction in intercropping varies widely across studies. A meta-analysis of cereals mixed with faba bean estimated an average disease reduction of 33%, but this ranged from 20% (± 9%) to 51% (± 21%) depending on the crop and disease (Zhang et al., 2019). Another meta-analysis, covering a broader range of crops, estimated that disease incidence decreased from an average of 36% when sole cropping to 22% when intercropping, although variation in the reduction of disease was substantial (Li et al., unpublished manuscript). Pathogen species, crop family, or the combination of host species and pathogen only partially explained observed disease suppression arising from intercropping.

Disease suppression in intercrops has been attributed to several mechanisms that are introduced by introducing a companion species. These mechanisms include an altered microclimate in the host canopy (i.e., microclimate modification; Boudreau, 1993; Castro et al., 1992; Gómez-Rodríguez et al., 2003; Guo et al., 2021; Schoeny et al., 2010), reduced density of the host crop (i.e., host dilution; Boudreau, 2013; Finckh et al., 2000; Zhang et al., 2019), the companion species acting as a barrier for the dispersal of disease propagules (i.e., the barrier effect; Gao et al., 2021; Gómez-Rodríguez et al., 2003; Schoeny et al., 2010), and companions influencing host plant resistance, through biotic or abiotic interactions (hereafter referred to as induced resistance; Finckh et al., 2000; Gómez-Rodríguez et al., 2007). Host dilution is frequently proposed to be the most important mechanism for disease suppression (Boudreau, 2013; Finckh et al., 2000; Zhang et al., 2019). Reducing the density of the susceptible host (by replacing it with the companion) leads to a reduction in the proportional area of susceptible hosts in a plot, and an increased distance inoculum must travel to infect new hosts (Burdon & Chilvers, 1982). In our study, we use the term 'host dilution' to refer specifically to these spatial effects of host dilution on disease dispersal. This should not to be confused with the term 'dilution effect', which refers to the phenomenon of reduction of disease risk with increased biodiversity (Keesing & Ostfeld, 2021).

By introducing a companion crop, multiple mechanisms are simultaneously evoked to suppress disease. For example, in a pea-cereal intercrop, reduction in *Ascochyta* blight was explained by host dilution, lowered relative humidity, and reduced splash dispersal (Schoeny et al., 2010). Similarly, in a pepper-maize intercrop, the density of anthracnose spores was decreased, along with increased relative humidity, and reduced temperature and sunlight intensity (Gao et al., 2021). These factors were found to be significantly associated with anthracnose disease incidence. In another study, the suppression of tomato early blight in tomato intercropped with marigold or pigweed was attributed to both plants acting as a barrier for spore dispersal and reducing relative humidity (Gómez-Rodríguez et al., 2003). Additionally, marigold exhibited allelopathic effects that inhibited in-vitro spore germination, a response not observed with pigweed.

While these studies shed light on the complex interplay of mechanisms leading to disease suppression in intercrops, they also emphasize the challenges in assessing the contribution of individual mechanisms to overall disease suppression. Disentangling these mechanisms from field experiments can be difficult as the mechanisms may behave differently depending on the introduced companion crop, and they may interact synergistically or in opposition. Most studies fall short of identifying the relative importance of each factor in disease suppression, as they often focus on a single variable or, when assessing multiple factors, only demonstrate correlations without quantifying the relative importance of individual factors to disease suppression. Process-based modelling, and in particular scenario-analysis, can help to disentangle the importance of different mechanisms and quantify their relative contribution. As such it can help to understand how different types of companion crops achieve disease suppression.

Here, we parameterize a process-based epidemiological model using an extensive dataset from a strip-crop field experiment, and by means of scenario analysis we quantify the relative importance of individual mechanisms to overall disease suppression in strip-crop systems. Strip intercropping (or strip cropping) is a form of intercropping where species are alternated in multi-row strips. We use late blight (*Phytopthora infestans*) in potato (*Solanum tuberosum)* strip-cropped with three different companion crops as a model pathosystem for analysing these individual mechanisms. This system is particularly useful because of the dependence of potato late blight on relative humidity and temperature, and these dynamics have been well captured by process-based epidemiological models (Andrade-Piedra, Hijmans, Forbes, et al., 2005; Andrade-Piedra, Hijmans, Juárez, et al., 2005; Bruhn & Fry, 1981; Hjelkrem et al., 2021; Skelsey et al., 2009), making it effective for studying how intercropping influences canopy microclimate and disease development. We use data from field experiments, in which potato was strip-cropped with either faba bean (*Vicia faba)*, ryegrass (*Lolium perenne)*, or maize (*Zea mays)*. These companion crops have different characteristics, such as contrasting stature, and are expected to influence disease dynamics through different mechanisms.

5.2 Methods

5.2.1 Theoretical framework

The approach to quantify the relative importance for disease dynamics of mechanisms introduced by strip cropping consisted of four steps: (1) field measurements were analysed to estimate multipliers for the effect of host dilution, barrier effect and induced resistance on disease in strip crops, (2) baseline parameters of an epidemic model were calibrated using microclimate measured in the monoculture to replicate disease progress as observed in the monoculture, (3) strip-crop microclimate input data and effect multipliers for the additional three mechanisms (host dilution, barrier effect, and induced resistance) were toggled in the epidemic model in different combinations to simulate disease progress assuming various mechanisms to be (in)active, and in (4) these scenarios were compared to severity observed in the field in the contrasting strip crops. A conceptual diagram of the approach described is shown in Fig. 5.1.

The methods are structured as follows. We start by describing the process-based epidemic model of late blight, followed by a description of the measurements that were made in the field. We continue with descriptions of steps 1-4. In step 1, we estimated how model parameters change in response to strip cropping. Next, in step 2 we describe how the model was calibrated to the monoculture disease severity data. In step 3, we ran the model experiments with mechanisms on/off, and in step 4 we compared them to field observations.

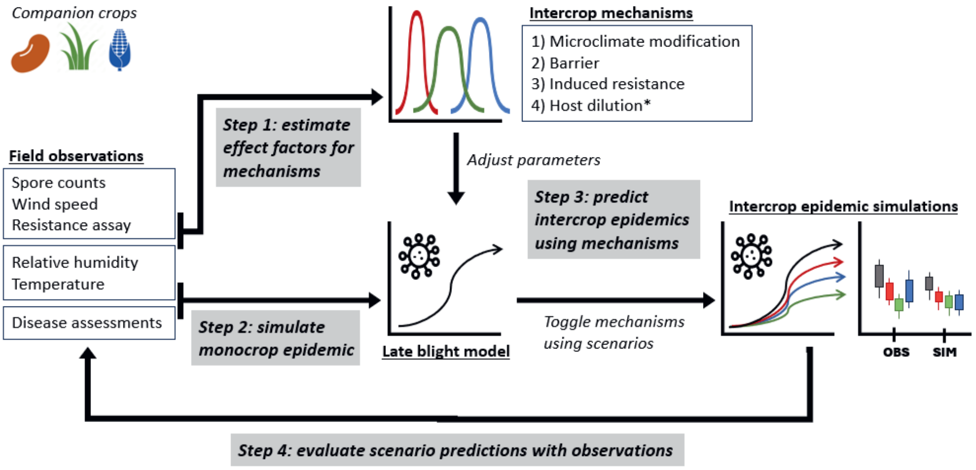


Fig. 5.1 Conceptual diagram of the modelling approach. This diagram outlines the methodology used in this paper to model the effect of disease-suppressive mechanisms in strip crops on late blight epidemics in potato, which consists of four steps. Step 1: field observations are used to estimate effect multipliers which describe the effect of several mechanisms in strip crops relative to the monoculture. Effect multipliers are used (in Step 3) to change the rate parameters in the late blight model. Step 2: a general late blight epidemic model is parametrised to fit observed disease progress in the monoculture. Step 3: disease progress in strip-crop treatments is predicted by inputting companion-specific strip-crop canopy microclimate data and changing model parameters according to the effect multipliers estimated in Step 1; mechanisms are toggled ON/OFF in a full factorial design. Step 4: disease progress under all scenarios is compared with observed disease severity. Refer to the text for more details. *The effect of host dilution was estimated using a spore dispersal model and parameters estimated in a previous study (Paysour & Fry, 1983; Skelsey et al., 2005).

5.2.2 Model description

For the epidemic model, we used an existing process-based model that simulates late blight progression in a potato canopy (BLIGHTTIME, Skelsey et al., 2009). The model takes times series of relative humidity (RH), temperature, and precipitation as input values to calculate rate variables for processes in the infection cycle (e.g. deposition efficiency, infection efficiency, latency progression rate) in addition to host growth (e.g. leaf growth rate, leaf death rate). A conceptual diagram of the model is shown in Fig. 5.2. The model integrates these microclimate-dependent variables to produce an hourly disease severity output—calculated as the proportion of total leaf area that is diseased—over the duration of input data, starting from planting date of the potatoes. We model four different ways that intercropping can potentially affect disease severity. The first is through a changed microclimate. Microclimate data (RH and temperature) measured in the various strip-cropped potato canopies is inputted to the epidemic model to predict how modification of microclimate by companion crops influences disease progression. This is because microclimate affects numerous disease processes and is used in the calculation of nearly all disease rate parameters (blue arrows in Fig 5.2: infection efficiency, lesion growth rate, latency progression, sporulation efficiency, spore deposition efficiency, and lesion inactivation; see Skelsey et al., 2009 for details). Secondly, the effects of host dilution, barrier effect, and induced resistance on disease progress are introduced by modifying corresponding disease process rate parameters with effect multipliers. Specifically, host dilution and barrier effect adjust the deposition efficiency parameter (the proportion of spores landing on potato leaves), while induced resistance adjusts the infection efficiency parameter (the probability that a spore successfully infects a leaf; see Fig. 5.2). See Methods, section ‘Step 1: estimating the effects of companion crops on disease processes’, for details on how these effect multipliers are estimated relative to the monoculture from field data.

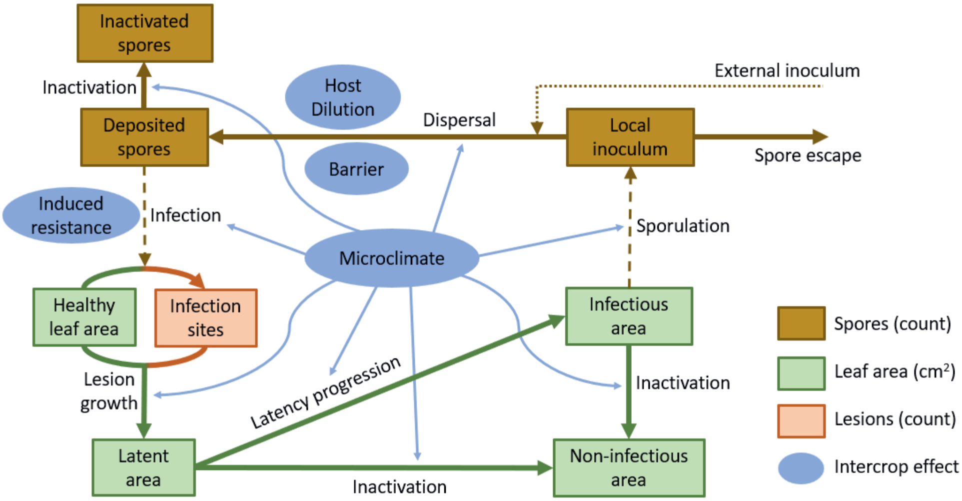


Fig. 5.2 Conceptual diagram of the process-based late blight model and disease processes affected by intercropping. The model was used to predict late blight disease progress as a function of hourly relative humidity (RH), temperature, and precipitation. Disease progress in strip crops is modelled through introducing disease-suppressive mechanisms of strip-cropping. Disease-suppressive mechanisms are represented by the blue ovals and are positioned adjacent to the disease process they affect. For the effect of microclimate modification, blue arrows indicate the processes dependent on microclimate. Green boxes represent host leaf area state variables (healthy and diseased), brown boxes are spore number state variables, and the single red box represents the number of lesions, which is required to model variable latency progression. Solid green and brown arrows indicate flows within leaf area or spore number state variables, respectively. Dashed brown arrows depict the flow between leaf area and spore number state variables, either through the deposition of spores on leaves and subsequent infection, or through sporulation from leaves. The dotted brown arrow represents the initial introduction of external inoculum into the system. The host growth model components have been excluded for simplicity. Note that rainfall does not vary in response to treatment, but it is used in the estimation of leaf wetness upon which infection is dependent.

To illustrate how effect multipliers for disease-suppressive mechanisms have been implemented in the model, we provide an example for how infection efficiency is calculated within the model for potato grown with different companions. Infection efficiency (IE_{it}) at time t, for potato intercropped with crop *i* is calculated as:

$$IE_{it} = IE_{max} * f(T_{it}, RH_{it}) * rIE_i$$

IE_{max} is a model parameter for the maximum infection efficiency possible in a monoculture. IE_{max} is adjusted according to the temperature and relative humidity in treatment i at time t by multiplying by $f(T_{it}, RH_{it})$, which represents the effects of temperature and relative humidity on infection efficiency and as such accounts for differences in microclimate induced by strip cropping with companion crop *i*. The infection efficiency can be further adjusted by multiplying with rIE_i, a parameter that accounts for the effect a companion crop i has on infection efficiency, for example by inducing resistance (e.g., as measured in a detached leaf assay). In all monoculture simulations this multiplier (rIE_i) is set to 1. Fig. 5.3 provides a visual example for how infection efficiency varies depending on temperature and RH (at 100% and 90%), and mock treatment 'Strip A' lowers the infection efficiency compared to the monoculture.

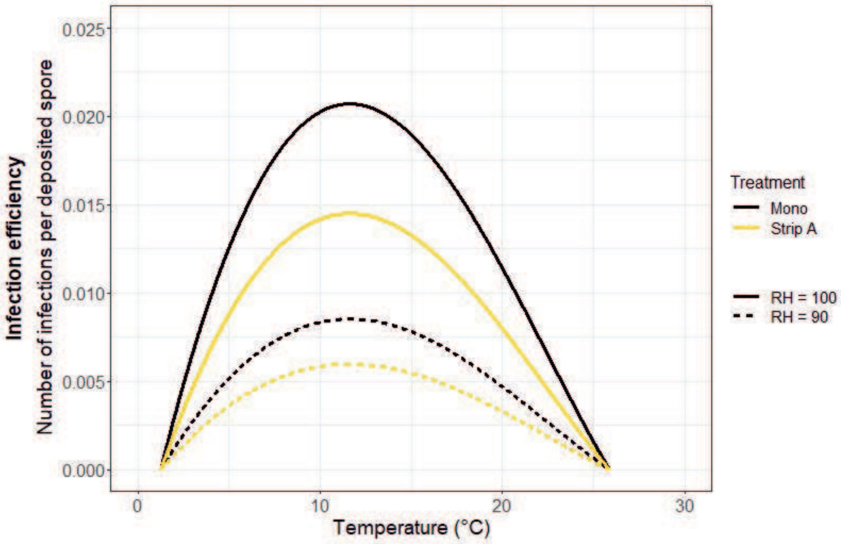


Fig. 5.3 Illustrative example of how the effect of companion crops on infection efficiency is implemented in the model. The maximum infection efficiency IE_{max} for monoculture is 0.021 at approximately 11.6°C; the real infection efficiency is calculated at each time step dependent on measured hourly relative humidity and temperature. If a strip crop is simulated, this is then modified both by using the measured microclimate data specific to the strip crop and by multiplying the infection efficiency with the effect multiplier representing the effect of induced resistance (as measured through a detached leaf assay). The relative infection efficiency effect multiplier used for Strip A is 0.7; this is a mock value which is used in this figure as an example (the effect of strip cropping may also be disease enhancing).

5.2.3 Field set-up and experimental measurements

The main data used in our approach was collected in a field experiment conducted at the organic experimental farm of Wageningen University, the Netherlands (51.99°N, 5.65°E), between April and August 2022 (Chapter 3). The experiment included four treatments with four replications each, divided across two locations about 800 m apart: (1) a monoculture potato treatment (‘mono’), and (2) potato-faba bean (‘bean’), (3) potato-ryegrass (‘grass’) and (4) potato-maize (‘maize’) strip-intercropping treatments. Each plot measured 21 m x 24 m. A replacement design was used, with strip-crop plots divided into 7 strips of equal 3 m width, alternating over four companion strips and three potato strips. In all plots, potato (cv. Agria) was planted on 17 May 2022 at a row distance of 75 cm and an intra-row distance of 40 cm; in the strip-crop plots this resulted in strips of four rows. Agria is moderately resistant to foliar late blight. In respective plots, faba bean (cv. Cartouche) was planted on 3 May in six-row strips, while maize (73% autens KWS/27% LG30.179) was planted on 29 April in four-row strips. Ryegrass was also sown on 29 April.

Throughout the growing season, measurements were collected for (1) disease severity, (2) canopy microclimate, (3) spore dispersal and (4) host resistance (Table 5.1). Disease severity (1) was assessed for 24 potato plants in each plot seven times between the first observation of late blight symptoms on 8 July 2022, until termination of the crop on 11 August 2022; the plants to be monitored were selected with stratified random sampling. Initially, infected leaflets were counted, and later severity was visually estimated. In three plot repetitions of each treatment, canopy temperature and relative humidity (2) was logged every 10 minutes from 16 June until 9 August at either the center of the monoculture plots, or at two central positions in each strip-crop plot: within the middle potato strip, and at the border row of the middle potato strip. Before June 16, local weather data was used to simulate leaf area growth in potato. To evaluate spore dispersal (3), wind speed was measured at the periphery of the field every 10 minutes. A trap equipped with three microscope slides for catching incoming particles was positioned at the center of each plot at a height of 10-20 cm above the canopy; spores were collected from 16:00 until 9:00 every 1-3 days from 29 June to 1 August. The numbers of particles with a size similar to *P. infestans* spores (estimated with a cross-sectional area within 314-1257 mm^2) were counted from four microscope images (20 mm^2) per slide, for a total of 12 counts per plot for 21 collection dates. To assess *P. infestans* resistance (4), a detached leaf assay (DLA) was performed on June 23, prior to the first field observation of *P. infestans*. From each plot, 14 randomly sampled potato leaflets were inoculated with ten isolated droplets of *P. infestans* spore suspension; the number of successful infections per leaflet was counted after five days.

Table 5.1 List of data used for modelling late blight epidemics in monoculture and strip-crop potato systems. There are two sources of relative humidity and temperature data; these time series were experimentally measured in-situ, and weather station data was used to impute missing/erroneous readings and data outside of the date range of experimental measurements. The steps of the methodology in which these data were used are listed (refer to the text for details).

	Measurement	**Frequency/Date**	**Measurement source**	**Step(s) used**
Late blight severity	Number of infected leaflets per plant	July 11-12, 14-15, 18-19, 21-22, 25-26, 29-30 August 3-4	In-situ	2, 4
	Estimated severity (%)			
Microclimate	Relative humidity (%)	10 min	In-situ	2, 3
		Hourly	Local weather station	
	Temperature (°C)	10 min	In-situ	2, 3
		Hourly	Local weather station	
	Precipitation (mm/hr)	Hourly	Local weather data	2, 3
Spore dispersal	Number of trapped particles per slide image	Every 1-3 days	In-situ	1
	Wind speed (m/s)	10 min	In-situ	1
Host resistance	Number of lesions per detached leaflet	June 23	In-situ	1

Step 1: estimating the effects of companion crops on disease processes

Field measurements were used to derive estimates of how the rate parameters in the BLIGHTTIME model change in response to strip cropping.

Companion Crop Microclimate Modification

The effect of strip cropping on microclimate was captured by individually inputting the field- measured RH and temperature time series from the potato monoculture canopy and the potato canopy of the three strip-crop treatments into the BLIGHTTIME model (see Methods, section ‘Step 2: standardisation of the host-pathogen model with monoculture field data’). For each times series, measurements taken at 10-minute intervals were aggregated to hourly means for the duration of the season.

Estimating the barrier effect of companion crops

As an indicator of the barrier effect of companion crops, longitudinal aerial particle counts were analysed as a response variable using a generalized linear mixed effect model, with treatment (categorical), mean daily wind speed (continuous) and their interaction specified as fixed effect predictors, while sampling location (categorical; microscope slides nested in particle traps, one trap per plot, with plots nested in field location) and date of collection (categorical) were specified as random effects. A negative binomial distribution with log link was used to model the distribution of the particle counts. The maximum likelihood estimates of particle count per treatment, including their uncertainty as represented by their standard errors were used to generate probability distributions for relative spore counts (rS_i, Eqn. 5.1). Assessed with the monoculture treatment as the reference, these estimates were used as effect multipliers to modify the spore deposition efficiency parameter for strip crops in the BLIGHTTIME model.

$$S_{ijt} \sim NegBin(\mu_{ijt}, k_{ijt})$$

$$\log(S_{ijt}) = \beta_0 + \beta_{1i} + \beta_2 W_t + \beta_{3i} W_t + \alpha_t + \alpha_f + \alpha_{fp} + \alpha_{fps}$$

$$rS_{it} = \frac{S_{it}}{S_{mono,t}} = \frac{\exp(\beta_0 + \beta_{1i} + \beta_2 W_t + \beta_{3i} W_t)}{\exp(\beta_0 + \beta_2 W_t)} = \exp(\beta_{1i} + \beta_{3i} \times W_t)$$

$$rS_i = \frac{\sum_{t=1}^{n} \exp\,(\beta_{1i} + \beta_{3i} \times W_t)}{n}$$

(Eqn. 5.1)

S_{ijt} is the spore count of observation *j* sampled from slide *s*, of trap *t*, of field *f*, for each collection date *t*. Spore counts were modelled with a negative binomial distribution; μ_{ijt} is the estimated mean spore count, and k_{ijt} is the dispersion parameter. β_0 represents the constant intercept for spore counts in monoculture, and β_{1i} are the effects of strip-crop treatments on spore counts. W_t is the mean wind speed during spore collection intervals for each date, and β_2 is the marginal effect of wind speed on spore counts. β_{3i} represents the interaction between wind speed and strip-crop treatment. $\alpha_t, \alpha_f, \alpha_{fp}, \text{and } \alpha_{fps}$ are the random effects of collection date, and nested field, trap, and slide sampling location for each observation. rS_{it} represents the relative spore dispersal under strip-crop treatments, relative to the monoculture, at time t. rS_i aggregates a mean relative spore dispersal which accounts for differences in wind speeds across collection dates. A distribution of rS_i is calculated which accounts for uncertainty in β_{1i} and β_{3i}.

Estimating the effect of induced resistance due to intercropping

For induced resistance, detached leaf assay infection counts were analysed as the indicator response variable using a generalized linear mixed effect model, with treatment as the only fixed effect predictor, while sampling location (plot nested in field location) was specified as a random effect. A zero-inflated binomial distribution with logit link was used to model the distribution of infection counts. Similar to the barrier effect, distributions for multipliers for the effect of induced resistance were estimated using monoculture as the reference treatment (rIE_i, Eqn. 5.2) and used to modify the infection efficiency parameter for strip crops in the BLIGHTTIME model.

$$Icount_{ij} \sim Bin(10, \pi_{ij}) \cap Bernoulli(p_i)$$

$$\log\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) = \beta_0 + \beta_{1i} + \alpha_f + \alpha_{fp}$$

$$rIE_i = \frac{\pi_i}{\pi_{Mono}} = \frac{\left[\frac{\exp(\beta_0 + \beta_{1i})}{1 + \exp(\beta_0 + \beta_{1i})}\right]}{\left[\frac{\exp(\beta_0)}{1 + \exp(\beta_0)}\right]}$$

(Eqn. 5.2)

$Icount_{ij}$ is the infection count recorded for the leaflet *j* sampled from plot p, of field f for treatment i. π_{ij} is the estimated proportion of inoculation sites which resulted in a successful infection, and p_i is the probability that a zero count is observed (zero-inflation). β_0 represents the constant intercept for infection counts in monoculture, and

β_{1i} are the effects of strip-crop treatments. α_f and α_{fp} are nested random effects for the field and plot sampling locations of leaflets.

Simulating the effect of host dilution

To account for the proportion of spores in strip crops that land on hosts versus non-hosts after they enter the field or are dispersed as secondary inoculum, a dispersal model was used. The reduction in deposited spores, as a result of host dilution, was assumed to be dependent on the density and spatial arrangement of the host, but independent of the companion crop. The layout of experimental plots was modelled to scale, according to the spatial arrangement of a monoculture or strip-crop plot, with a grid (21 m x 24 m) containing rectangular (75 cm x 40 cm) host plant grid cells and (only in the strip crops) non-host grid regions representing companion strips. To obtain the proportion of spores that land on hosts versus non-hosts, we first assumed that all host grid cells released the same number of spores and that their deposition distances were described by identical radial Laplace dispersal kernels. The steepness of the kernels was parametrised with a dispersal gradient factor, α, which was estimated to be 0.82 and 1.09 m^{-1} in a study of *P. infestans* spore dispersal (Paysour & Fry, 1983). Through integration of the dispersal kernels (which overlap due to the proximity of hosts), the number of spores deposited on any grid cell was calculated as a function of its distance from each of the host plants in the grid. Thus, the total number of spores deposited on all hosts plants relative to total the number of spores released gave the overall probability of spores landing on host plants. The effect of host dilution was calculated as the ratio of this successful deposition probability in the strip-crop arrangement relative to the monoculture arrangement. Uncertainty in α was accounted for by using a plausible uniform distribution of $a \sim U(0.685, 1.225)$ [m^{-1}] which is double the range reported by Paysour & Fry (1983). This yielded a distribution of ratios for the relative reduction in spore deposition in strip-crop plots with specified experimental dimensions. These were used as the effect multipliers to reduce the deposition efficiency rate parameter for strip crops in the BLIGHTTIME model. See Supplementary material Method S5.1 for details.

Step 2: standardisation of the host-pathogen model with monoculture field data

The BLIGHTTIME model was developed to predict the seasonal development of late blight epidemics in potato (Skelsey et al., 2009). As described before, it uses hourly climate time series data to predict the initiation and growth of lesions and the subsequent production and deposition of spores (Fig. 5.2). Modifications to this model included: a leaf wetness infection requirement (blight hour function), a maximum lesion age, a maximum lesion number per plant, temperature-dependent latency progression and high-temperature lesion inactivation. The blight hour function sets a temperature-dependent leaf wetness duration requirement for infection to occur at any given hour (Hartill et al., 1990; Hjelkrem et al., 2021; Rotem et al., 1970; Zwankhuizen & Zadoks, 2002). The maximum lesion age inactivates lesions after 15 days (Bruhn & Fry, 1981), while the maximum lesion number sets a limit to the number of lesions which can be initiated on a host plant over a season. The temperature-dependent latency progression function modulates the rate that lesion area progresses from latent to infectious according to temperature (Narouei-Khandan et al., 2020), and the high-temperature lesion inactivation function inactivates lesions as temperatures reach a high temperature threshold (Crosier, 1934; Wallin & Hoyman, 1958). These functions were added to account for the extreme temperatures that were observed in 2023, and the effect the high heat had on lesion growth, which could not be accounted for in the original model. For further details on these modifications, refer to Supplementary material Method S2.

Using replicate microclimate data from the monoculture, certain model input values were adjusted to calibrate the simulation of disease progression in the monoculture to match field observations of disease progress in the monoculture. Specifically, input values related to the initiation of the epidemics were set using this monoculture data. The date of inoculation was set following the procedure of Andrade-Piedra et al. (2005). Inoculation load was set so that the simulated rate of disease progression in the monoculture matched the observed disease severity data. These settings were maintained in all subsequent strip-crop simulations (see Methods, section ‘Step 3: prediction of strip intercropping disease dynamics’).

Step 3: prediction of strip intercropping disease dynamics

Using the effect multipliers that were derived in Step 1, and the microclimate data measured in the strip crops, the disease progress in the strip crops was predicted.

Additionally, the importance of different disease-suppressive mechanisms in strip cropping was explored in a full factorial design in which the four mechanisms are presumed to be active or inactive, leading to 16 different scenarios. When mechanisms are activated, effect multipliers for the mechanisms modify the associated disease process rate parameter: host dilution and barrier effect modify the spore deposition efficiency, while the effect of induced resistance modifies the infection efficiency (see Fig. 5.2). Conversely, when mechanisms are inactive, these parameters are assumed to be equal to the monoculture. Note that barrier effect and induced resistance use companion crop-specific effect multipliers, while host dilution does not, assuming instead that this mechanism acts identically for all companion crops.

The uncertainty in the effect multipliers on disease progress is incorporated by representing these multipliers with probability distributions and by propagating their uncertainty to the modelled disease severity output. The uncertainty in microclimate modification was modelled using confidence bands produced using the hourly mean and standard error of replicate RH and temperature time series. For each simulation run, RH and temperature time series were independently randomly sampled as confidence band contours. In scenarios with microclimate modification inactivated, microclimate was randomly sampled from monoculture microclimate confidence bands. 500 replicate simulations were run per treatment per scenario, with randomly sampled effect multipliers or microclimate time series contours. Relative area under the disease progress curve was calculated for each simulation ($rAUDPC_{sim}$) and observations ($rAUDPC_{obs}$) using the span of observed severity dates, generating distributions which could subsequently be compared (see Methods, section ‘Step 4: ranked evaluation of mechanisms of disease suppression’).

Step 4: ranked evaluation of mechanisms of disease suppression

For each strip-crop treatment, under each scenario, a mean disease progress curve (DPC) was calculated from the DPCs produced from individual microclimate replicates. Mean absolute error (MAE) was calculated as the mean residual variance between observed severity assessments and DPCs. Scenarios were ranked within and across treatments, with the lowest MAE indicating the best prediction.

When considering uncertainty in the mechanisms, observed $rAUDPC_{obs}$ values were compared against scenario-treatment $rAUDPC_{sim}$ distributions. The prediction accuracy of simulated data was assessed by ranking the scenarios by predictive likelihood, which reflects the likelihood of the data being accurately described by model predictions (under each scenario). The likelihood of $rAUDPC_{obs}$ values was obtained by using the predicted distributions in $rAUDPC_{sim}$ as a probability distribution. Lower negative-log-likelihood (NLL) indicated an improved prediction accuracy.

5.3 Results

5.3.1 Estimation of effects of strip intercropping on disease processes (Step 1)

Companion crop microclimate modification

Microclimate differed consistently between the different strip-crop treatments. Overall, mean hourly RH was consistently highest in potato strip-cropped with maize (‘potato-maize’; see Fig. S5.5a for 24-hour mean measured canopy RH). During the nighttime hours, the second highest RH was observed in the monoculture. Mean RH was generally lowest in potato strip-cropped with ryegrass (‘potato-ryegrass’), although monoculture showed lower RH extremes. This skewed the hours spent below 60% and 50% RH thresholds to a higher number in monoculture than in potato-ryegrass (Table 2). RH in potato strip-cropped with faba bean (‘potato-faba bean’) was lowest during the night, but remained higher than in monoculture and in potato-ryegrass during the daytime. Clear patterns distinguishing mean temperature between treatments were not observed (Fig. S5.5b).

Considering the sensitivity of *P. infestans* to RH, as accounted for in the host-pathogen model, the mean daily number of hours that measured RH values fell above or below critical BLIGHTTIME RH thresholds were calculated (Table 5.2). These indices corroborate findings from mean hourly RH (Fig. S5.5a), showing that potato-maize and the potato monoculture spent the most hours above high RH thresholds (95% for sporulation and 87% for leaf wetness). The monoculture also spent the most hours below low RH minimum thresholds (60% for infection of a leaf and 50% for lesion growth). Potato-ryegrass spent the fewest hours above high RH thresholds and the second most hours below low RH thresholds.

Table 5.2 Mean number of hours per day in July 2022 that relative humidity falls above or below model thresholds for host-pathogen processes. This is calculated as a mean for each treatment from relative humidity (RH) in measured in monoculture (‘mono’), potato-faba bean (‘bean’), potato-ryegrass (‘grass’), and potato-maize (‘maize’) plots. RH thresholds in the epidemic model of 95% and 87% are the minimum RH required for sporulation and the minimum RH required for leaf wetness, respectively. The 60% and 50% thresholds are the minimum RH at which infection and lesion growth can still occur, respectively. Means are presented ± 1 SD. The bolded/italics values are the two highest means in each threshold category.

Treatment	RH ≥ 95% (hrs/day)	RH ≥ 87% (hrs/day)	RH < 60% (hrs/day)	RH < 50% (hrs/day)
Mono	***7.87 ± 0.66***	***10.99 ± 0.80***	***7.00 ± 0.86***	***6.49 ± 0.87***
Bean	6.67 ± 0.68	10.83 ± 0.75	6.60 ± 0.78	5.41 ± 0.82
Grass	6.55 ± 0.75	10.34 ± 0.78	***6.79 ± 0.80***	***5.64 ± 0.80***
Maize	***8.04 ± 0.72***	***11.84 ± 0.76***	5.83 ± 0.81	4.82 ± 0.95

Effect of strip intercropping host dilution

Applying dispersal kernel models to the experimental layout of monocrop and strip-crop plots, 88% and 58.3% of released spores landed on host plants in the experimental plots, respectively (evaluated for the mean dispersal gradient, $\alpha = 0.955\ m^{-1}$). Thus, the mean proportion of spores that are deposited on hosts in strip crops is 66% of the deposition on hosts in the monoculture. Over the range of uniformly distributed α assessed, this relative deposition was approximately uniformly distributed from 60% to 72% compared to the monoculture.

Effect of companion crop barrier and induced resistance

In assessing spore counts relative to monoculture, the treatment predictor coefficient estimates on a log scale (estimate ± SE) were positive for potato-bean and potato-ryegrass (although insignificant), and significantly negative for potato-maize showing that spore deposition is reduced when potato is strip-cropped with maize (see Table S5.1 for generalized linear mixed effect model coefficients). Indicating a reduction in deposition in strip-crop plots as wind speeds increase, the treatment-wind interaction predictor estimates were negative for all companion crops. Assembling these coefficient estimates using Eqn. 5.1 and propagating their uncertainty produces distributions for the multipliers for the barrier effect which indicate an increase in relative deposition efficiency compared to monoculture (mean ± SD) in potato-ryegrass and a decrease for potato-faba bean and potato-maize (Table S5.1, Fig. 4a).

Coefficient estimates on a logit scale (estimate ± SE) for the treatment predictor of detached leaf assay infection rates were positive for all companion crops. Effect multipliers (mean ± SD) of infection efficiency representing the effect of induced resistance were generated using Eqn. 2. Susceptibility to *P. infestans* is increased to varying degrees in the strip crops (Table S5.1, Fig. 4b).

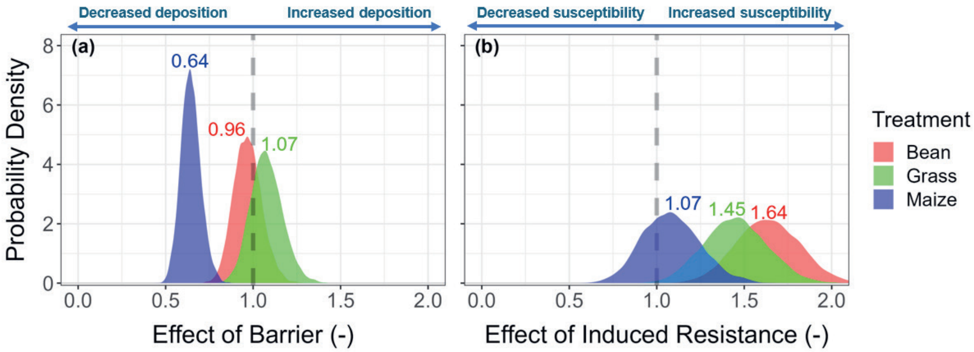


Fig. 5.4 Probability density curves for estimated effect multipliers representing the effect of companion crops on (a) spore deposition efficiency through the barrier effect mechanism and (b) infection efficiency through the induced resistance mechanism. Effect multipliers were derived from experimental measurements and are calculated relative to the monoculture (vertical dashed grey line). The distributions are labelled with their respective means.

5.3.2 Simulating monocrop epidemics (Step 2)

Date of inoculation and inoculation load were adjusted to improve the fit of simulated monoculture DPCs to observed monoculture disease severity data. The mean monoculture DPC (Fig. 5b; $R^2 = 0.57$) was simulated with inoculation date set to July 2 (6 days prior to the first field observation of late blight symptoms) and inoculation load set to 3500 spores/plant for two consecutive hours. These settings were used in all subsequent strip-crop simulations across all scenarios (Fig. 5.5).

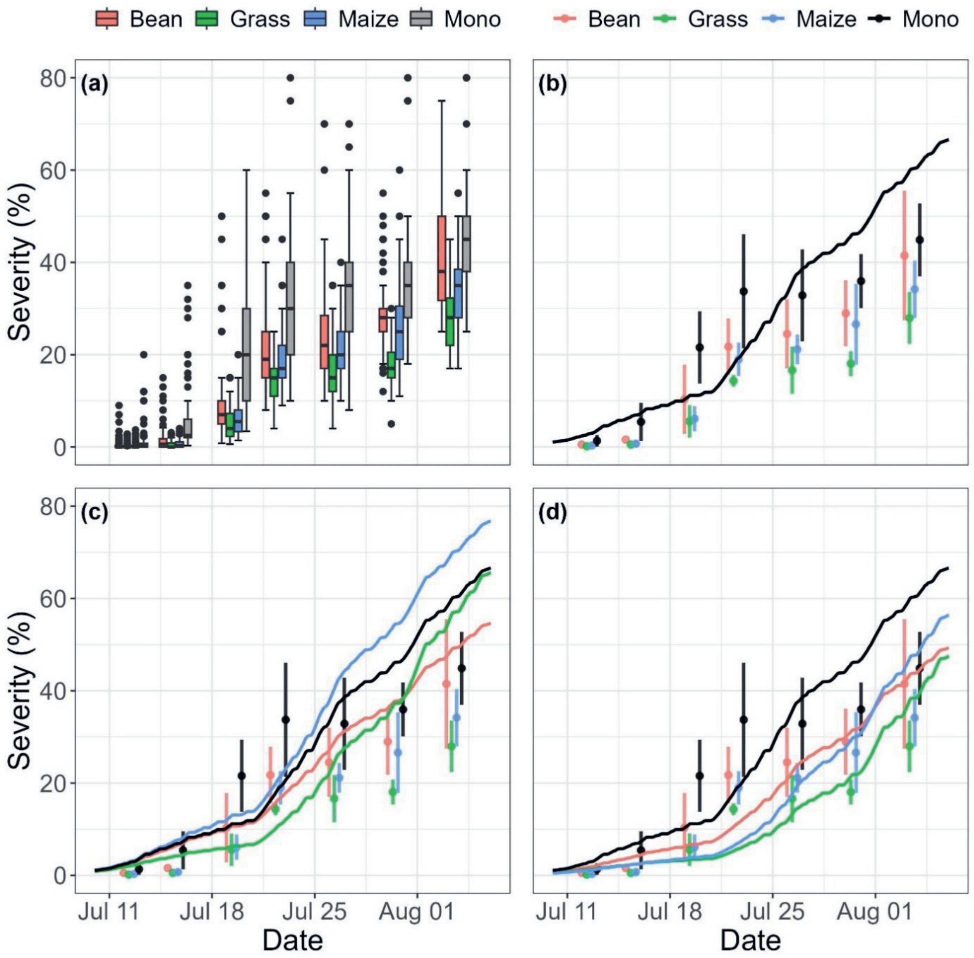


Fig. 5.5 Comparison of observed disease severity and disease severity simulated in selected strip-cropping scenarios. Boxplots of observed disease severity, which was assessed seven times between 11 July and 4 August 2022 for randomly selected plants from four replicate plots of each treatment (a). Lines in (b-d) represent the predicted disease progress curves (DPCs) in the monoculture (b), including the effect of measured canopy microclimate in the strip crops on disease severity (c; 'MM'), and the predicted DPC when combining the effects of host dilution, microclimate modification, and the barrier effect (d; 'HD + MM + B'). Scattered points with error bars represent the observed mean severity ± 1 SD, representing the same observed data depicted in (a). Only three of 16 scenarios are shown (refer to Supplementary material Fig. S5.6 for figures of all scenarios). Mechanism abbreviations: HD (host dilution); MM (microclimate modification); B (barrier effect).

5.3.3 Scenario analysis of strip intercropping disease dynamics (Steps 3 & 4)

First, individual microclimate replicates were used to simulate DPCs across all 16 scenarios, consisting of a full factorial design which toggled the four mechanisms—host dilution (HD), microclimate modification (MM), barrier effect (B), and induced resistance (IR)—which were presumed to be active or inactive. Visually, the mean DPCs of the scenario which combined host dilution, microclimate modification, and the barrier effect ('HD + MM + B') most closely fitted the observed severity (Fig. 5.5), which was supported by this scenario ranking 1st in terms of MAE (Fig. 5.6). Ranked overall, seven of the eight highest-ranking scenarios included the mechanism host dilution, five scenarios included microclimate modification and barrier, while only two scenarios included induced resistance. Inclusion of induced resistance resulted in a high overestimation of severity in potato-faba bean and potato-ryegrass. Induced resistance was included in the highest-ranking scenario of potato-maize, which combined host dilution, barrier effect, and induced resistance ('HD + B + IR'), but this required the exclusion of microclimate modification, since both of these mechanisms were predicted to promote late blight in potato-maize. Microclimate modification had a disease-suppressive effect in potato-ryegrass and in potato-faba bean, although there was higher variation in potato-faba bean (Fig. 5.5c); this suppression was driven by reduced relative humidity compared to the monoculture, in particular during the nighttime. Conversely, microclimate modification in potato-maize promoted disease due to elevated RH compared to the monoculture. Interestingly, the effect of mechanisms on disease severity are of comparable magnitude for certain companion crops. For example, host dilution leads to a reduction in disease severity of 25% in all strip crops, the barrier effect induced by maize decrease disease severity by 28%, and the altered microclimate due to strip cropping with grass reduces severity by 24% (Fig. 5.7).

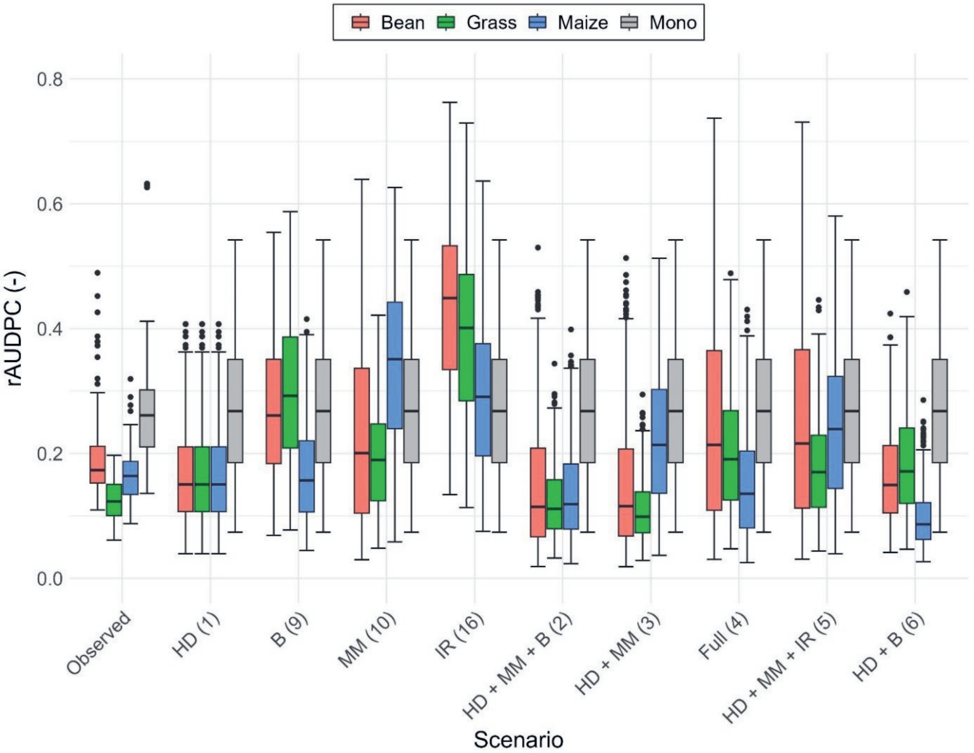
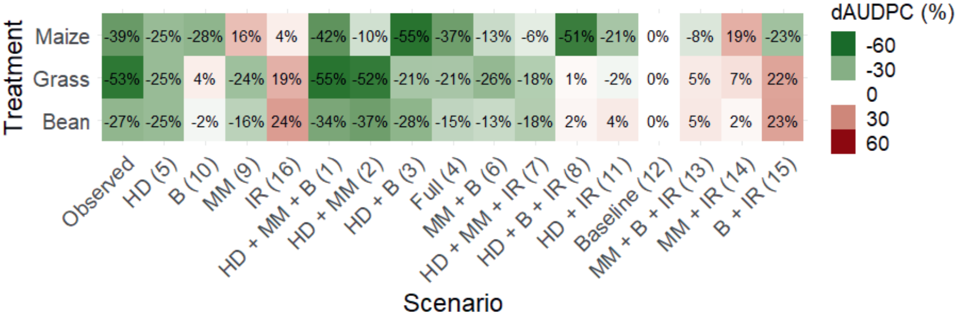


Fig. 5.6 Comparison of observed rAUDPC$_{obs}$ and rAUDPC$_{sim}$ simulated in selected strip-cropping scenarios accounting for uncertainty in the mechanisms of disease suppression (500 runs per scenario-treatment). Scenarios were combinations of toggled active mechanisms. The leftmost five boxplots respectively depict observed disease, followed by scenarios with single mechanisms assumed active (HD, B, MM or IR respectively). This is followed by the best ranking scenarios. Numbers in brackets indicate the ranking that was determined using a log-likelihood analysis of observed rAUDPC compared to simulated rAUDPC. Mechanism abbreviations: HD (host dilution); MM (microclimate modification); B (barrier effect); IR (induced resistance). Refer to Supplementary material Figs. S5.7-9 for figures of boxplots for each strip-crop treatment under all scenarios.

rAUDPC$_{sim}$ distributions, generated through propagation of uncertainty in the effects of disease-suppressive mechanisms (Fig. 6), generally agreed with mean simulated DPCs (Fig. 5, Fig. S5.6). The scenario which combined the effects of host dilution, microclimate modification, and the barrier effect ('HD + MM + B') ranked 2nd overall in NLL (instead of 1st with MAE), following the scenario which only considered the effect of host dilution ('HD'), which had ranked 1st with NLL, but 5th with MAE. Nonetheless, comparing distributions visually suggests that scenario 'HD + MM + B' most appropriately detects differences in disease suppression between companion crops, which ‘HD’ is unable to predict, given that this mechanism alone simulates all strip-crops identically (as the proportional area and arrangement of host plants is identical in all strip crops). Compared to the ranking by MAE, ranking by NLL slightly improves the scenarios with activated induced resistance. Nonetheless, induced resistance failed to be included in any of the three best scenarios ranked by NLL.



Treatment	Observed	HD (5)	B (10)	MM (9)	IR (16)	HD + MM + B (1)	HD + MM (2)	HD + B (3)	Full (4)	MM + B (6)	HD + MM + IR (7)	HD + B + IR (8)	HD + IR (11)	Baseline (12)	MM + B + IR (13)	MM + IR (14)	B + IR (15)
Maize	-39%	-25%	-28%	16%	4%	-42%	-10%	-55%	-37%	-13%	-6%	-51%	-21%	0%	-8%	19%	-23%
Grass	-53%	-25%	4%	-24%	19%	-55%	-52%	-21%	-21%	-26%	-18%	1%	-2%	0%	5%	7%	22%
Bean	-27%	-25%	-2%	-16%	24%	-34%	-37%	-28%	-15%	-13%	-18%	2%	4%	0%	5%	2%	23%

Fig. 7 Heatmap of percent change in rAUDPC (dAUDPC) in strip-crops relative to monoculture as observed and simulated in strip-cropping scenarios. The leftmost ‘Observed’ dAUDPCs were calculated from observed disease severity. This is followed by dAUDPCs calculated from disease progress curves (DPCs) simulated in scenarios of single active mechanisms (HD, B, MM, or IR), and then by those scenarios combining toggled active mechanisms. The scenarios are ranked by mean absolute error (MAE) from left (best fit) to right (worst fit); rankings are indicated in parentheses. ‘Baseline’ represents the scenario in which no disease-suppressive mechanisms are active, and strip-crops are identical to the monoculture. ‘Full’ represents the scenario in which all mechanisms are active. Mechanism abbreviations: HD (host dilution); MC (microclimate modification); B (barrier effect); IR (induced resistance).

5.4 Discussion

In this study, we used field data combined with a modelling approach to quantify the relative importance of four different mechanisms potentially driving disease suppression in intercrop systems. These mechanisms include host dilution, microclimate modification, barrier effect, and induced resistance. We examined these mechanisms for the suppression of potato late blight in potato strip-cropped with different companion crops (faba bean, ryegrass, and maize) and compared this to potato grown as a monoculture. By measuring the various mechanisms in the field and by subsequently incorporating these in a standard epidemiological model, we were able to quite accurately predict disease progression. Predictions of disease severity in the strip crops were most accurate when the combined effects of host dilution, microclimate modification and barrier effect were considered. As hypothesised, the relative importance of each mechanism varied depending on the companion crop introduced.

Host dilution is often proposed as the most important mechanism for disease suppression in intercrops (Boudreau, 2013; Finckh et al., 2000; Zhang et al., 2019). Reducing the density of the susceptible host, by replacing it with a companion crop, leads to spores landing on non-hosts, rendering them ineffective. In our case study, we estimated that on average 66% of released spores are deposited on hosts in strip crops, compared to the monoculture, which led to an estimated reduction of disease severity by 25% (Fig. 7). In addition to host dilution, which was assumed to be identical for each strip-crop treatment, the other mechanisms can further modify the level of disease suppression than what is achieved through host dilution alone.

Numerous studies show that intercropping can modify the canopy microclimate and suggest that these modifications, especially relative humidity (RH), play an important role in disease suppression (Boudreau, 1993; Boudreau & Mundt, 1992; Boudreau & Shew, 2006; Gao et al., 2021; Gómez-Rodríguez et al., 2003; Schoeny et al., 2010). In our case study, without consideration of other mechanisms, simulations using only microclimate modifications of the strip crops, resulted in a 24% reduction in $\mathrm{rAUDPC_{sim}}$ in the strip crop with ryegrass compared to the monoculture, while a 16% increase was simulated for the strip crop with maize. It may seem that differences in observed RH are small or even inconsequential in their contribution to disease suppression. For example, in July 2022, the daily average RH was 78.9% in the potato monoculture, 77.8% in the potato-grass, 80.6% in the potato-maize, and 79.4% in the potato-faba bean. However, these small differences partly arise from taking a daily average, not taking into account the variation in the daily amplitude of RH across strip crops (Fig. S5.5). Additionally, microclimate influences many key processes in the disease cycle of *Phytophthora infestans*, and other pathogens, including spore germination and infection, lesion growth, and sporulation (Crosier, 1934; Harrison & Lowe, 1989; Zwankhuizen et al., 1998). Consequently, small differences in RH can accumulate over the season by influencing various disease processes resulting in significant differences in disease severity, which can be either beneficial or detrimental compared to the monoculture.

Similarly, the barrier effect could either promote or suppress disease, depending on the companion crop and its stature or canopy density. Potato plants strip-cropped with maize received fewer spores than the monoculture, and simulations considering only the barrier effect estimated a 28% reduction in disease severity in the strip crop with maize compared to the monoculture. In contrast, potatoes strip-cropped with ryegrass were exposed to slightly increased spore deposition. In the strip crop with faba bean, no clear barrier effect was observed. Lastly, the effect of induced resistance led to higher severities in all strip crops, but more so for the strip crop with faba bean or ryegrass than maize.

Interestingly, no single mechanism could explain the majority of the variation in observed disease levels between the various strip crops. Only when multiple mechanisms were combined could we capture the observed disease severity, suggesting that several mechanisms are important for disease regulation. While host dilution is often recognised as the most important disease-suppressive mechanism, we exemplify that contributions of other mechanisms are of a similar magnitude, and must be considered for evaluating overall suppression. The combinations of mechanisms varied in their capacity to replicate the observed disease progress curves, but overall, the most successful scenario integrated the effects of host dilution, microclimate modification, and barrier effect.

Disease reduction in intercropping varies widely across studies (Li et al., unpublished manuscript; Zhang et al., 2019). This study suggests that substantial variation in disease suppression can be attributed to the fact that the strength and direction of each disease-suppressive mechanism changes based on the choice of the companion crop. Different companion crops evoke these mechanisms at varying strengths, and the interplay of these mechanisms can result in varying levels of disease suppression. Notably, the effects of disease-suppressive mechanisms are not necessarily complementary. For instance, in the strip crops with ryegrass and maize, the effect of microclimate modification and barrier effect counteracted. Maize provided a strong barrier effect, intercepting inoculum which might otherwise be deposited on host potato plants, resulting in an estimated 28% reduction in severity, but it increased the duration of high RH in the potato canopy, which promotes the establishment and growth of *P. infestans*, which in isolation was estimated to increase severity by 16%. Conversely, in the strip crop with ryegrass, potato plants benefitted from a reduced RH, resulting in an estimated 24% drop in severity, yet were exposed to higher spore deposition, leading to a 4% increasing in severity. Nevertheless, the net effect of the two mechanisms resulted in disease suppression in both strip-cropping systems.

5.4.1 Application

On a more fundamental level, modelling disease-suppressive mechanisms helps to understand how species mixtures contribute towards disease suppression, demonstrating that different companion crops can reduce disease pressure, even if the mechanisms operate differently. We tested this modelling approach on data from a field trial with a similar setup conducted in 2021 (Supplementary material Fig. S5.10). Simulations of the 2021 epidemic that included canopy microclimate (as measured in 2021) and host dilution accurately predicted disease progression in the strip crops. However, when simulations also included the barrier effect (as measured in 2022), disease suppression in the strip crop with maize was overpredicted. This overprediction may be due to an overestimation of the barrier effect, as maize was planted four weeks later than potato that year, resulting in maize being only slightly taller than potato and thus less effective as a barrier, compared with 2022 (Supplementary material Fig. S5.11; Homulle et al., 2024). Modelling the 2021 season suggests our approach can be generalised to other years, but the strength of the mechanisms depends on the characteristics of the companion species (e.g. its height). Furthermore this points towards the importance of management decisions (such as planting date) for the strength of disease suppression.

Furthermore, this approach can be used to explore how intercrop design affects disease suppression. To do so, data on microclimate and the barrier effect under various intercropping arrangements, or reliable methods to predict them, would be necessary since the spatial arrangement of species, and their identity can impact the strength of these mechanisms. For example, as the ratio of maize in pepper-maize and bean-maize intercrops increased, the relative humidity compared to respective monocultures also increased (Boudreau, 1993; Gao et al., 2021). The proportion of maize in an intercrop could also lead to trade-offs with its effectiveness as a barrier and the spatial effect of host dilution on spore dispersal. If the model is made to be more spatially-explicit, the intercrop design, such as strip width, may be investigated and potentially optimised.

Lastly, our approach of modelling disease suppression may also be combined with decision support system (DSS) models in the context of strip intercropping. This integration could determine a spraying schedule for strip-cropping systems, and assess whether conditions in strip crops allow for less (frequent) spraying or delaying the first application (Boudreau et al., 2016; Yan et al., 2024). Ultimately, it could help investigate potential reductions in fungicide application in intercrops, contributing to more sustainable crop protection.

5.4.2 Model uncertainties

In our approach, estimation of effect multipliers for mechanisms underlying disease suppression of strip intercropping compared to monoculture relies on several simplifying assumptions, especially with respect to spore dispersal. We attempted to isolate the spatial effect of host dilution from the barrier effect, although host dilution implicitly interacts with the particle collection data which was used to estimate the barrier effect, leading to a possible overestimate of disease suppression compared to the monoculture when these mechanisms are combined in simulations. Furthermore, we assumed that the barrier effect was only dependent on wind speed, and wind direction and turbulence were not explicitly considered, but these aspects can impact disease dynamics. For example, in a strip-crop system, the orientation of potato strips with respect to the wind direction affected the observed reduction in late blight, with the greatest reductions in plots planted perpendicular to the wind (Bouws & Finckh, 2008). Wind turbulences may affect the movement of disease propagules, potentially leading to inoculum loss outside the plot, but these patterns are complex and likely change with crop growth stage, architecture of the neighbour, and planting pattern (e.g., strip versus row intercrops; Boudreau, 2013; Boudreau & Mundt, 1992).

The data from the in-vitro detached leaf assay indicated that defense responses are down-regulated in the intercrops compared to the monoculture, leading to increased infection rates of late blight by 7-64%. These results are inconsistent with typically observed resistance levels (Kessel et al., 2010; Skelsey et al., 2009; Vleeshouwers et al., 1999), suggesting that the assay may have overestimated the impact of companion crops on potato plant resistance. Furthermore, including induced resistance in the model simulations worsened the predictions compared with the observed disease severities, indicating that the magnitude of the effect of induced resistance as observed in-vitro may not have been present to the same extent in the field. This highlights the need to further investigate the role of induced resistance in field conditions to better understand its contribution to disease regulation.

While previous studies have reported on disease-suppressive mechanisms in intercrop experiments (Gao et al., 2021; Gómez-Rodríguez et al., 2003; Schoeny et al., 2010), assessing the contribution of individual mechanisms to overall disease suppression can be challenging. Introducing an additional species in intercropping brings a range of mechanisms that may interact synergistically or in opposition. Where other studies attribute changes in disease pressure to differences measured in the crop, such as in relative humidity, we propose that these measurements can be used to quantify the contributions of intercrop companions to disease suppression. By incorporating field measurement in an epidemiological model, we were able to predict disease severity in a strip-crop system. This helped to accomplish disentangling the importance of different mechanisms and quantifying their contribution to disease suppression. Our study has shown that, for instance, small differences in microclimate induced by strip cropping can significantly influence disease severity, effectively quantifying the accumulation over a growing season of the effect of microclimate modifications. This study is the first to our knowledge to use a mechanistic simulation approach to disentangle the mechanisms leading to disease suppression in strip-cropping systems.

5.5 Conclusion

This study describes a novel approach used to model the effects of strip-crop related disease-suppressive mechanism, using late blight in potato as a case study. Field data was used to estimate parameters for host dilution, microclimate modification, induced resistance and barrier effects. These were then integrated into a mechanistic late blight simulation model, which characterizes the effect of environmental variables on host-pathogen interactions. The model predicts that even small differences in microclimate as induced by different companion crops can significantly affect disease severity. The severity of disease in strip-cropping systems could only be reproduced by a combination of mechanisms, suggesting that all those mechanisms are relatively important. This methodology sets a premise for modelling the effects of strip cropping on disease dynamics, as well as the development of other approaches that may be used to further study and optimize disease-suppression in intercrop systems.

Acknowledgements

We would like to thank all colleagues that assisted in the management of the field experiments which generated data used in this study. We recognize Paola Cassiano and Viacheslav Shevchuk for their contributions towards collection of data used in this study. Furthermore, we would like to thank Peter Skelsey and Wopke van der Werf for the original development of the late blight model BLIGHTTIME that was modified for our study. Additionally, we thank Wopke van der Werf, Geert J.T. Kessel, Alejandro Morales for valuable advice provided for interpretation and analysis of the data.

Notes

Li W.F., Douma J.C., Makowski D., Homulle Z., van der Werf W. Intercropping consistently but variably decreases plant disease incidence: a global meta-analysis. Unpublished manuscript

Supplementary material

Methods S5.1 Simulation of the effect of host dilution

The effect of host dilution on spore dispersal was simulated with a static, spatially explicit simulation model. Individual host plants are represented in a grid as they are arranged in the field, in either monoculture or strip-crop arrangements. Subsequently, each host plant releases spores according to identical dispersal kernels superimposed across the entire grid, and the distribution of deposited spores across the grid are evaluated to estimate the percentage of spores that land on either 1) host plants, 2) non-host (companion) plants, or 3) escape the plot.

Two dispersal kernels were analyzed in the estimation of the effect of host dilution on spore dispersal: a radial Laplace and a radial Gaussian kernel. Cross-sections of the dispersal kernels (centered on each host plant) are shown in Fig. S5.1A. Ultimately, it was chosen to use the radial Laplace kernel, as this kernel was similarly applied in the previous analysis of Skelsey et al. (2005). Furthermore, comparison between the two dispersal kernels in their estimation of the effect of host dilution shows relatively small differences (Fig. S5.1B).

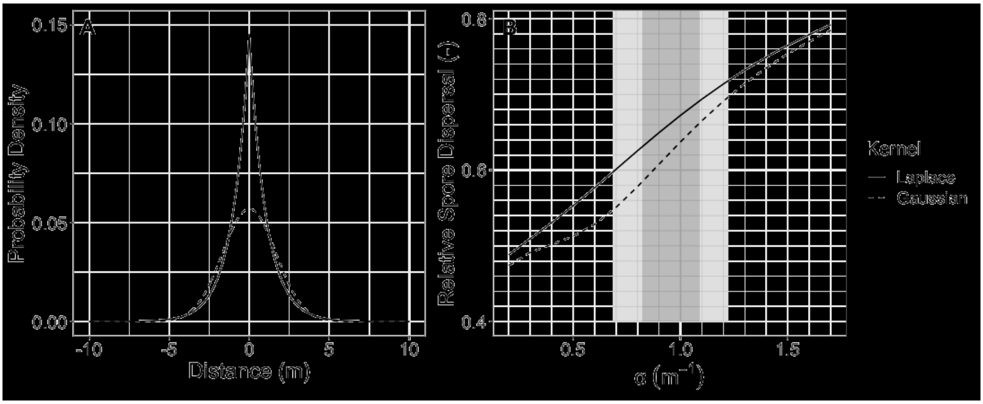


Fig. S5.1 Dispersal kernels tested for the estimation of the host dilution effect of intercrops. (A) Cross-section of 2-dimensional Gaussian and Laplacian dispersal kernels with α=0.955 m^{-1}. (B) Relative spore deposition simulated in the strip-crop grid compared to monoculture grid across a range of α from 0.2 to 1.7 m^{-1}. The relative spore deposition for a Laplacian kernel was ultimately used to estimate the effect of host dilution. The distribution of effect multipliers for host dilution was simulated from a uniform distribution of α ranging from 0.685 to 1.225 m^{-1}, shaded in light-gray. This sampled range is double the range of α reported in literature, 0.82 to 1.09 m^{-1}, shaded in dark-gray (Paysour & Fry, 1983).

See Fig. S5.2 for a graphical representation of the spore dispersal across monoculture and strip-crop plots. In the monoculture grid, using a dispersal gradient of $\alpha = 0.955\ m^{-1}$, 88% of released spores landed on potato cells, while the remaining 12% escaped the bounds of the grid. For the strip-crop grid, 58.3% of released spores landed on potato plant grid cells, 37.2% of spores landed on non-host cells, and the remaining 7.2% escaped the plot. Thus, for the strip-crop and monoculture plots, respectively, 58.3% and 88% represent the proportion of released spores that land on hosts (versus landing on non-hosts or escaping the plot). These values are used as the estimate of the rate of spore deposition in strip-crop and monoculture plots. The effect of host dilution was calculated as the ratio between these deposition rates, re-scaling the relative spore deposition in the strip-crop to 66% compared to the monoculture. Notably, this is only for $\alpha = 0.955\ m^{-1}$ under the given experimental plot dimensions. This calculation was repeated across a gradient $\alpha{\sim}U(0.685, 1.225)$ [m^{-1}] resulting in relative spore deposition ranging from approximately 0.60 to 0.72 in the strip crops relative to the monoculture. This distribution was sampled for multipliers for the effect of host dilution on spore dispersal and deposition.

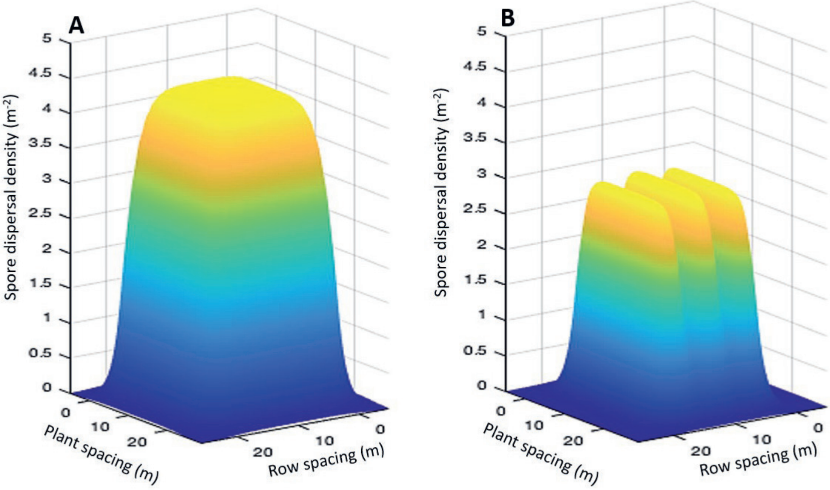


Fig. S5.2 Surface plots of spatial spore dispersal density in A) monoculture, and B) strip-crop plots. The Laplacian dispersal kernel was used to generate these density surfaces, with α=0.955 m^{-1}. Individual plants were homogenously modelled as spore sources in sole and strip crop arrangements, matching the spatial arrangement of the experimental plots. Integration was used to calculate the cumulative spore deposition across the plot grid and for host and non-host strips in the strip-cropping system. The figures were generated using MATLAB version R2023a.

Methods S5.2 Modifications to the BLIGHTTIME model

The ‘BLIGHTTIME' model (Skelsey et al., 2009) was used to simulate microclimate-dependent late blight epidemics. Slight modifications were made to the original model, including: a leaf wetness infection requirement (blight hour function), a maximum lesion number per plant, a maximum lesion age, temperature-dependent latency progression and high-temperature lesion inactivation. Additionally, the structure of the model was modified to simultaneously track the number of lesions produced at each times step, and the area that is divided across various stages of infection (latency, infectious, non-infectious) of lesions produced at each time step.

The original BLIGHTTIME model uses a Leslie matrix approach, keeping track of the number and radius of lesions of all ages for each time step. Lesions are transitioned through consecutive age classes, which account for the duration of latency and infectiousness of lesions. We modified the structure of the model to a compartmental approach, drawing inspiration from BLIGHTSIM (Narouei-Khandan et al., 2020). Instead of complete transition of lesion (age) classes to consecutive classes at each time step, lesion area progresses through classes at a variable rate. This allows for a variable, microclimate-dependent latency period. Lesions classes LAT1-LAT5, INF, and NINF represent how the area of each lesion is divided across all lesion ages classes. LAT1-LAT5 approximately corresponds to individual days of a five-day latency (although the microclimate-dependent latency progression rate can accelerate or prolong the period that lesion area remains in each category). INF stores the lesion area that is infectious, while NINF stores the lesion area that is no longer infectious. A separate vector records the number of lesions initiated at each time step, which is used for functions which act on whole individual lesions.

Lesion growth rate (LGR) determines the rate of radial expansion of lesions; calculated lesion growth is removed from healthy leaf tissue (H) and added to the first latent class (LAT1). Individual lesions can only grow to the border of a leaflet, which is modeled as a circle with a set radius of 0.03 m; development of a lesion continues until its corresponding area has fully progressed to NINF. Latency progression rate (LPR) defines the rate of transition of area from LAT1 through the consecutive LAT compartments and into INF. Under optimal LPR conditions 1/24th of each latent compartment is progressed to the next compartment at each hourly time step. Lesion area sporulates for as long as it remains in the INF compartment, before progressing to the NINF compartment. A modified function for lesion death (described below) can accelerate the removal from LAT and INF compartments, by inactivating whole lesions and thus any corresponding lesion area (across all stages LAT, INF, NINF) in these compartments; this process is separate from hourly INF inactivation, which progresses 1/24th of INF area to NINF at each time step, accounting for the approximate one-day infectious period of lesion area.

Spore production is calculated as a function of INF area. All spores are pooled and immediately dispersed and deposited for each time step during which sporulation occurs (according to microclimate conditions and the presence of infectious lesion area). The rate of spore deposition at each time step is determined by the deposition efficiency (DE). Deposition is a prerequisite for the initiation of a new lesion. Lesions can only be initiated if the blight hour requirement is met (the blight hour function is described below), and if so, the infection rate of spores resulting in a new lesion is determined by the infection efficiency (IE). At the end of each time step, spores that failed to initiate a lesion are permanently removed.

Blight hour function

This function relates to the temperature-dependent requirement of extended leaf wetness for infection to occur (Crosier, 1934). It is a modification of the blight day function of the original BLIGHTTIME model, which specifies that a minimum number of consecutive “infection-hours” with RH > 90% and temperature between 10 and 27°C must be met for infection to be able to occur on a given day. The minimum number of hours that is required for a blight day depends on the average temperature over the consecutive infection-hours (Rotem et al., 1970; Zwankhuizen & Zadoks, 2002). An approach similar to that of the Nærstad model was used, which calculates infection risk at any given hour contingent on microclimate conditions in the following hours (Hjelkrem et al., 2021).

The following operation is performed for every hour to determine whether it is a ‘blight hour’ in which infection may occur. Including the starting hour, at least three consecutive leaf wetness are required for infection, however, as average temperature deviates from the optimal range of 15 to 20°C, the required duration increases (Hartill et al., 1990; Rotem et al., 1970). Leaf wetness is assumed for any hour with RH ≥ 87%. If the first three-hour consecutive hours of leaf wetness do not meet the temperature requirement, additional hours of leaf wetness are no longer consecutively required, but within an 11-hour interval, a sufficient threshold of hours of leaf wetness must be met, determined by the average temperature over the entire period. To qualify the hour at the beginning of the period as a blight hour, the average temperature over the duration of leaf wetness hours must fall above the line shown in Fig. S5.3.

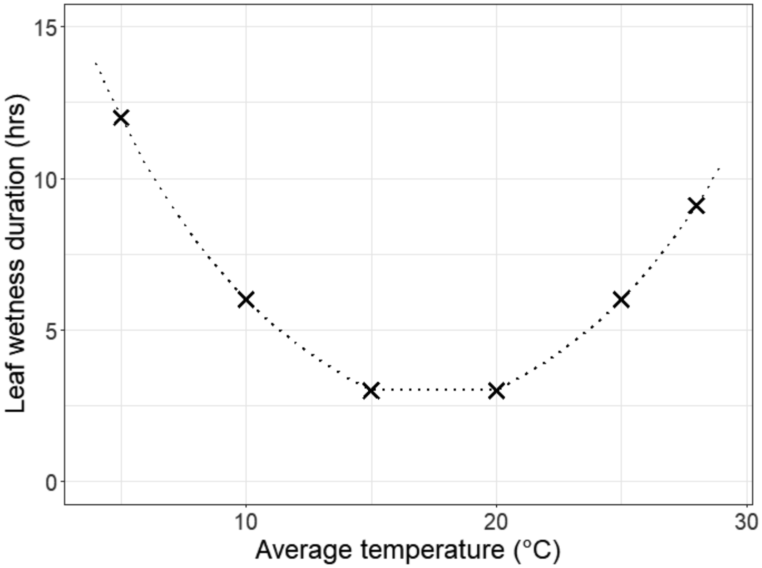


Fig. 5.3 Duration of leaf wetness and average temperature required for *P. infestans* germination as modified for the late blight epidemic model (Rotem et al., 1970). As optimal temperatures for germination (15-18°C) are approached, leaf wetness duration requirements become less stringent and vice versa.

High-temperature lesion inactivation

Pre-existing late blight models rarely include functions which inactivate lesions under high temperature and/or low humidity conditions. Quantified relationships between these conditions and lesion survival are not well described, although qualitative observations have been made (Crosier, 1934). LATEBLIGHT inactivates all lesions if daily mean temperature exceeds 41°C for three consecutive days (Wallin & Hoyman, 1958). An alternative method is proposed for this study, although it was not experimentally tested. Lesion death rate, LD_t, is calculated as the proportion of lesions which inactivate at each time step depending on the time step temperature:

$$LD_t = 1 - \left[\frac{1}{1 + \exp(T_t - T_{thres})}\right]^{\Delta t}$$

with T_t as the temperature (°C) at time t and Δt as the duration of a time step (1 hour). T_{thres} is the temperature at which $LD = 0.5$ if T_{thres} is maintained for 24 hours.

All pre-existing functions are factored by 1/24 to convert daily rates to hourly rates, but such an approach for LD would imply that a maximum limit of 1/24 lesions can be killed at any hour. To overcome this limitation, the proposed relationship raises survival rate to the power of Δt and takes the difference from 1 as the death rate. Thus, at 30°C, $LD \approx 0$, while at 37°C, $LD \approx 0.15$ for one hour (Fig. S5.4).

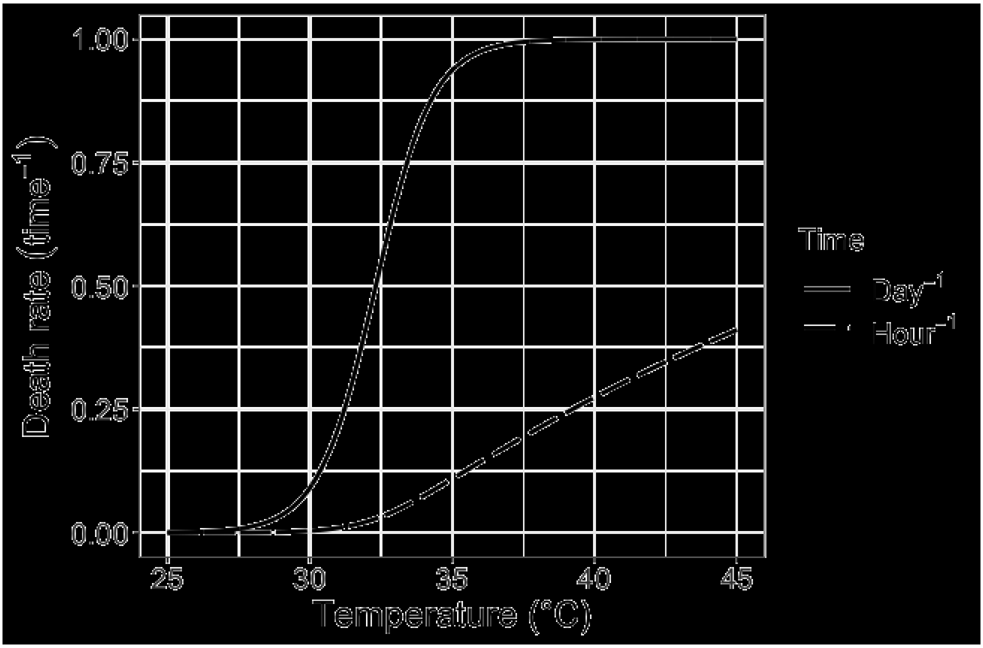


Fig. 5.4 The total number of active lesions is reduced by LD and the area of these lesions allocated to LAT and INF compartments is moved to the NINF compartment. Additionally, if temperature exceeds 34°C during the 24 hours following initiation of new lesions, they will inactivate (Crosier, 1934; Wallin & Hoyman, 1958). This condition is checked at the time step of lesion initiation, and these inactivated lesions will not contribute towards the total lesion number. Any inactivated lesion will no longer continue to grow or develop.

Latency progression rate

The modification of the original BLIGHTTIME structure from a Leslie matrix to a compartmental structure was done to allow for variable latency progression. The age classes of the BLIGHTTIME model were originally structured by hour but were converted to day compartments L1-L5. The latency progression rate modifies the rate that area moves between compartments relative to an unmodified rate $LPR = 1$, which should theoretically transfer each lesion age category to the next stage. That being said, the modified version transfers 1/24th of each compartment at each time step; thus transfer is in fact modeled as an exponential decay with a decay factor of 1/24, which is modified by the temperature-dependent LPR.

Maximum lesion age

As a result of the addition of a variable latency progression rate, and the accompanied compartmental lesion area tracking, an individual lesion can never progress through all stages (latent, infectious, non-infectious) completely (although area will approach zero). To account for this, and the slightly retarded progression due to the exponential decay, individual lesions are inactivated 15 days after initiation, as was done in LATEBLIGHT (Arneson et al., 1993; Bruhn & Fry, 1981).

Maximum lesion number

A maximum lesion number per plant is set, using a logistic relationship relating deposition to lesion number; as lesion number increases DE is reduced according to the relationship:

$$DE_{red,t} = \frac{n_{les,max} - n_{les,t}}{n_{les,max}}$$

with DE_{red} as the reduction factor (0: no deposition can occur; 1: DE can take maximum value), n_t is the number of lesions at time t, and $n_{les,max}$ is the maximum lesion number.

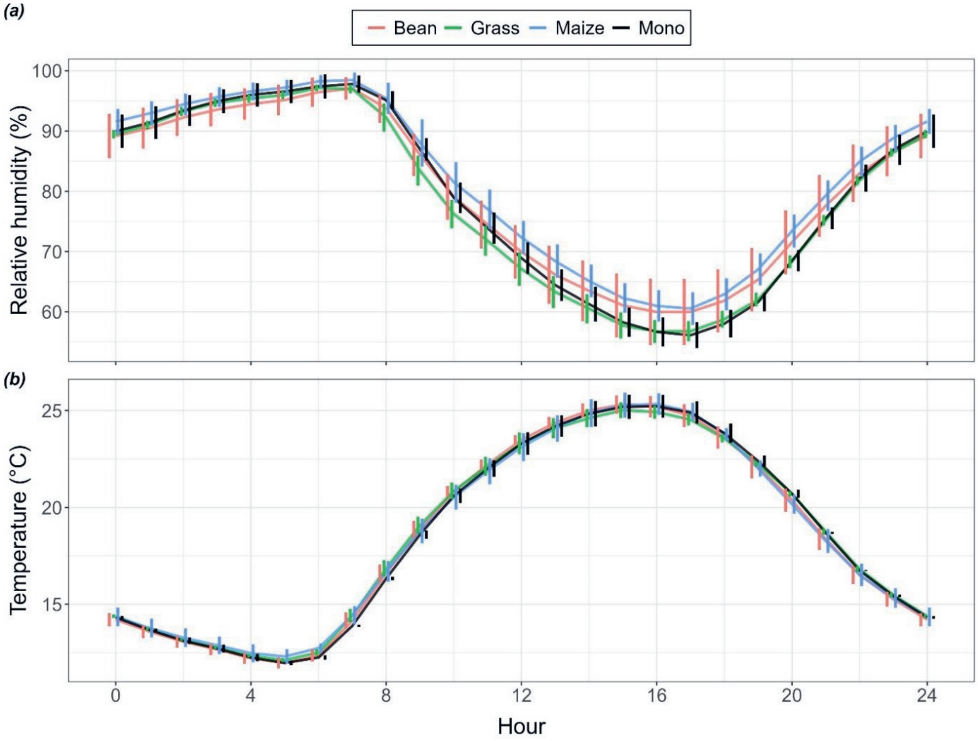


Fig. S5.5 Mean hourly canopy relative humidity (a) and temperature (b) for monoculture ('mono') and strip-crop treatments in July 2022. Relative humidity (RH) and temperature were measured at 10-minute intervals for n=6 microclimate time series replicates in potato-faba bean ('bean'), potato-ryegrass ('grass'), and potato-maize ('maize') plots (2 replicates per plot, for three plots each) and for n=3 microclimate time series for mono (1 replicate per plot, for three plots). Hourly means represent the mean temperature for a given hour across every day in July 2022. The month of July is used to highlight differences in relative humidity (RH) and temperature between treatments as this was the period when most experimental observations of late blight were made. Curves connecting hourly means are interpolations to improve readability of the figures. Error bars denote ± 1 SD of the mean hourly RH or temperature between replicates.

Table S5.1 Generalized linear mixed effect model coefficients used to estimate effect multipliers for the effect of companion crops on deposition efficiency and infection efficiency. Only the coefficients necessary for calculating the effect multipliers (according to Eqns. 5.1 and 5.2) are shown, with subscript i indicating the companion crop treatment. Coefficients for estimating the barrier effect are on the log scale and both are companion-specific. Coefficients for estimating induced resistance are on the logit scale; the intercept coefficient is the logit-transformed infection rate observed in the monoculture treatment, which is necessary to calculate the relative infection rate in the strip crops in combination with the companion-specific treatment coefficient. †, P < 0.1; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

Mechanism	**Parameter**			**Bean**	**Grass**	**Maize**	**Mono**
Barrier effect	GLMM coeff.	Intercept: treatment	$\boldsymbol{\beta_0}$	2.715***			
		Slope: treatment	$\boldsymbol{\beta_{1i}}$	0.063	0.127†	-0.238**	0
			$\mathbf{SE}_{\beta_{1i}}$	0.072	0.072	0.075	0
		Intercept: wind speed	$\boldsymbol{\beta_2}$	0.017			
		Slope: treatment-wind speed interaction	$\boldsymbol{\beta_{3i}}$	-0.177**	-0.101	-0.377***	0
			$\mathbf{SE}_{\beta_{3i}}$	0.067	0.067	0.077	0
	Effect multiplier (mean ± SD)			0.96 ± 0.08	1.07 ± 0.09	0.64 ± 0.06	1.00
Induced resistance	GLMM coeff.	Intercept: treatment	$\boldsymbol{\beta_0}$	-0.7885**			
			$\mathbf{SE}_{\beta_0}$	0.248			
		Treatment	$\boldsymbol{\beta_{1i}}$	0.833***	0.596**	0.112	0
			$\mathbf{SE}_{\beta_{1i}}$	0.226	0.229	0.234	0
	Effect multiplier (mean ± SD)			1.64 ± 0.18	1.45 ± 0.18	1.07 ± 0.17	1.00

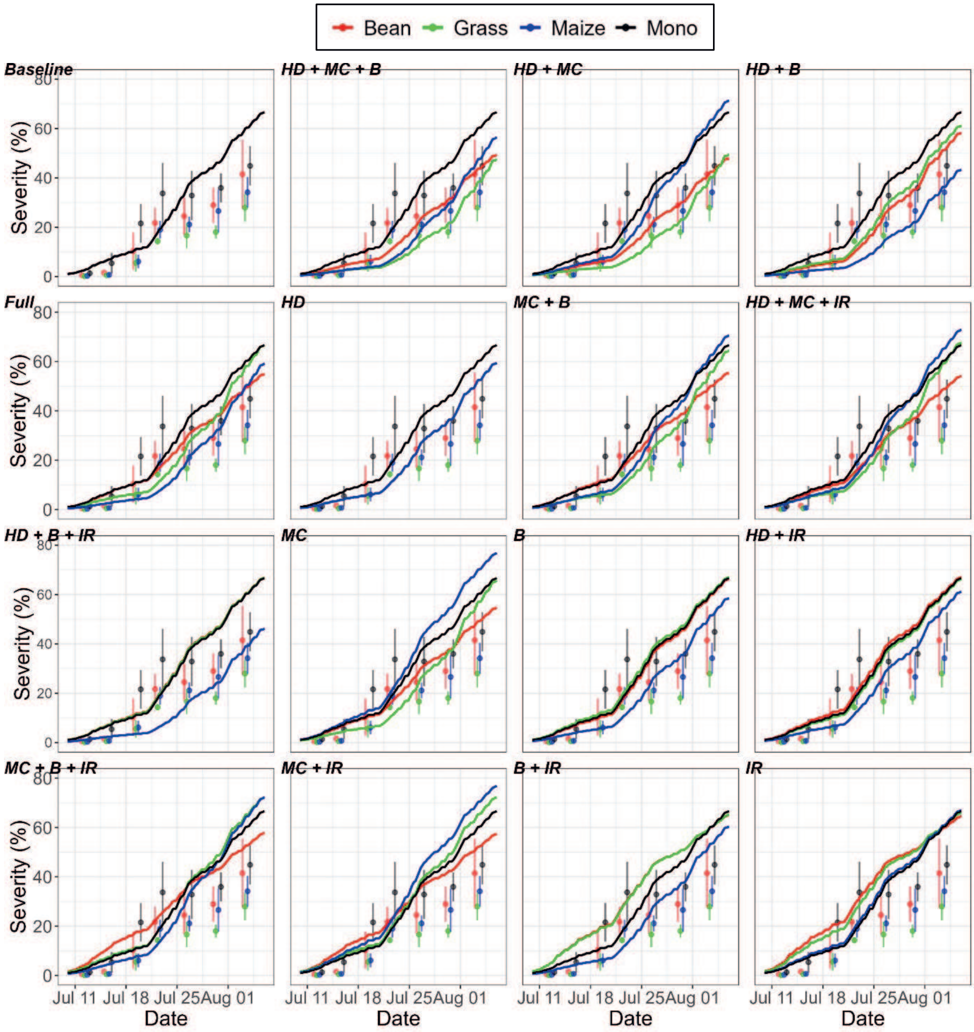


Fig. S5.6 Comparison of simulated and observed severity across all strip-crop scenarios. For each plot panel, lines represent mean simulated disease progress curves (DPCs) for each treatment under the given scenario. Scattered points with error bars represent the observed mean severity ± 1 SD, which was assessed seven times between 11 July and 4 August 2022 for randomly selected plants from four replicate plots of each treatment. Labels in the upper-left corner of plot panels indicate the scenario. Mechanism abbreviations: HD (host dilution); MM (microclimate modification); B (barrier effect). The 'baseline' scenario corresponds to the simulation of disease progress in the monoculture, and the strip-crop scenario with all strip-crop mechanisms inactivated. Following the 'baseline' plot panel, panels are ordered from left-to-right, and top-to-bottom in order of increasing mean absolute error (MAE) calculated from mean simulated DPCs and observed disease severity (i.e., 'HD + MC + B' is the highest-ranking scenario in MAE, and 'IR' is the lowest-ranking scenario). 'Baseline' was included out of order, as the monoculture reference; this scenario ranked 12th in MAE, after scenario 'HD + IR'.

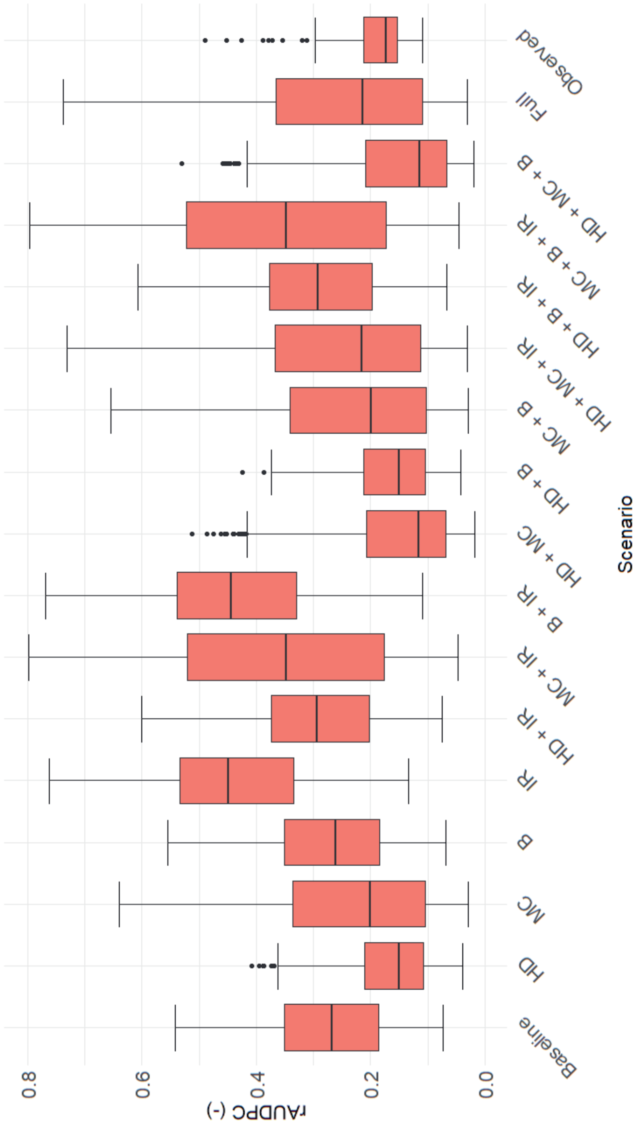


Fig. S5.7 Comparison of observed $rAUDPC_{obs}$ and $rAUDPC_{sim}$ simulated for potato strip cropped with faba bean across all strip-cropping scenarios accounting for uncertainty in the mechanisms of disease suppression (500 runs per scenario). Scenarios were combinations of toggled active mechanisms (HD, B, MM and/or IR respectively). The 'Observed' boxplot represents rAUDPC which were calculated from observed disease severity, which was assessed between 11 July and 4 August 2022 for randomly selected plants from four replicate plots of each treatment. 'Baseline' represents the scenario in which no disease-suppressive mechanisms are active, and disease in the strip-crops is identical to the monoculture. 'Full' represents the scenario in which all mechanisms are active. Mechanism abbreviations: HD (host dilution); MM (microclimate modification); B (barrier effect); IR (induced resistance).

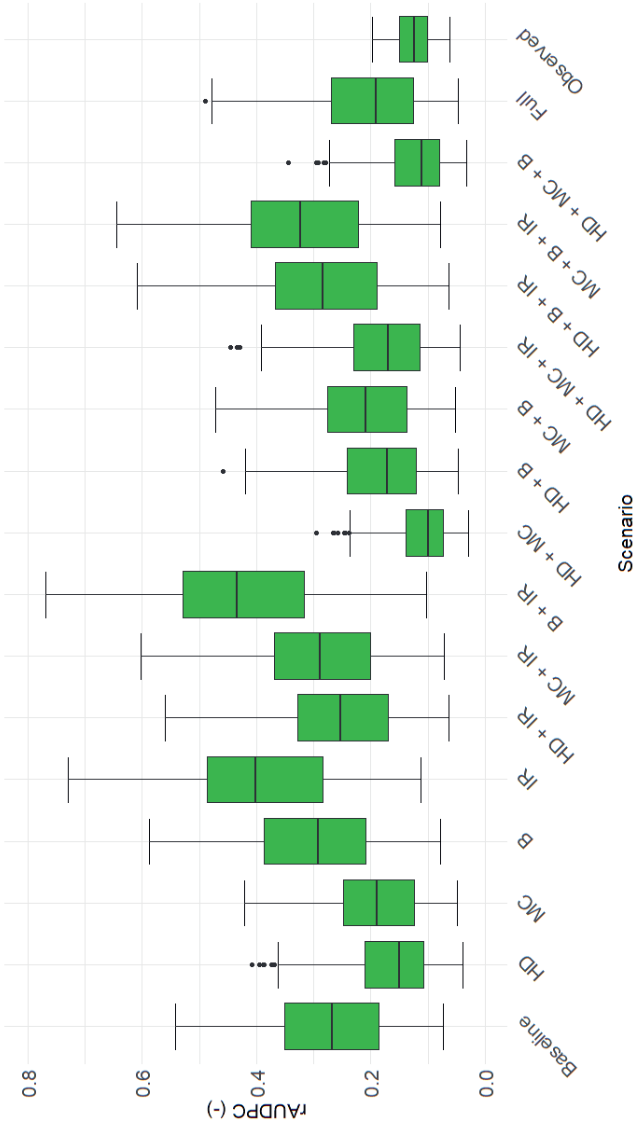


Fig. S5.8 Comparison of observed rAUDPC$_{obs}$ and rAUDPC$_{sim}$ simulated for potato strip cropped with ryegrass across all strip-cropping scenarios accounting for uncertainty in the mechanisms of disease suppression (500 runs per scenario). Scenarios were combinations of toggled active mechanisms (HD, B, MM and/or IR respectively). The ‘Observed’ boxplot represents rAUDPC which were calculated from observed disease severity, which was assessed between 11 July and 4 August 2022 for randomly selected plants from four replicate plots of each treatment. ‘Baseline’ represents the scenario in which no disease-suppressive mechanisms are active, and disease in the strip-crops is identical to the monoculture. ‘Full’ represents the scenario in which all mechanisms are active. Mechanism abbreviations: HD (host dilution); MM (microclimate modification); B (barrier effect); IR (induced resistance).

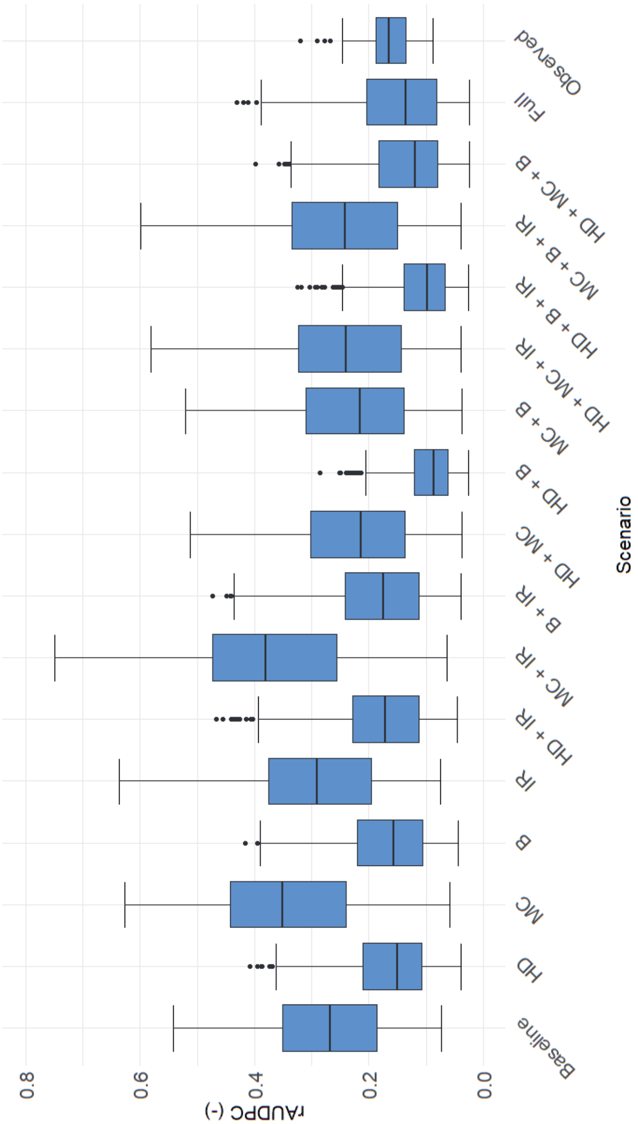


Fig. S5.9 Comparison of observed $rAUDPC_{obs}$ and $rAUDPC_{sim}$ simulated for potato strip cropped with maize across all strip-cropping scenarios accounting for uncertainty in the mechanisms of disease suppression (500 runs per scenario). Scenarios were combinations of toggled active mechanisms (HD, B, MM and/or IR respectively). The 'Observed' boxplot represents rAUDPC which were calculated from observed disease severity, which was assessed between 11 July and 4 August 2022 for randomly selected plants from four replicate plots of each treatment. 'Baseline' represents the scenario in which no disease-suppressive mechanisms are active, and disease in the strip-crops is identical to the monoculture. 'Full' represents the scenario in which all mechanisms are active. Mechanism abbreviations: HD (host dilution); MM (microclimate modification); B (barrier effect); IR (induced resistance).

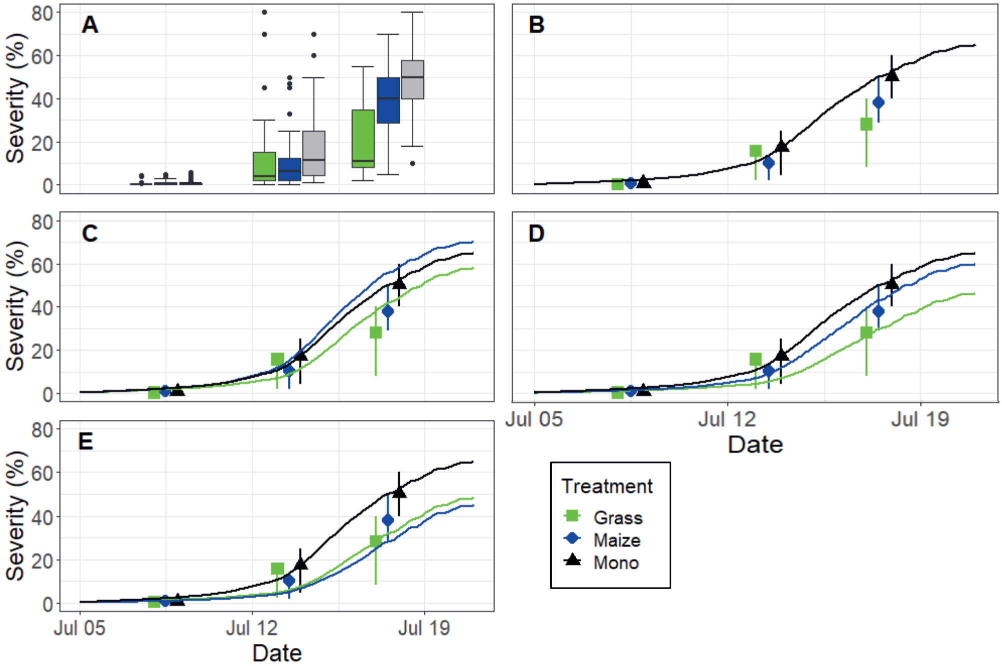


Fig. S5.10 Validation of late blight simulation model for strip-cropping treatments of 2021. (A) Boxplots of observed plant-level disease severity are depicted. Field observations took place on three dates, July 8, 13 and 17 2021. (B-E) Mean simulated DPC are shown for monoculture and two strip-crop treatments (potato strip-cropped with maize or ryegrass) under various scenarios. Trials of potato strip-cropped with faba bean were not conducted in 2021. Plotted points represent the mean observed disease severity, assessed per plant, and error bars represent upper and lower quartiles. The simulated scenarios that are depicted are: (B) monoculture (C) with the effect of microclimate modification ('MM'), (D) with the combined effects of host dilution and microclimate modification ('HD + MM'), and (E) with the combined effects of host dilution, microclimate modification, and the barrier effect ('HD + MM + B'). Mechanism abbreviations are: HD (host dilution); MC (microclimate modification); B (barrier effect); IR (induced resistance).

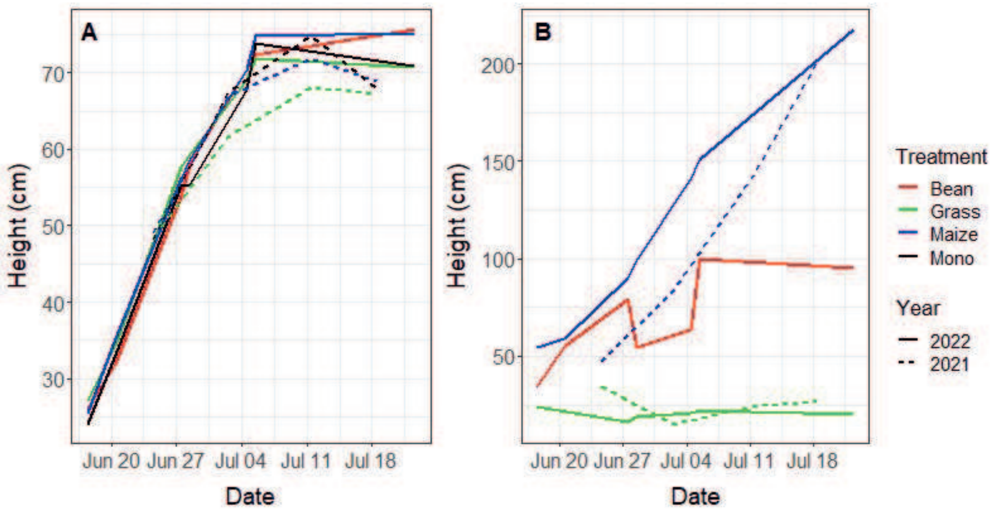


Fig. S5.11 Mean height of potato and companion crops in 2021 and 2022. In 2021, there were two plots of each treatment, monoculture potato, and potato strip-cropped with ryegrass or maize. In 2022, there were four plots of each treatment: monoculture potato, and potato strip-cropped with faba bean, ryegrass, or maize. The height of potato plants and companion plants were measured across all plots from June 24 to July 18 in 2021, and from June 17 to July 22 in 2022. (A) Height of potato plants planted in monoculture or strip-cropped with different companions. (B) Height of the companion plants of potato in strip-cropped plots. Note that potato was only strip-cropped with faba bean in 2022, not in 2021. In both 2021 and 2022 late blight symptoms were first observed in the field on July 8.

Chapter 6

General Discussion

The intensification and specialisation of agriculture have resulted in highly efficient and productive agricultural systems. However, this mode of agriculture also comes at a cost; it contributes to numerous forms of environmental degradation, biodiversity loss, and land and water pollution. Intercropping, simultaneously growing more than one crop species on the same field, could be a way to bring more diversity back to agricultural fields, and reduce these negative impacts. This diversity can have many positive effects, among which is disease suppression. In this thesis I aimed to improve our understanding of disease-suppressive mechanisms in (strip)intercrop systems.

I started with a broad meta-analysis of patterns in disease suppression across various intercrop combinations and pathosystems (Chapter 2). Although this approach provided insights in general patterns (or lack thereof), it did not allow for a detailed examination of the specific mechanisms driving disease suppression. Therefore, in the subsequent chapters I zoomed in on one specific system, namely potato late blight in strip cropping. Chapter 3 presented data from a three-year strip-crop field experiment to study the effect of strip cropping potato with companion crops of different stature, on the epidemic development of *Phytophthora infestans*. I then delved deeper into the mechanisms underlying disease suppression, such as microclimate, barrier effect, and host resistance (Chapter 4). Finally, in Chapter 5, we went one step further and used the data from the field experiment in a modelling approach to quantify the relative importance of individual mechanisms in overall disease suppression.

6.1 Overview of key findings

The meta-analysis presented in Chapter 2 clearly showed that intercropping suppresses plant diseases across a wide variety of systems and pathogens compared to monocropping. Intercropping reduced both the initial incidence and the apparent infection rate. This indicates that intercropping decreases both the primary infection of a crop and the subsequent spread of a pathogen within the crop. This effect was quite robust across a wide variety of crop combinations and planting patterns. Furthermore, I found that tall companion species significantly suppressed vectored plant pathogens more than companions of similar or shorter height than the focal crop, confirming a barrier effect of the companion crop as an overall relevant driving mechanism. Due to the interactions among traits of the focal host, companion species, the pathogen, weather and climate, and the variability in experimental design between studies (e.g. the moment of disease observation), it was challenging to tease apart the effects of different causal factors on plant disease incidence. Within each specific focal host-companion-pathogen combination, different (combinations of) disease-suppressive mechanisms are likely at play with different strengths, and different types of intercrop systems may achieve disease suppression in different ways.

The disease-suppressive potential of intercropping (Chapter 2) was also confirmed for strip cropping (a specific form of intercropping) using field experiments (Chapter 3). Strip cropping potato with grass or maize lowered the severity of potato late blight compared with potatoes grown in monoculture. Across three years of experiments, the average severity over the observation period was significantly lower in the strip-crop with grass or in the strip-crop with maize than in the potato monoculture. Strip cropping with faba bean did not significantly reduce disease severity, which could have been due to the relatively (compared to maize) poor development of the bean canopy as a barrier against spore dispersal.

When looking at the underlying mechanisms behind this disease reduction (Chapter 4), I found that strip cropping significantly altered the microclimate in the potato strip; relative humidity was lower in potato-grass than in the potato monoculture. Strip cropping with faba bean did not significantly change the microclimate. Changes in the duration of humid conditions are considered highly relevant for the epidemiology of potato late blight (Crosier, 1934; Harrison & Lowe, 1989; Zwankhuizen et al., 1998) because daily patterns of humidity and leaf wetness duration impact several components of the pathogen’s lifecycle and relatively small differences in wetness duration can greatly affect infection chance and disease progress.

Furthermore, potato strip-cropped with maize generally received the lowest number of particles over the growing season (a proxy for incoming spores) among all treatments, indicating that maize formed a barrier for spore dispersal. Within this system, there was a trade-off between this barrier effect and the microclimate effect, which was time dependent. The humidity increased in the potato strips next to maize, especially later in the season when maize was taller than potato and when late blight already had established. While maize functions as a barrier, it may inadvertently create more conducive conditions to infection. The balance of these effects greatly depends on the timing of both the disease and growth and stature of the crop species in the mixture.

By integrating these mechanisms into a microclimate-dependent late blight simulation model (Chapter 5), we confirmed that the small differences in relative humidity, due to companion crops, (for example, in July 2022, relative to the potato monoculture, the daily average RH was −1.1% in the potato–grass, +1.7% in the potato–maize, and +0.5% in the potato–faba bean), significantly impacted disease dynamics. Similarly, simulations considering only the barrier effect confirmed that this would have led to a reduction in disease severity in the strip crop with maize compared to the monoculture if acting in isolation. The model most accurately predicted disease suppression when combining host dilution, microclimate modification and barrier effect, suggesting that each of these mechanisms played a relevant role. For each companion crop, mechanisms suppressed disease in different degrees, and the mechanisms also partly counteracted each other (particularly microclimate modification and barrier effect), but their overall effect remained disease suppressive.

6.2 Limitations of meta-analyses

This research employed a combination of research methods to investigate disease-suppressive mechanisms in (strip)intercrop systems. We used a meta-analysis to explore broad patterns in disease suppression across various intercrop systems and species combinations and pathosystems (Chapter 2). This was followed by field experiments allowing us to study one specific system in detail (Chapter 3 and Chapter 4). Lastly, we applied a modelling approach using data from the field experiments to disentangle different disease-suppressive mechanisms, and quantify their relative importance in overall disease suppression. Each method had its own strengths and brought its own insights. Some methods also complemented and extended each another. For instance, by using field experiments we could measure changes associated with potential disease-suppressive mechanisms, such as a modified microclimate in potato strips intercropped with grass. However, because multiple mechanisms operate simultaneously in the field, it was difficult to attribute the individual contribution of each mechanism to the observed disease suppression. The modelling work complemented and enhanced this data from the field experiment; by using a model, we were able to quantify the contribution of each mechanism to disease suppression.

In hindsight, the meta-analysis may not have been an effective research method for identifying specific patterns of disease suppression across systems. This limitation likely stems from the complexity of intercrop-related disease-suppressive mechanisms. In the field, several mechanisms are at play simultaneously, and these can be working synergistically or in opposite directions in different type of systems. Additionally, weather conditions during the growing season can affect the canopy development of the companion crops, including the timing at which the companion crop reaches a certain height, which can influence the timing and strength of various mechanisms. For instance, in our field experiment (Chapter 3, 4), sowing time and weather conditions influenced the growth of maize. In the relatively cold spring of 2021, maize grew slowly and was therefore ineffective as a barrier for spore dispersal, whereas warmer conditions in 2022 allowed maize to grow taller more quickly, reaching sufficient height before the start of the epidemic.

However, such detailed information is rarely reported in scientific studies, making it unavailable for inclusion in the meta-analysis. As a result, aggregating findings across diverse systems may have obscured rather than revealed patterns. This could be one of the cases where (agro)ecological studies are too heterogeneous to be combined statistically in a meaningful way (Whittaker, 2010) and where context-specific case studies provide better mechanistic understanding than identifying generalised metrics (Simberloff, 2004, 2006). Counterintuitively, then, when the goal is to generate generalisable insights for designing disease-suppressive systems, it may be more effective to develop methods and tools that gain mechanistic understanding of one specific system, that can then be translated or adapted to other systems, than to find patterns across systems.

6.3 Multifunctionality

(Agro)ecosystems are capable of providing a wide range of ecosystem functions and services. Ecosystem functions are the array of biological, geochemical and physical processes that occur within an ecosystem, while ecosystem services relate to the extent to which these function meet some human needs (Manning et al., 2018). Although this thesis primarily focused on disease suppression in intercrop systems, (agro)ecosystems are inherently multifunctional, i.e. they simultaneously provide multiple ecosystem functions and services. Ideally, intercrop systems should support multiple agronomic and ecological functions, such as yield stability, weed suppression, natural pest control, efficient resource use, and resilience to environmental stresses like drought and flooding. However, identifying or designing systems that successfully promote multiple functions and services is challenging.

While intercrop systems can suppress disease, it is not a given that they will simultaneously provide other ecological services. For instance, in the meta-analysis (Chapter 2), we saw that some systems managed to achieve both disease suppression and a yield increase of the host crop (win-win), while there were also systems that only achieved one of those functions (trade-off), and some systems that had both an increase in disease and a reduction in yield of the host crop (lose-lose) (Fig. 2.7). A closer examination of the characteristics of these systems reveals that the type of pathogen involved (fungi, virus, or bacteria) does not appear to determine whether an intercrop system results in a win-win, trade-off, or lose-lose outcome (Fig. 6.1). Notably, though not entirely unexpected, systems with taller companion crops are often associated with reduced yield in the host crop. Interestingly, in systems employing a strip cropping pattern, a greater proportion of cases fall into the win-win category compared to other intercrop arrangements.

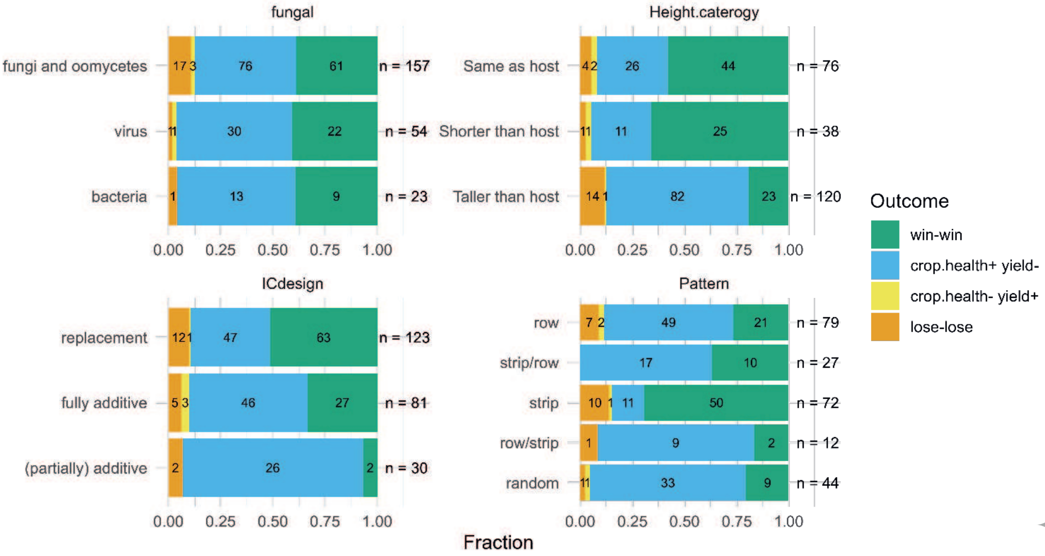


Fig. 6.1 Distribution of outcome categories of the meta-analysis (Chapter 2) across intercropping system characteristics. 'Win-win' systems achieved both disease suppression and yield increase of the host crop. 'crop.health+ yield-' indicates reduced disease incidence with a yield decrease, while 'crop.health- yield+' involves increased disease incidence but higher yield. 'Lose-lose' systems had both increased disease incidence and decreased yield. Bars represent the percentage of outcome category per system category. Each subplot corresponds to a specific system aspect (e.g. type of pathogen, height of companion, intercrop design).

The types of intercrop systems that are chosen in experimental studies already give an insight into which crop combinations are favourable for promoting certain ecological functions. For example, meta-analyses studying the yield gain of intercropping as compared with sole crops, had mainly mixtures of maize/legume, small grain/legume, and maize/small grain in their dataset (Li et al., 2020, 2023) (Fig. 6.2). Similarly, a meta-analysis studying the weed suppressive effect on intercropping found most data centred on intercrop systems consisting of maize/legume or small grain/legume (Gu et al., 2021). In contrast, the meta-analysis on disease suppression (Chapter 2) included more records involving 'other' (not maize/small cereal-legume combinations) crop types, such as zucchini (*Cucurbita pepo*) and members of the Solanaceae family (e.g., potato, tomato, pepper, tobacco). This suggests that while maize/legume and small grain/legume systems may be effective for enhancing yield and suppressing weeds, disease suppression might be more closely associated with intercrop systems other than the common cereal-legume combinations. Conversely, it might also suggests that these 'different' systems may be less effective, or at least less frequently used, for achieving yield gains or weed suppression.

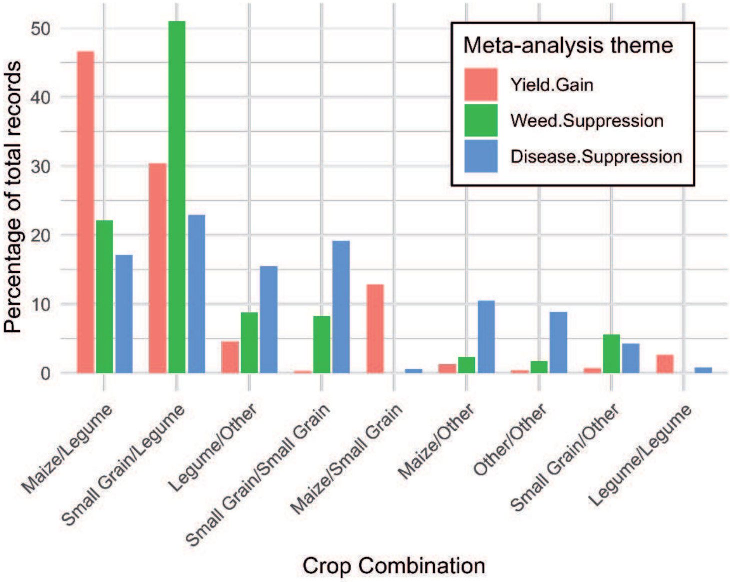


Fig. 6.2 Percentage of data points for different crop combinations in intercropping studies across three separate meta-analyses, each with a different focus. The total number of data points was 934 for the meta-analysis on yield gain (Li et al., 2020, 2023), 339 for weed suppression (Gu et al., 2021), and 484 for disease suppression (Chapter 2).

Going from this broad comparison of multifunctionality across different intercrop systems, another example of multifunctionality can be found when looking at one specific example from the strip-crop experiment (Chapter 3). Potato plants are subjected to multiple stressors, next to potato late blight. The Colorado potato beetle (*Leptinotarsa decemlineata*), is a major pest problem in potato production mainly due to the foliage feeding by its larvae (Chittenden, 1907; Ferro et al., 1985; Weber, 2003). During the 2022 growing season of the potato strip-crop experiment described in Chapter 3, we counted Colorado beetles on the potato plants grown in strip-crop or in monoculture. During this season, strip cropping did not reduce the number of beetles (adults and larvae) compared with monoculture, and the number was actually higher in the strip-crop with faba bean or maize (Fig. 6.2). At 10 weeks after planting, the strip-crop with faba bean had a significantly higher number (p = 0.02), and 11 weeks after planting the strip-crop with maize had a significantly higher number (p=0.001) than the monoculture.

Although diverse systems are often accredited to enhance natural pest suppression (Alarcón-Segura et al., 2022; Bianchi et al., 2006; Cuperus et al., 2023), and some studies have found that Colorado potato beetle numbers decrease in more diverse cropping systems (Alioghli et al., 2022; Tajmiri et al., 2017), the strip-crop systems that we tested may not have been sufficiently diverse to disturb the beetles from finding the host plants. Including the practice of strip cropping in farm operations might actually increase build-up of beetles over the years. The proximity of potato strips from year to year, relative to the wider spacing in large monocultures, may facilitate their movement from overwintering sites in the soil of previous year's crops to the new potato crop. Over time, this could potentially increase pest pressure in strip-cropped systems, as beetles emerge near favourable habitat with reduced dispersal distance.

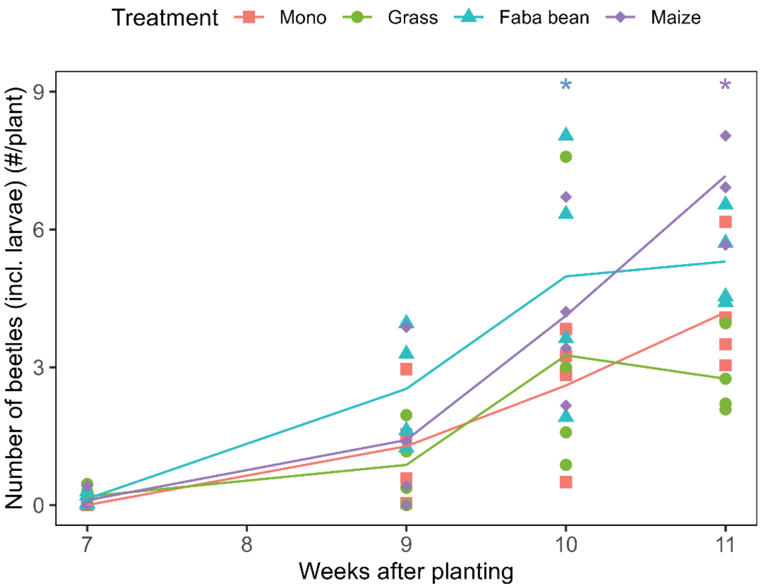


Fig. 6.3 Number of Colorado potato beetles (adults and larvae) on the potato plants grown as monoculture (Mono) or strip-cropped with either grass, faba bean, or maize during the 2022 growing season. The points (symbols) represent the mean number of beetles (including larvae) per plot based on visual observations on 24 plants per plot. The lines are drawn between the midpoints of the four plots for each treatment. Stars indicate a significant difference between the strip-crop and the monoculture in a given week; blue for the strip-crop with faba bean, purple for the strip-crop with maize.

Research on ecosystem functioning often takes an approach whereby it attempts to isolate a single function to better understand underlying mechanisms and to identify clear cause-effect relationships. However, this approach misses the complexity of real-life ecosystems and potential trade-offs and synergies that typically exist between different ecosystem functions. In a time in which crop production faces multiple demands, such as achieving high yields of quality crops, using resources efficiently, enhancing resilience to climate and environmental change, and preserving biodiversity while minimising its environmental impact (Baekelandt et al., 2023; Harbinson et al., 2021; United Nations, 2021), knowledge of these potential interactions can be critically important when designing intercrop systems. While studying individual functions can deepen our understanding of specific mechanisms, research needs thus to take a more integrated approach to understand how multiple functions interact. If multiple functions can be achieved simultaneously without compromise, there is no problem. But if promoting one function goes at the cost of another function, it becomes important to consider which functions are the most important in a given context. For example, in potato-based systems, where late blight drives heavy pesticide use and resistance is a growing concern, disease suppression may take priority in intercrop design, but as my results suggest e.g., the combination with maize could enhance Colorado beetle incidence while income generation from grass-clover is relatively low.

6.4 Implementation of strip-cropping

The agricultural sector faces increasing pressure to meet multiple demands (producing high yields, using resources efficiently, minimising environmental impact, etc.). Meeting these challenges requires a transition toward more sustainable production systems. While intercropping has numerous benefits, to enhance its broader implementation, challenges faced by farmers in its execution need to be addressed. One of the challenges identified is the lack of agroecological knowledge and practical experience in planning and implementing mechanised strip cropping systems (Juventia, 2024). For farmers, strip cropping is not merely having strips of different crops next to each other, they need to figure out what combination of crops works and how to adjust machinery to fit the chosen strip width and fit this in a cost-efficient, and legally permitted crop-rotation plan. Research into better understanding of the ecological interaction between crop species could help farmers in selecting crop combinations based on their objectives. For instance, the strip-crop experiment described in Chapter 3 showed that strip cropping potato with grass suppressed late blight and enhanced potato yield within the potato strips in comparison to potatoes grown as a sole crop. In Chapter 4, I showed that strip cropping with grass lowered the relative humidity in the potato canopy, reducing the daily duration of favourable conditions for infection by almost two hours. Understanding these mechanism helps extend disease suppression strategies beyond the specific companion crops tested, and could inform the design of new strip-cropping systems. In the given example it is likely that other short companion crops could produce similar microclimate effects, although more research is needed to verify the generality of this mechanism.

The transition to ecology-based agriculture requires not only understanding of ecological interactions, but also practical knowledge, technological innovations, and institutional support. One practical challenge is finding the right width of the strips to be feasible with current machines (Juventia, 2024). A strip-crop farmer from the CropMix[1] consortium began with strips of 3-meter wide when he first implemented strip cropping, but changed to strips of 18-meter after the first year due to inefficiency of machinery, because his harvester works on 9-meter width. For another strip-crop farmer finding the right strip width was also a puzzle. When they first implemented strip cropping on the farm, they started with strips of 39 meter - the width of the sprayer boom. The next year they experimented with a strip width of 19.5 meters (half the spray boom), and later with 12 meters, which matched the width of their harrow (Dutch: ‘eg’). They are now considering 24-meter strips (twice the harrow width) as a potentially better fit for both the harrow and sprayer (C. Lugtenburg, personal communication, 7 November 2024).

While being a practical puzzle, strip width plays an important role in determining the ecological benefits of strip cropping. Narrower strips allow for more interaction between crop species and generally enhance disease-suppressive effects (Ditzler et al., 2021). Yield benefits of growing species in alternating strips rapidly drop as strips become

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[1] CropMix is a research consortium funded by the Dutch government which aims to drive the transition to robust agro-food production ecosystems, in which biodiversity and resilience are the starting point for coping with external threats. The consortium consist of researchers from various disciplines (agronomy, ecology, economics and social scientists), 25 strip-crop farmers, and partners of civil society organisations and market parties involved in the food chain.

wider (van Oort et al., 2020), yet wider strips are more compatible with existing mechanised systems—particularly for conventional farmers. For instance, a conventional strip-crop farmer in the CropMix consortium currently uses strips of 27-meter to match the width of his sprayer. For him it is (mechanically) not feasible to go to narrower strips (P.H. Mulder, personal communication, 12 February 2025). Thus, in order to be able to enhance the ecological benefits of strip cropping, the feasibility of implementing and managing small strips has to be improved.

The development of small-scale autonomous machines would enable farmers to more easily and efficiently manage small strips. Innovations in strip-crop technology also enable farmers greater flexibility and creativity in designing their strip-crop system. However, currently, technological development is not supporting a transition towards more diverse cropping systems, but rather focuses on optimising existing systems with increasingly more precise techno-fixes (Ditzler, 2022). This orientation towards reducing input use through increased efficiency is a step in the right direction but does not necessarily change the fundamental structures of industrial agriculture and may thus not lead to a redesign of our farming systems (Altieri et al., 2017; Clapp & Ruder, 2020).

Technology for Ecology

Shifting current farming practices from optimisation with precision agriculture and precision livestock farming technologies, towards “next-generation agricultural production systems that are sustainable, circular and regenerative”[2], is central to the concept Technology for Ecology that is being developed within the Dutch Science Foundation (NWO)-funded Synergia consortium in which this PhD research project is embedded. The overall aim is to work on Technology for Ecology-based Farming, where biological/ecological principles in farming lead the development of new farming systems, and by that the required technological knowledge, principles and tools. Farming technologies that support ecology-based systems cannot be easily defined; they are highly context-dependent and shaped by the practices through which they are applied (Webster & and Gardner, 2019). In the case of sensing technology, sensors can enable different types of knowledge: oversight, which helps farmers to get an

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[2] https://technology4ecology.org/

oversight of the current state in order to optimise the efficiency of production, and insight, which fosters a holistic and long-term understanding of ecological relations and how they affect production (Gorissen et al., 2025). For the technology of sensors to be more ecology-based, they should not only provide oversight, but also give farmers insights. Getting insight goes beyond short-term decision-making, focusing instead on improving and nurturing ecological interactions. More generally, new technologies should help prevent farmers from getting ‘stuck’ at the initial efficiency-focussed level, where they reduce external inputs, by giving farmer the necessary insights to replace these inputs with natural processes.

Continuing on the concept of Technology for Ecology, one central aspect is that biological and ecological principles should guide the development of new farming systems (rather than technologies). This means that ideally, by better understanding ecological interactions, we can design (diverse) farming systems in which the ecological interactions enhance the functioning of the system. Only then do we develop the technology that is needed to set-up, manage and harvest such a system. However, there is not a “one-size-fits-all” approach when it comes to designing these systems. The functioning of the ecological interactions is quite dependent on the context and the objectives of the system. For example, when it comes to disease suppression, the ‘most efficient’ system depends on multiple contextual factors, such as the crops being grown and the specific pathogens involved (Chapter 2). Furthermore, the objectives of the farmer (or of broader political or societal stakeholders) will further shape what the system will look like. A system optimised for disease suppression may look very different from one prioritising higher yields across both/all crops. Consequently, the technologies needed to support these systems may also have to be diverse and context-specific. Thus, instead of starting with available technology and trying to fit it to ecological aims, we must start with ecological system design, and then develop or adapt technologies that support it.

6.5 The actual contribution of strip cropping in the transition

As discussed throughout this thesis, agriculture exerts considerable pressure on the environment—particularly through the use of chemical inputs. Intercropping is often mentioned as a key diversification strategy in agriculture to reduce external inputs for fertilisation and crop protection (Timaeus et al., 2022; Yan et al., 2024). However, the implementation of (strip)intercropping does not automatically lead to input reduction. While it is easy to conclude that a lower disease severity in (strip)intercrops (Chapter 2, 3) would translate to reduced pesticide use, it is not necessarily the case. To understand the role of (strip)intercropping in the transition to towards sustainable agriculture, it is crucial to understand how farmers manage intercrops in practice, and whether intercropping actually reduces dependency on chemical inputs.

When looking at the different types of farmers, conventional farmers have the greatest potential to reduce the use of chemical inputs, since organic and biodynamic farmers are generally already using less inputs and no chemical inputs. As previously discussed, conventional strip-crop farmers, however, will likely adjust their strip width to the working width of their existing machinery, including their sprayer boom, to avoid having to invest in new machinery. As a result, these conventional strip-crop farmers are spraying their strip-cropped fields in the same way as they would do in monocultures, without adjusting their crop protection strategy (C. Lugtenburg, personal communication, 7 November 2024; P.H. Mulder, personal communication, 12 February 2025). This shows that implementing strip cropping thus does not automatically reduce external inputs.

For pesticide use to decrease, there must also be a change in management approach. One potential strategy might be to delay the first spray of the season. However, in our field experiments (Chapter 3) I did not observe a delay in first detection of late blight in the strip-crops plots compared with monoculture plots. For potato late blight, delaying the first spray under intercropping may thus not be feasible. The other strategy would be to reduce the total number of sprayings during the season. This approach would require integration of the ecological functions of strip cropping, such as its impact on microclimate, into decision support systems (DSSs). DSSs are applied management tools that can be used to interpret complex data (e.g. weather forecasts) and can help guide more nuanced, risk-based decisions about crop protection (Shtienberg, 2013). If decision-making tools accounted for the altered conditions in strip-cropped fields, they could support a reduction in pesticide applications.

Reformist change or radical transformation?

In this final section of the thesis I give a more personal view on agricultural transition. As mentioned above, the orientation towards reducing input use is only a first step in the transformation of industrial agriculture towards diverse ecology-based systems. Optimising current agricultural practices may provide (temporary) solutions to specific problems, but is unlikely to provide long-term solutions that more systemically and holistically address problems in agriculture. There is a need for advancing beyond mere input reduction to substituting exogenous inputs with ecological interactions.

Most current agricultural research aims to improve efficiency, reduce inputs, and address environmental degradation. Scientists are focussing on enhancing productivity while preserving natural resources. An example is precision agriculture, which employs drones and satellites to monitor fields and precisely adjust the quantity of inputs (water, fertilisers, and pesticides). In essence such practices entail that one finetunes existing practices e.g., reducing their environmental impact, but without changing the fundamentals of the system. This is what one could denote as a reformist approach (Adams, 2019; Watson, 2024). A reformist approach aims to reform current systems to make them more efficient and less harmful, without fundamentally challenging the system.

Radical transformation, in contrast, pushes for a more radical change, a complete redesign of the current food system (Boutaleb, 2025; Watson, 2024). The goal is then not to use fewer inputs, such as pesticides, but to create a system that does not require them in the first place. This goes beyond improving field-level diversity such as through strip cropping. Changes at the landscape scale are needed as well, promoting greater crop diversity across the landscape, rather than having a few single crops, such as potato, dominate the landscape. However, looking more critically, achieving transformative change is actually quite complex and requires “a fundamental, system-wide reorganization across technological, economic and social factors, including paradigms, goals and values” (Pickering et al., 2022). While changes needed for transformation are often envisaged as taking place at the farm level (such as for the practice of strip cropping), the wider context—the political, economic, cultural and social dynamics—is just as important. Transformations need to be considered at the whole food system level, not just at the farm or field level.

Going beyond the ecological side, I think a crucial aspect of this radical transformation is a change in power structures (Anderson et al., 2021b); a change in what in social sciences is called the ‘dominant regime’. The dominant regime, in the case of the agricultural system, refers to the prevailing system of industrial agriculture and policies that prioritise profit, efficiency, and global markets (Anderson et al., 2021b). Practices such as climate-smart agriculture, regenerative agriculture, conservation agriculture, precision agriculture, or other forms of alternative farming practices, though aiming for sustainability, often fail to deliver radical change, because they leave existing power dynamics in place and remain embedded in the dominant regime. Some approaches, such as organic agriculture, had a radical and transformative agenda that, over time, in many aspects has been twisted to conform to the dominant regime (Anderson et al., 2021a). Co-optation is the process by which a dominant regime incorporates a practice or idea into its structure, reshaping it to neutralise it and maintain control. In the case of strip cropping, this might occur when the practice is adopted with wide strip sizes and conventional management, resulting in few or no benefits of ecological interactions. In the process of co-optation, only certain incremental changes are taken up, those that do not alter power structures, that support technical fixes in reductionist ways, and that otherwise lack a holistic approach to enable social, cultural, political and economic dimensions of transitions to sustainable food systems. This process of co-optation is not only carried out by people and institutions of the dominant regime, it can be a more subtle process, often perpetuated by well-meaning researchers and institutions.

Fortunately, there are also interventions that support transformative change. Social movements, organisations, activists, critical scholars are working to deconstruct aspects of the current regime. Through participatory decision-making and grassroots action, they help reshape the food system from the ground up. They are establishing new rules or institutions, fostering new practices, processes or technologies, or building new networks and social groups to legitimately challenge the regime. For example, protests against pesticides (pesticide vrij-dag (Parkinson Vereniging, 2025)), or legal action to object to the use of certain pesticides containing glyphosate (Parkison Vereniging, 2025), help deconstruct the regulatory frameworks that have enabled monocultural chemical-dependent agriculture. These actions can thereby encourage the emergence of alternatives.

Now coming back to the practice of strip cropping, a practice alive with transformative potential, but vulnerable to being co-opted. When the practice is adopted by farmers, within the current industrialised framework without broader systemic change, it may lead to a geometric change of the landscape from large intensely managed rectangular plots to more narrow but still intensely managed strips. This does not mean strip cropping is pointless, nor is it a reason for discouragement, it is a reminder that transformation is not a single act or solution, but an ongoing, collective process. With attention to context, power, purpose, and collaboration, practices like strip cropping can become meaningful steps toward more just, resilient, and sustainable food systems.

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Summary

The mechanisation, specialisation and intensification of agriculture have resulted in highly efficient and productive agricultural systems. However, this mode of agriculture also comes at a cost; it contributes to numerous forms of environmental degradation, biodiversity loss, and land and water pollution. Monocultures - (large-scale) fields where a single crop type is grown - are a key element of such agricultural systems, and relatively vulnerable to pests and diseases. Due to the low plant diversity, a single pathogen can spread relatively unhindered, potentially destroying the whole crop. One of the most notorious examples is the potato late blight epidemic caused by oomycete *Phytophthora infestans* that caused the Irish potato famine in the 1840s. Intercropping, simultaneously growing more than one crop species on the same field, could be a way to bring more diversity back to agricultural fields, and reduce negative impacts associated with modern agriculture. This diversity can have many positive effects, among which is disease suppression.

Despite the overwhelming evidence that intercropping can suppress diseases, it is not clear which management practices, pathogen traits or host or companion crop characteristics influence the strength of the suppression. Although different disease-suppressive mechanisms have been hypothesised and studied, it is largely unknown whether and how the mechanisms can be influenced by the identity and traits of the companion species, and how the effects of different mechanisms work out in combination (i.e., to what extent are there trade-offs or synergies). While GPS-aided mechanisation makes strip cropping more feasible than mixed or row intercropping, the typical strip widths that are compatible with machinery could reduce some of the benefits, because the benefits supposedly depend on the proximity of the different species. There is, however, little information on the effectiveness of disease control in strip cropping systems.

In this thesis, I used a two-fold approach to improve our insight into what drives disease suppression in intercropping. First, I used a meta-analysis to identify factors across different intercrop systems, such as characteristics of the pathogen, the crops in the

mixture or management choices, that might influence the disease-suppressive mechanisms. Although this approach provides insights into general patterns (or lack thereof), it does not allow for a detailed examination of the specific mechanisms and their interactions. Therefore, I followed this meta-analysis with a more in-depth study of one specific system, namely potato late blight in strip cropping. Potato late blight is a major stressor for potato production, driving heavy pesticide use, and growing chemical resistance and the ability of *Phytophthora infestans* to rapidly overcome host resistance pose ongoing challenges for potato production.

In Chapter 2, I analysed published experiments on disease suppression across various intercrop combinations and pathosystems, to identify patterns across these different systems and to gain insights into the disease-suppressive mechanisms at play across these systems. I showed that intercropping suppresses plant diseases across a wide variety of systems and pathogens compared to monocropping. Intercropping reduced both the initial incidence and the apparent infection rate of pathogens. This indicates that intercropping decreases both the primary infection of a crop and the subsequent spread of a pathogen within the crop. This effect was quite robust across a wide variety of crop combinations and planting patterns. Furthermore, I found that companion species that were taller than the focal crop significantly suppressed vectored plant pathogens in the focal crop more than companions of similar or shorter height, suggesting a potentially important role of the barrier effect. Interactions among traits of the focal host, companion species, the pathogen, weather and climate, and the variability in experimental design between studies (e.g. the moment of disease observation), likely made it challenging to tease apart the effects of different causal factors on plant disease incidence. Aggregating findings across diverse systems obscured rather than revealed patterns.

To study disease-suppressive mechanisms more in depth, in Chapter 3 I focused on one specific pathosystem. I conducted three years of field experimentation on disease suppression and yield in potato strip cropping in Wageningen, the Netherlands. The experiments tested the effect of strip cropping potato with companion crops of different stature, each planted in alternating 3-meter wide strips, on the epidemic development of *Phytophthora infestans* and tuber yield. This chapter confirms that strip cropping has the potential to suppress disease. Strip cropping potato with grass or maize lowered the severity of potato late blight compared with potatoes grown in monoculture. Across three years of experiments, the average severity over the observation period was significantly lower in the strip-crop with grass or in the strip-crop with maize than in the potato monoculture. Strip cropping with faba bean did not significantly reduce disease severity.

In Chapter 4, I delve deeper into the mechanisms underlying disease suppression. In the field experiments described in Chapter 3, I measured along with the epidemiological variables, various factors that affect disease development, such as microclimate, spore dispersal, and host resistance. This chapter explores how different companion crops influence these factors. Strip cropping significantly altered the microclimate in the potato strip; relative humidity was lower in potato-grass than in the potato monoculture. Strip cropping with faba bean did not significantly change the microclimate. Furthermore, potato strip-cropped with maize generally received the lowest number of particles over the growing season (a proxy for incoming spores), indicating that maize formed a barrier for spore dispersal. Within this system, there was a trade-off between this barrier effect and the microclimate effect, which was time dependent. The humidity increased in the potato strips next to maize, especially later in the season when maize was taller than potato and when late blight already had established. While maize functions as a barrier, it may inadvertently create more conducive conditions to pathogen development. The balance of these effects greatly depends on the timing of both the disease and growth and stature of the crop species in the mixture.

In Chapter 5, I go one step further and use the findings from the field experiment in a modelling approach to quantify the relative importance of individual mechanisms in overall disease suppression, and the interactions between mechanisms. By integrating these mechanisms into a microclimate-dependent late blight simulation model, I confirmed that the small differences in relative humidity, due to companion crops, significantly impacted disease dynamics. Similarly, simulations considering only the barrier effect confirmed that this would have led to a reduction in disease severity in the strip crop with maize compared to the monoculture if acted in isolation. The model

most accurately predicted disease suppression when combining host dilution, microclimate modification and barrier effect, suggesting similar importance of these mechanisms. For each companion crop, mechanisms suppressed disease at different strengths, or counteracted (particularly microclimate modification and barrier effect), but their combined effect remained disease suppressive.

In the final chapter, Chapter 6, I synthesized the findings from the previous chapters, placing them within a broader context. I reflect on the usefulness of a meta-analysis to identify disease-suppressive mechanisms in cropping systems. Additionally, I discuss the challenges of designing disease suppressive strip-crops as well as challenges related to the practical implementation of strip cropping in conventional farming, and discuss its contribution to lowering dependence on chemical inputs. Lastly, I stress the importance of looking beyond optimisation and (short-term) techno-fixes, advocating instead for a radical transformation of the food system and a change in power structures in order to actually address the negative side effects of modern agriculture.

Samenvatting

Mechanisatie, specialisatie en intensivering van de landbouw hebben geleid tot zeer efficiënte voedselproductie. Deze vorm van landbouw heeft echter ook een keerzijde: het veroorzaakt milieuschade, leid tot verlies aan biodiversiteit en vervuiling van de bodem en het water. Monoculturen –velden waarop één gewas wordt geteeld – vormen een belangrijk onderdeel van het huidige landbouwsysteem, maar ze zijn ook vatbaar voor plagen en ziekten. In een perceel met geen gewasdiversiteit kan een pathogeen zich makkelijk verspreiden en mogelijk het hele gewas aantasten. Een bekend historisch voorbeeld is de aardappelziekte, veroorzaakt door de oömyceet *Phytophthora infestans*, die bijdroeg aan de Ierse hongersnood in de jaren 1840. Mengteelt, waarbij meerdere gewassen gelijktijdig op één veld worden geteeld, kan een manier zijn om de biodiversiteit op landbouwgrond te vergroten en zo de negatieve effecten van intensieve landbouw te verminderen. Mengteelt kan verschillende voordelen opleveren, waaronder het verminderen van ziektedruk.

Hoewel er vaak aangetoond is dat mengteelt ziekte aantasting kan verminderen, is het nog niet bekend welke teeltstrategieën, eigenschappen van pathogenen of kenmerken van de gewassen in de menging bepalend zijn voor de mate van ziekteonderdrukking. Er zijn verschillende mechanismen voorgesteld en onderzocht, maar het blijft grotendeels onduidelijk of, en hoe, deze beïnvloed worden door eigenschappen van het buurgewas. Ook is weinig bekend over hoe verschillende mechanismen op elkaar inwerken: versterken ze elkaar, of werken ze elkaar tegen? Dankzij GPS-gestuurde mechanisatie is strokenteelt een praktisch beter uitvoerbare en daarbij meer haalbare manier om diversiteit aan te brengen dan mengteelt op rijniveau of volledige gewasmenging in de huidige westerse vorm van akkerbouw. Toch kunnen de strookbreedtes die nodig zijn voor machinale bewerking bepaalde voordelen verkleinen, omdat de effectiviteit van mengteelt deels afhangt van de fysieke afstand tussen verschillende soorten. Hoe effectief strokenteelt ziekten kan onderdrukken is grotendeels onbekend.

In dit proefschrift heb ik op twee manieren onderzocht hoe ziekteonderdrukking in mengteelt werkt. Eerst heb ik door middel van een meta-analyse onderzocht hoe het gewas, het buurgewas, het type pathogeen, en het management van de mengteelt ziekteonderdrukking beïnvloed. Deze aanpak geeft inzicht in algemene trends, maar biedt weinig ruimte om dieper in te gaan op specifieke interacties tussen mechanismen. Daarom heb ik daarna een gedetailleerde studie uitgevoerd binnen één systeem: Phytophthora in aardappel-strokenteelt. Deze ziekte heeft een grote impact op de aardappelteelt, met grootschalig gebruik van bestrijdingsmiddelen als gevolg. De snelle resistentieontwikkeling van *Phytophthora infestans* tegen zowel chemische middelen als resistente rassen bemoeilijken de teelt van aardappel in noordwest Europa.

In hoofdstuk 2 analyseerde ik gegevens uit eerdere studies over ziekteonderdrukking bij verschillende mengteeltcombinaties en ziekten. Mijn doel was om patronen en mechanismen te identificeren. Uit de analyse bleek dat mengteelt in het algemeen leidt tot lagere ziekte incidentie dan in monocultuur. Het verlaagde zowel de initiële ziektedruk als de snelheid waarmee ziektes zich opbouwen. Dit wijst erop dat mengteelt zowel de introductie als verspreiding van een ziekte kan afremmen. Dit effect bleek robuust in uiteenlopende combinaties van gewassen en mengteelt ontwerpen. Ook ontdekte ik dat buurgewassen die hoger zijn dan het hoofdgewas effectiever vector-overdraagbare ziektes verminderen dan buurgewassen die even hoog of lager dan het hoofdgewas zijn, waarschijnlijk vanwege hun functie als fysieke barrière. Het gebrek aan duidelijke patronen in de meta-analyse is waarschijnlijk het gevolg van interacties tussen gewas-, pathogeen- en klimaat en verschillen in onderzoeksopzet.

In hoofdstuk 3 richtte ik mij op één specifiek systeem om dieper in te gaan op de ziekte-onderdrukkende mechanismen, en de interactie tussen deze mechanismen. Hiervoor heb ik drie jaar lang veldproeven uitgevoerd in Wageningen. Daarbij onderzocht ik de invloed van strokenteelt met verschillende buurgewassen (van verschillende hoogtes), geplant in stroken van drie meter, op de ontwikkeling van Phytophthora in aardappel. De resultaten bevestigen dat strokenteelt ziektes kan onderdrukken. Drie jaar aan experimenten lieten zien dat de gemiddelde ziekte aantasting significant lager was in de strokenteelt met gras of in de strokenteelt met maïs dan in de aardappelmonocultuur. Strokenteelt met veldbonen gaf daarentegen geen significante afname van ziekte.

In Hoofdstuk 4 verdiepte ik mij verder in de onderliggende mechanismen van ziekteonderdrukking. Naast epidemiologische gegevens heb ik ook andere factoren gemeten, zoals het microklimaat, inkomende deeltjes en vatbaarheid van aardappel planten. Deze factoren werden beïnvloed door het soort buurgewas. Zo was de relatieve luchtvochtigheid in aardappelstroken naast gras lager dan in monocultuur. Een lage luchtvochtigheid is minder gunstig voor de verspreiding van *P. infestans*. Stroken met veldboon hadden daarentegen weinig effect op het microklimaat. Stroken met maïs bleken het beste sporen te weren: het aantal inkomende deeltjes (een maat voor inkomende sporen) was daar het laagst. Later in het seizoen zorgde maïs, door zijn hoogte, juist weer voor een hogere luchtvochtigheid in aangrenzende aardappelstroken, wat de ziekteontwikkeling kon bevorderen. Kortom, er is sprake van een trade-off tussen het barrièreeffect en het microklimaat, waarbij zowel de timing van het begin van de epidemie als de gewasgroei belangrijke factoren zijn.

In hoofdstuk 5 combineerde ik de veldgegevens met een model om de afzonderlijke invloed van verschillende mechanismen te kwantificeren en hun onderlinge interacties te begrijpen. Door ziekteontwikkeling te modelleren onder invloed van veranderingen in microklimaat door een ander buurgewas, kon ik bevestigen dat zelfs kleine verschillen in luchtvochtigheid de groei van de ziekte beïnvloeden. Ook het afzonderlijke effect van een fysieke barrière, zoals bij maïs, bleek in simulaties effectief in het verminderen van ziekte. Het model voorspelde ziekteonderdrukking het best wanneer drie mechanismen gecombineerd werden: gastheerverdunning, microklimaatverandering en het barrièreeffect, wat suggereert dat al deze mechanismen van belang zijn. Afhankelijk van het buurgewas werkten sommige mechanismen sterker dan anderen, en soms werkte ze elkaar tegen (zoals bij microklimaat en barrièreeffect), maar gezamenlijk hadden ze een positief effect op ziekteonderdrukking.

In het afsluitende hoofdstuk, hoofdstuk 6, vat ik de belangrijkste bevindingen samen en plaats ik ze in een breder perspectief. Ik reflecteer op de waarde van meta-analyses voor het identificeren van ziekte-onderdrukkende mechanismen in mengteelt. Ook bespreek ik de uitdagingen bij het ontwerpen van effectieve strokenteeltsystemen en de praktische uitvoering ervan in de gangbare landbouw. Daarnaast ga ik in op hoe strokenteelt kan bijdragen aan het verminderen van het gebruik van chemische bestrijdingsmiddelen. Tot slot pleit ik voor een bredere kijk op de verduurzaming van de landbouw: niet alleen optimalisatie en technologische oplossingen, maar ook fundamentele veranderingen in machtsverhoudingen zijn nodig om de negatieve gevolgen van de moderne landbouw écht aan te pakken.

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Finally, as the last words I will write for my thesis, meaning that it is almost time to celebrate, I want to thank my paranymphs, David and Ellen, for helping me over the last hurdle and being at my side during the defence!

About the author

This PhD thesis is written by Zohralyn Homulle, as can be seen on the cover of this book. Zohralyn was once born like everyone. She was born in Den Haag, a popular city to get born in as it is the 3rd largest municipality in the Netherlands, on 20 August 1997. Zohralyn was a very sweet baby and could only lie down in the first few months. When she was a toddler she liked to colour — in the colouring book, not on the walls! Zohralyn had a normal childhood. When she finished primary school she went to high school. During that time she was also a lifeguard on the shores of Scheveningen. Afterwards, she did a bachelor's in Plant Sciences at Wageningen University and did an exchange programme in Wales. There, she bought the famous ugly face mug that she still uses to this day. When she finished her bachelor's, she was still not done with studying, but wanted a change of scenery. So she joined the Master's in Agroecology, which is an international programme to obtain a double degree in Agroecology. This programme took her to Norway, Austria, France and Scotland. She made a lot of friends there but did not obtain new mugs. When Covid struck however, she had to go back to the Netherlands. At that time she was working on her thesis in Scotland, which had to be put on pause because it was a greenhouse experiment. In the meantime she wrote a literature review that got published — Zohralyns first scientific paper! When travel opened up again she went back to Scotland to finish her thesis and graduated. She was apparently still not done studying as in 2021, she started a PhD at the Centre for Crop Systems Analysis at Wageningen University. You can read all about it in this book! As the potatoes grew in her field, Zohralyn saw herself grow as well. She still remembers the harvest of the potatoes fondly and how everyone would come to help her. Now she harvests her work and will get another diploma as a reward.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 30 ECTS (= 20 weeks of activities)

Review/project proposal (4.5 ECTS)

- Intercropping as a tool to reduce Phytophthora infestans in potato

In-depth / Topical / On-site Postgraduate Courses (3 ECTS)

- What's Bugging You?, PE&RC, 2023
- Transition to sustainable, ecology-based agriculture, CropMix, 2025

Methodological / Statistical Postgraduate Courses (1.5 ECTS)

- Structural Equation Modelling, PE&RC, 2023

Deficiency, refresh, brush-up courses (3 ECTS)

- Ecological Modelling and Data Analysis in R, WUR, 2021
- Plant Pathology and Disease Epidemiology, WUR, 2022

Invited review of journal manuscripts (3 ECTS)

- Plant and Soil, Quantitative assessment of the damage by faba bean chocolate spot and faba bean yield loss during intercropping when using nitrogen fertilizers, 2021
- Plant and Soil, Improving management methods to progress sustainability of organic cabbage and beetroot production: effects of intercropping and fertilization strategies on the plant - soil system, 2022
- Plant and Soil, Intercropping with wheat and faba bean alleviated phytotoxic effects of cinnamic acid on the root cell wall structural resistance of faba bean reduced Fusarium wilt occurrence, 2022
- Plant and Soil, Nitrogen fixation by beans in crop mixtures is influenced by functional traits of associated species, 2022
- Plant Pathology, Wheat–faba bean intercropping can control Fusarium wilt in faba bean under *F. oxysporum f. sp. fabae* and ferulic acid stress as revealed by histopathological analysis, 2022
- Plant and Soil, Effects of spring wheat / faba bean mixtures on early crop development, 2022
- Field Crops Research, Modelling the impact of *Phytophthora infestans* on potato production under climate change. Relevance of the time of infection and rate of disease growth on yield losses, 2022
- Plant and Soil, Faba bean-wheat intercropping controls the occurrence of faba bean Fusarium wilt by improving the microecological environment of rhizosphere soil, 2023

Competence, skills and career-oriented activities (3.74 ECTS)

- PhD Competence Assessment, WGS, 2021
- Effective and efficient communication in academia and beyond, WGS, 2021
- Presenting with impact, Wageningen in'to Languages, 2021
- Mobilising your - scientific – network, WGS, 2022
- Supervising BSc & MSc students, WGS, 2022
- Writing propositions for your PhD, WGS, 2025
- Last Stretch of the PhD Programme, WGS, 2025

Scientific Integrity/Ethics in science activities (0.3 ECTS)

- Ethics in Plant and Environmental Sciences, WGS, 2021

PE&RC Retreat, PE&RC Day, and other PE&RC events (2.4 ECTS)

- PE&RC First year's weekend, 2021
- PE&RC Midterm weekend, 2023
- PE&RC Last Year retreat, 2025
- PE&RC Writing week, 2023

National/local scientific meetings, seminars, and discussion groups (5 ECTS)

- Toekomstvisie Gewasbescherming 2030, een andere weg inslaan?, KNPV Voorjaarsbijeenkomst, 2021
- WEES seminars, 2021
- Synergia Arable Use-Case meetings, 2022-2025
- Sustainable Intensification of Agricultural Systems, discussion group, 2022-2023
- Symposium - Crop diversification: new perspectives beyond agronomy, 2022
- Symposium Red de Lente - 60 jaar na Silent Spring, KNPV, 2022

International symposia, workshops and conferences (9.8 ECTS)
- Euroblight, Ascona, Switzerland, 2022
- The Canadian Tri-Society meeting of the Canadian Phytopathological Society, the Canadian Society of Agronomy and Canadian Society for Horticultural Science, Ottawa, Canada, 2023
- European Association for Potato Research, Pathology and Pests Section Meeting, Arras, France, 2023
- Netherlands Annual Ecology Meetings, Lunteren, Netherlands, 2024
- Euroblight, Lunteren, Netherlands, 2024

Lecturing/Supervision of practicals/tutorials
- Soil-Plant Relations, 2022-2024
- Integrated Pest Management, 2021, 2022, 2024
- Advanced Agronomy, 2022-2024
- Agroecology, 2022
- Biosystems Engineering, 2022
- Research Methods in Crop Science, 2022
- Seagriculture: Seaweed Biology and Cultivation, 2023
- Research Methods in Crop Science, 2024

BSc/MSc thesis supervision
- Research topic 1: Morphological changes in potato as induced by strip cropping with grass and maize and its role in disease suppression of late potato blight
- Research topic 2: Potato late blight infection in strip-intercropping and its relation to potato morphological changes compared to potato monoculture
- Research topic 3: Effect of strip intercropping of potatoes on pest populations, late blight disease severity and tuber yield
- Research topic 4: The potential role of companion crops as barrier in the spread of late blight in potato-intercropping systems
- Research topic 5: Quantifying the relative importance of disease-suppressive mechanisms in species mixtures: a case study of late blight in strip-intercropped potato
- Research topic 6: Modelling yield and gross revenue of potato-based strip intercropping systems. Impact of competition for light and late blight suppression on field level performance.

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