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# Etude de la dynamique paysagère de *Pseudocercospora fijiensis* en Martinique : détermination des leviers territoriaux pour une gestion durable

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**Le 17 février 2023**

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*A Garance et Margaux, les meilleures nièces du monde*

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# Avant-Propos

Les techniques de lutte agroécologiques sont essentielles pour développer une agriculture durable. Cette thèse s'inscrit dans la dynamique de développement d'une production de banane plus respectueuse de l'environnement, en limitant les traitements chimiques contre les ravageurs, l'enherbement et les maladies. Les deux tiers de la thèse et les expérimentations se sont déroulés en Martinique. La période d'écriture s'est déroulée au CIRAD de Montpellier.

Pour répondre aux différentes questions de recherche, un travail de modélisation de données de maladie et des essais expérimentaux ont été réalisés. Les données de maladie s'étendent du 1er janvier 2015 au 31 décembre 2019 et ont été collectées par la SICA-CERCOBAN, organisme de conseil pour les traitements de cercosporiose en Martinique. Les essais ont été menés du 18 juin 2020 au 29 mars 2022 sur de multiples sites en Martinique, et les incubations en serre ont été réalisées sur le site du CAEC (Campus Agro-Environnemental Caraïbe).

La thèse a été financée par le CIRAD et le projet Banamosaïc qui avait pour objectifs :

- De développer la gestion territoriale collective des bioagresseurs des bananiers en Martinique,
    - i) en développant des moyens agroécologiques de lutte
    - ii) en proposant une coordination territoriale de la gestion de cette maladie
- D'identifier des éléments paysagers qui structurent le territoire,
- De faire émerger une gestion multi-échelle selon les conditions pédoclimatiques et le contexte paysager.

Le projet s'est intéressé à deux ravageurs, la cercosporiose noire et le charançon noir du bananier, faisant chacun l'objet d'une thèse pour étudier quels leviers territoriaux pourraient être efficaces dans la lutte agroécologique contre ces ravageurs. Dans le cadre de ce projet, nous avons mené des entretiens et organisé des ateliers pour co-concevoir avec les agriculteurs et les techniciens, des méthodes de lutte collectives et territoriales, en sollicitant les différents leviers de gestion.

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# Liste des Publications

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# CHAPITRE 1. Introduction générale



## A. Les maladies fongiques et les enjeux de la réduction des fongicides

L'agriculture est l'activité primordiale à l'existence humaine. Le changement climatique, l'augmentation de la population mondiale et l'émergence de nouveaux ravageurs rajoutent de nouveaux défis aux productions agricoles dès aujourd'hui et pour le siècle à venir. La recherche et les chercheurs ont un rôle à jouer essentiel dans ces problématiques, en optimisant les rendements de production, en 'redesign-ant' les systèmes de cultures et en développant des techniques agroécologiques de lutte pour une agriculture durable.

Pour de nombreuses productions agricoles, les maladies fongiques représentent une des plus grandes contraintes, entrainant des pertes en moyenne de 15% au niveau mondial (Oerke and Dehne 2004). *Magnaporthe oryzae*, *Fusarium oxysporum, Fusarium graminearum, Mycosphaerella graminicola, Puccinia* spp., *Botrytis cinerea*, font partie des pathogènes fongiques les plus ravageurs à l'échelle mondiale (Dean et al. 2012). Ils infectent de nombreuses cultures essentielles à l'alimentation humaine, le riz, le blé et plus largement les céréales mais aussi de nombreux fruits et légumes. Ils provoquent des grandes pertes de rendement allant de 10 % à la destruction totale de certaines cultures (Dean et al. 2012). Aujourd'hui, l'utilisation de fongicides est la méthode la plus commune pour les contrôler. Chez les productions fruitières, les maladies fongiques sont responsables de la majeure partie des traitements chimiques, par exemple en culture de pommes et de bananes en France, cela représente respectivement 65% et 76% des quantités de pesticides appliquées (AGRESTE 2021).

En 2020, 26 000 tonnes de fongicides ont été vendus en France. Les fongicides sont autant vendus que les herbicides, loin devant les insecticides (AGRESTE 2021). Il a été observé que l'exposition aux substances chimiques contenues dans les pesticides entrainait le développement de pathologies (maladie de Parkinson, cancers, perturbations endocriniennes…) (INSERM 2013). La réduction de leur utilisation est donc un sujet primordial pour réduire les risques sur la santé humaine et l'environnement. L'union européenne a donné comme objectif de réduire de moitié l'utilisation des « pesticides chimiques » dans l'agriculture d'ici 2030. Des méthodes de lutte agroécologiques doivent donc être développées pour réduire l'utilisation des fongicides et pratiquer une agriculture durable.

## B. Les méthodes agroécologiques de lutte contre les maladies fongiques

Le développement d'une maladie fongique se découpe en plusieurs étapes, avec des spécificités propres à chacune (Figure 1.1) (Rapilly 1991). Tout épidémie commence par un inoculum primaire qui vient infecter une zone saine et créer une pollution. Ensuite un cycle épidémique s'installe, une plante hôte est contaminée par le pathogène, une période d'incubation se déroule jusqu'au premier symptôme, en même temps qu'une période de latence qui se termine au moment de la sporulation. Commence alors la période contagieuse durant laquelle un inoculum secondaire est libéré puis disséminé qui va polluer puis contaminer un nouvel hôte. Enfin le premier plant contaminé meurt ou guérit de la maladie provoquée par le pathogène (Rapilly 1991).

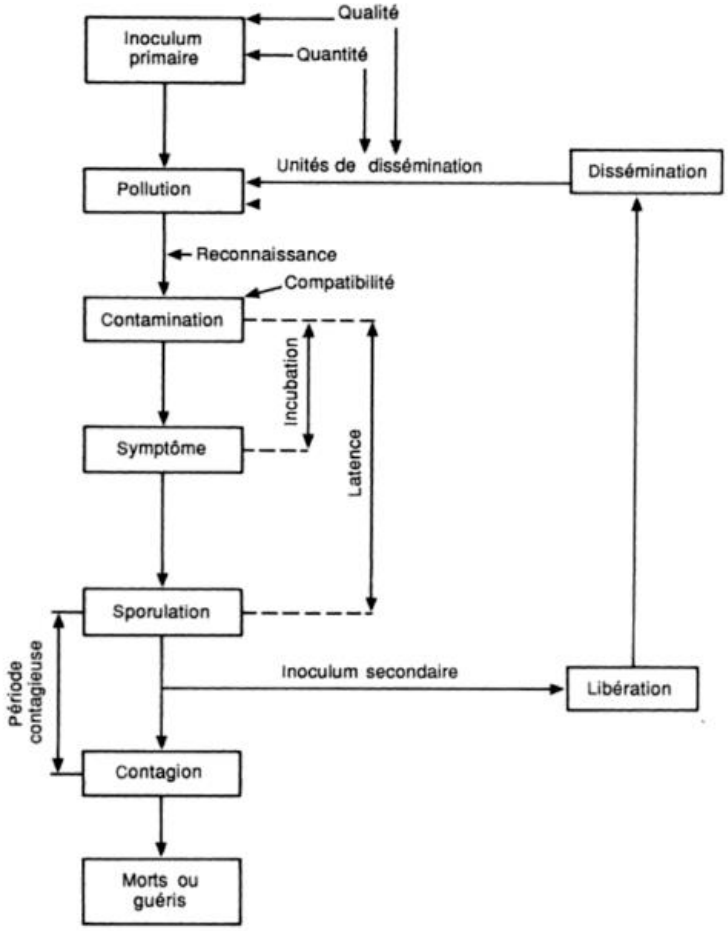



***Figure 1.1 :*** *Le cycle des variables d'états de la maladie : cycle de base de l'épidémie (Rapilly 1991)*

Les cycles épidémiques des maladies fongiques sont initiés par les processus de la propagation des spores qui peuvent être limités par différentes méthodes

agroécologiques (Figure 1.2). Les phases de contamination, incubation, latence et sporulation (Figure 1.1) sont les principales sur lesquelles des leviers agroécologiques peuvent être utilisés.

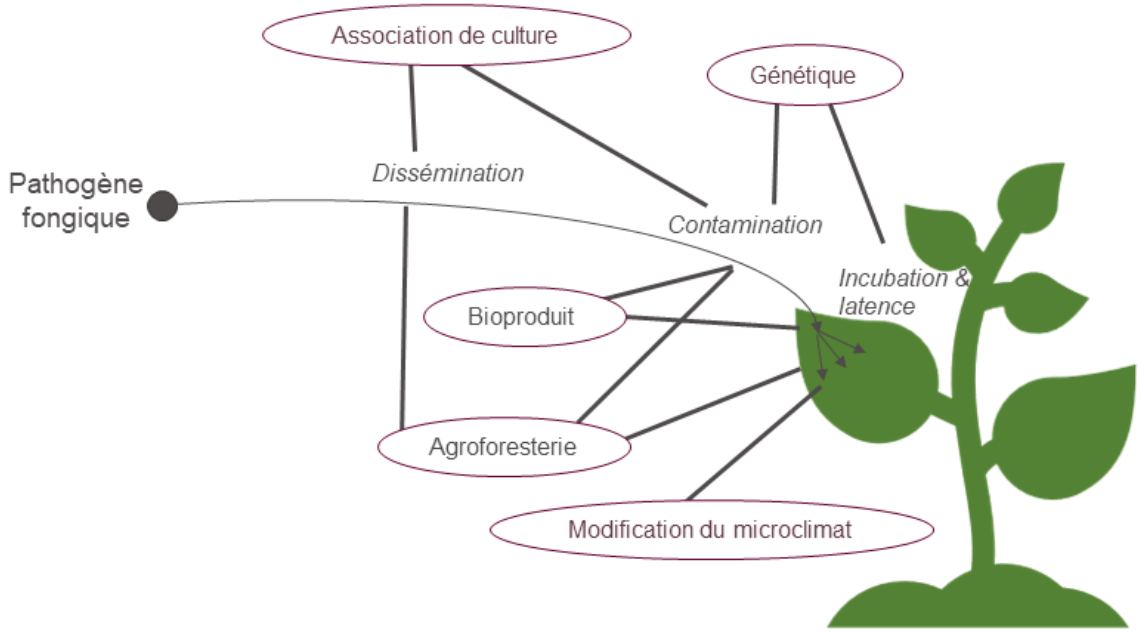



***Figure 1.2 :*** *Schéma d'intervention des leviers agroécologiques à différents moments du cycle épidémiologique d'un pathogène fongique*

Les associations de culture entre plantes hôtes et non-hôtes ou variétés sensibles et résistantes peuvent diminuer la progression épidémique des maladies en agissant sur différents facteurs : les niveaux d'auto et allo-inoculum, grâce à la dilution d'inoculum au sein de la parcelle (Boudreau 2013; Mundt 2002), la dissémination, en créant un effet barrière des spores vers les plants sensibles et diminuant ainsi les contaminations, mais aussi les périodes d'incubation et de latence et la diminution de la spécificité du pathogène, en ajoutant une diversité d'hôtes avec différents niveaux de susceptibilité, il y a plus de diversité génétique au sein de la population du pathogène avec différents niveaux de sévérité (Mundt 2002). L'architecture (densité, espacement, largeur d'inter-rangs…) de l'association de cultures et l'agencement des plants dans la parcelle peut être un levier pour réduire la progression de l'épidémie en fonction des modes et capacités de dispersion de la maladie (Bouws and Finckh 2008; Fernández-Aparicio et al. 2010; Mundt 2002; Sapoukhina et al. 2010; Villegas-Fernández et al. 2021). Dans certains cas, le pathogène peut également être inhibé par la présence d'une autre plante avec un pouvoir allélopathique. L'établissement d'inter-rangs avec ce type de plante, en plus

d'avoir une capacité d'interception des spores et donc de limiter la dissémination, permet aussi de limiter la contamination des plantes hôtes (Gómez-Rodriguez et al. 2003). La progression de l'épidémie dans la parcelle peut être limitée par le remplacement d'une variété sensible en une variété résistante (levier génétique) (Deguine 2017).

Au même titre que l'association de cultures, l'agroforesterie peut réduire la progression épidémique et l'abondance de spores dans une parcelle (Poeydebat et al. 2018; Schroth et al. 2000). Les arbres, en modifiant les flux d'air, diminuent la quantité d'auto-inoculum produit et disséminé. La modification du microclimat engendrée par la présence d'arbres peut agir à la fois sur la phase de contamination, d'incubation et de latence. La présence d'ombre réduit l'amplitude des variables météorologiques, cela peut à la fois rallonger (Schroth et al. 2000) ou raccourcir la période d'incubation et de latence (Motisi et al. 2021), ce qui va jouer un rôle déterminant sur la progression et la sévérité de la maladie au cours du cycle de production de la plante et donc sur les rendements et sur la qualité de la production agricole.

En substitution des traitements chimiques, l'application de bioproduits de manière préventive permet de diminuer la contamination (ex : application de cuivre contre le mildiou de la vigne) ou de manière curative durant les périodes d'incubation et de latence (ex : application de cuivre contre la tavelure du pommier ou du poirier).

## C. La dispersion des maladies fongiques

Cette thèse concerne une maladie fongique foliaire. La dispersion est une étape importante à prendre en compte dans l'épidémiologie d'une maladie de ce type, à dissémination aérienne (Lacey 1996). L'abondance de spores et la distance parcourue lors de la dispersion dépendent de chaque pathogène et plus particulièrement des spécificités de ses spores.

Dans de nombreuses études, les variables météorologiques ont montré une forte influence sur l'abondance de spores, aussi bien sur un intervalle de temps annuel et saisonnier (Crandall et al. 2020; Pakpour et al. 2015) que durant une journée (Lacey 1996). Elles sont souvent plus déterminantes que les éléments paysagers (Crandall and Gilbert 2017).

Les maladies fongiques peuvent être classées par mécanisme de dispersion, par l'air ou par l'eau (Lacey 1996; Rapilly 1991). Les mécanismes de libération des spores peuvent être passifs ou actifs, et peuvent nécessiter de l'eau (Lacey 1996). Dans les dispersions passives des maladies aériennes, le vent détache les spores de son hôte. La dispersion nécessite une vitesse suffisante dans ce cas, qui peut varier entre les types de spores et leurs caractéristiques (Lacey 1996; Mccartney and Fitt 2006). Dans les dispersions actives, les spores utilisent des mécanismes pour se projeter dans l'air puis sont dispersées par le vent (Mccartney and Fitt 2006). Les distances parcourues grâce au vent vont de quelques centimètres jusqu'à des centaines de kilomètres (Lacey 1996; Rapilly 1991). L'abondance de spores au sein d'une parcelle peut dépendre aussi de leur exposition au vent (Bouws and Finckh 2008; Zwankhuizen et al. 1998). Comme vu dans la partie B sur les leviers de gestion agroécologiques, l'hétérogénéité au sein d'une parcelle peut réguler les quantités d'inoculum. De la même manière, l'hétérogénéité et certains éléments paysagers peuvent être des leviers de gestion agroécologiques des pathogènes fongiques (Dupont et al. 2022).

## D. Le rôle du paysage dans la dispersion des maladies aériennes

L'effet du paysage pour la gestion des bioagresseurs a été principalement étudié dans le cas des ravageurs mais très peu des maladies fongiques. La présence d'habitats pour les ennemis naturels, d'habitats relais pour les ravageurs, la discontinuité du paysage et l'effet barrière d'éléments paysagers (plantes répulsives ou barrière physique) font partie des principaux leviers qui ont été décrits pour lutter contre un ravageur (Jeanneret et al. 2021). Malgré le manque de connaissances, le paysage semble aussi être un facteur important dans la régulation de maladies (Dupont et al. 2022; Etienne et al. 2022; Lacey 1996).

Il existe aujourd'hui peu d'études décrivant le rôle de la composition et de l'organisation du paysage sur les dynamiques des maladies fongiques (Delaune et al. 2021; Garedew et al. 2019; Plantegenest et al. 2007). En fonction de l'échelle d'analyse, les différents éléments n'auront pas le même impact sur le pathogène (positif, neutre ou négatif) (Delaune et al. 2021). A grande échelle, l'étude de la dispersion du pathogène permet de

comprendre les limites et les contraintes à sa dissémination et notamment la dissémination longue distance (Aylor 2003; García-Mozo et al. 2004). La dissémination longue distance permet au pathogène de coloniser des territoires sains et a une haute importance dans les cycles épidémiques (inoculum primaire). Par exemple, les zones réservoirs avec des plantes hôtes produisant de grande quantité d'inoculum, les zones semi-naturelles (forêts) influençant le microclimat, ou les haies pouvant avoir un effet relais, barrière ou sur l'aérologie, peuvent avantager ou contraindre le pathogène (Delaune et al. 2021). Les zones hôtes affectent, statistiquement, plus souvent positivement, la présence du pathogène et sa dynamique (sur une échelle de 0.2 à 1 km), contrairement aux zones semi-naturelles qui peuvent l'affecter aussi bien de manière positive ou négative en fonction du pathogène (principalement sur une échelle de 0.2 à 5 km) (Adrakey et al. 2022; Delaune et al. 2021; Plantegenest et al. 2007). Au-delà de sa composition, la discontinuité (hétérogénéité) du paysage est une variable qui influence la dissémination du pathogène et la contamination de plantes hôtes, en éloignant les zones hôtes et limitant la quantité de spores dispersées sur des plantes sensibles, ou en reliant les zones hôtes grâce à des axes de dispersion (routes ou corridor) facilitant la dissémination des spores (Laine and Hanski 2006; Pautasso 2013). L'architecture du paysage peut créer des corridors aériens permettant au pathogène de se disperser grâce aux vents (García-Mozo et al. 2004). La présence d'habitat relais comme la présence d'hôte secondaire permet au pathogène de survivre entre deux plantations et de se disperser entre des patchs de cultures hôtes (Adrakey et al. 2022). Ces connaissances permettent de mettre en place des techniques de gestion territoriale et collective.

Au sein des éléments paysagers, les haies font partie des leviers agroécologiques de lutte contre les bioagresseurs. Elles ont de nombreuses propriétés : habitat pour auxiliaires de cultures, apport de biodiversité, brise-vent, modification du microclimat (Forman and Baudry 1984). Elles ont un impact négatif sur les maladies fongiques en général, avec un effet optimal sur de courtes distances (0.8km) (Delaune et al. 2021). Un de leur mécanisme d'action contre la dispersion des maladies fongiques est l'effet barrière, en interceptant les spores ou en modifiant les flux d'air.

A l'échelle d'une exploitation ou d'une parcelle, moduler le paysage peut aussi être un levier de gestion des maladies, notamment en réduisant l'abondance d'inoculum. L'influence du paysage peut intervenir du macroscopique au microscopique, sur les

conditions abiotiques et biotiques, en modifiant la force et le sens du vent, et en modifiant le microbiome présent sur la parcelle. Le paysage peut agir sur divers mécanismes d'actions régulant le pathogène qui dépendent de l'échelle de travail (Figure 1.3).

Les méthodes de culture et le contexte paysager peuvent structurer les populations bactériennes et fongiques (Khatri et al. 2023; Schaeffer et al. 2021), pouvant ainsi réguler de manière biologique leur présence et ralentir le cycle épidémique du pathogène (Asad 2022).

La modification du microclimat a été souvent décrite comme un levier permettant de réduire ou accélérer les cycles épidémiques (Gómez-Rodriguez et al. 2003; Koech and Whitbread 2000). Au sein des systèmes agroforestiers, l'ombre apportée par les arbres implique des changements sur une multitude de variables climatiques qui sont des leviers potentiels de gestion de maladies fongiques (Gidoin et al. 2013) : la review de Schroth (2000), par exemple, fait état de la réduction des écarts de températures, de l'interception de la pluie ou de la réduction du vent dans les systèmes ombragés qui réduisent l'abondance d'inoculum au sein de la parcelle, limitent la dispersion des spores et la contamination des feuilles dans le cas des maladies foliaires. L'effet brise-vent des arbres ou des plantes associées aide à réduire la pression de la maladie par la limitation de dispersion par le vent au sein de la parcelle et par la réduction de contamination extérieure (Bouws and Finckh 2008; Schroth et al. 2000).

D'autres expérimentations des systèmes agroforestiers ont également démontré une réduction de la contamination via auto-inoculum et un ralentissement du développement des maladies fongiques (Cerda et al. 2020; Rao et al. 1997). La régulation des bioagresseurs est l'un des nombreux avantages de l'agroforesterie, ces systèmes contribuent aussi à l'amélioration de la fertilité du sol et à l'augmentation de la biodiversité dans les parcelles qui, indirectement, aident à lutter contre les pertes de rendements dues aux maladies (Cerda et al. 2020).

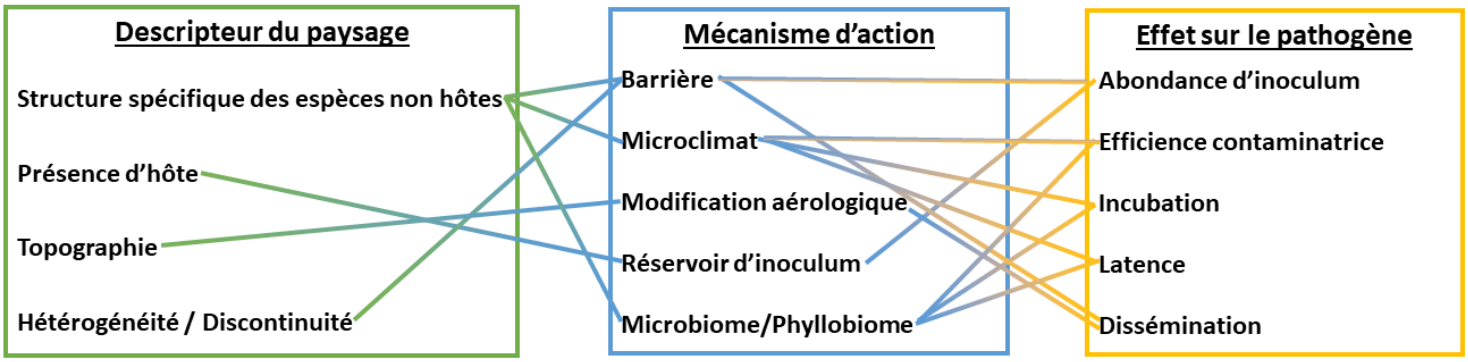



***Figure 1.3 :*** *Schéma de synthèse effet du paysage sur l'épidémiologie des maladies aériennes*

## E. Le modèle d'étude : la cercosporiose noire

Le bananier, *Musa* spp., est parmi les plus importantes cultures au monde. L'origine du genre *Musa* se trouve en Asie du Sud-Est et leurs diffusions à travers le monde remontent à des temps anciens (4000 an av. JC pour le plantain Afrique) (Lassoudière 2010). La banane fait partie de l'alimentation de base dans plusieurs parties du monde, notamment en Afrique de l'Ouest. Les bananes sont catégorisées en fonction de l'utilisation du fruit : banane dessert, banane à cuire, banane à bière. Les bananiers cultivés proviennent de milliers d'années de domestication et sont des diploïdes ou triploïdes issus de croisement entre *Musa acuminata* et *Musa balbisiana* (Lassoudière 2007). Il y a environ 130 millions de tonnes de bananes produites au niveau mondial, toutes variétés confondues (dessert et à cuire)(FAO 2022). La variété de banane dessert la plus cultivée et exportée est la Cavendish. Elle représente environ 50% de la production mondiale avec environ 60 millions de tonnes produites par an dont 20 millions de tonnes sont exportées (FAO 2022). Aussi surnommée banane export, elle est produite pour la majeure partie en Amérique latine (71%) (FRUITROP 2017). Elle souffre de nombreux bioagresseurs dont les plus importants à ce jour sont : les nématodes endoparasitaires des racines, les charançons noirs du bananier et la cercosporiose noire du bananier (Lassoudière 2007).

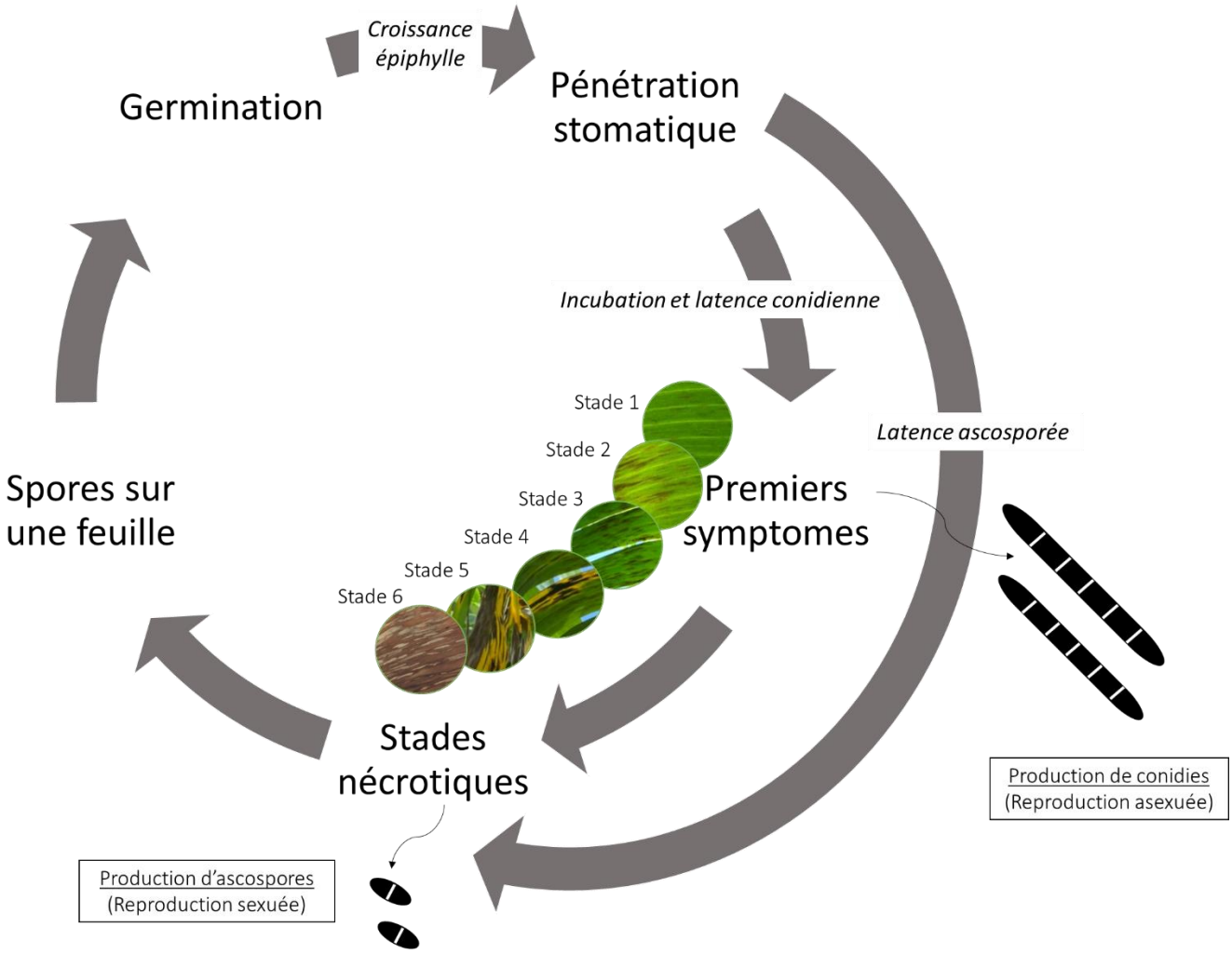



***Figure 1.4.*** *Schéma du cycle biologique et reproduction de la cercosporiose noire*

La cercosporiose noire est une maladie foliaire causée par *Pseudocercospora fijiensis*, un champignon hémibiotrophe de la famille des ascomycètes ; elle est aussi appelée la maladie des raies noires (MRN). La maladie se développe en six stades entre l'incubation et la sporulation ascosporée (Figure 1.4). Elle se caractérise par des raies noires sur la face inférieure des feuilles de bananier, les raies mesurent environ 1 millimètre au premier stade et s'agrandissent (stades 3-4), un halo jaune se forme autour de la lésion qui nécrose (stade 5) jusqu'à devenir de grandes plages nécrotiques (stade 6) (Meredith and Lawrence 1969). La maladie requiert un haut niveau d'humidité et une température d'environ 27°C pour avoir un développement optimal (Churchill 2011; Jacome et al. 1991). Le champignon *P. fijiensis* a deux types de reproduction (Figure 1.4) : sexuée, avec

la production d'ascospores par les périthèces, et asexuée, avec la production de conidies par les conidiophores (Meredith and Lawrence 1969).

Les conidies sont produites aux premiers stades de la maladie (stades 1-4) et se dispersent sur une dizaine de mètres autour du bananier, tandis que les ascospores sont produites aux stades nécrotiques (stades 5-6) et se dispersent sur des centaines de mètres (Rieux et al. 2014). Les conidies sont décrochées des conidiophores par le vent. Les périthèces doivent être imprégnés d'eau pour libérer les ascospores (Gaulh 1994). La libération des ascospores est généralement déclenchée par des évènements pluvieux (Brun 1964; Meredith et al. 1973). Concernant la germination des spores, l'humidité relative et la température semblent être des paramètres importants, spécialement chez les ascospores. L'humidité de la feuille est nécessaire pour sa contamination (Jacome and Schuh 1992). Les ascospores jouent un rôle important dans l'épidémiologie de la MRN et notamment dans la dispersion à longue distance (Rieux et al. 2014).

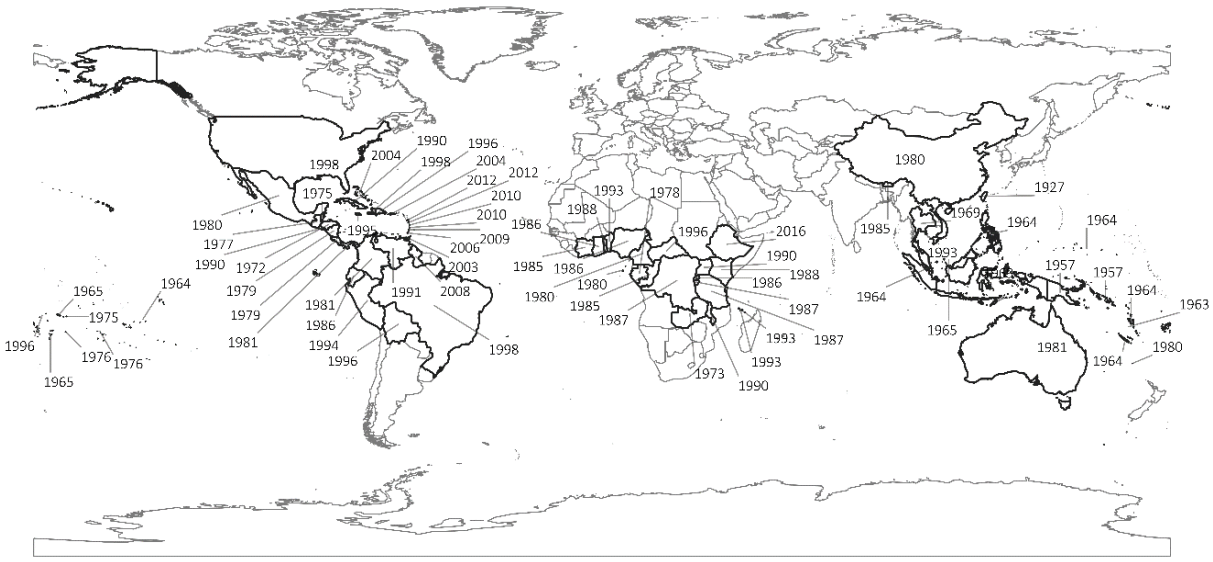



***Figure 1.5.*** *Dispersion de Pseudocercospora fijiensis depuis sa première observation (d'après Jones 2017)*

La cercosporiose noire du bananier a été décrite pour la première fois sur l'île Fidji en 1963 (Rhodes 1964) (Figure 1.5). Elle ressemble fortement à la cercosporiose jaune du bananier, causée par *Pseudocercospora musae,* mais ses symptômes sont plus sévères et elle cause des dégâts plus importants. La cercosporiose noire est aujourd'hui présente dans tous les pays exportateurs de banane (Figure 1.5). Dans la plupart des zones de production, elle a remplacé la cercosporiose jaune. C'est la maladie la plus problématique pour la production de bananes pour l'exportation. Les pertes de rendement peuvent s'élever jusqu'à 25% en présence de la maladie (De Lapeyre de Bellaire et al. 2010). La maladie mène à la nécrose des feuilles, qui réduit la capacité photosynthétique des bananiers (Figure 1.6) et les bananiers finissent leur cycle de production sans feuilles (Figure 1.7). En plus des pertes de rendement, les fruits perdent en qualité. Ils ont une durée de vie verte (DVV) plus courte ce qui handicape l'exportation (Churchill 2011; De Lapeyre de Bellaire et al. 2010). La durée de vie verte (phase préclimactérique) est très importante dans le processus d'exportation qui nécessite que le fruit reste vert jusqu'à arriver à la mûrisserie et jusqu'au consommateur. Comme sur la cercosporiose jaune, plus la sévérité de la maladie augmente (Gauhl et al. 1995; Stover 1971) au moment de la floraison, plus la DVV réduit (Chillet et al. 2009). Les pertes peuvent alors s'élever jusqu'à 100% (De Lapeyre de Bellaire et al. 2010).




***Figure 1.6.*** *Dégâts de cercosporiose noire sur CAVENDISH (Crédit photo : Scot Nelson)*

De nombreux cultivars (plantain et dessert) sont sensibles à la cercosporiose, avec différents niveaux de résistances (El Hadrami et al. 2003; Fouré and Moreau 1992; Meredith and Lawrence 1970). La banane Cavendish cultivée y est particulièrement sensible.



***Figure 1.7.*** *Dégâts de cercosporiose noire sur CAVENDISH : Bananier sans feuilles en fin de cycle (Photo Luc De Lapeyre De Bellaire)*

*Pseudocercospora fijiensis* a colonisé l'Amérique centrale puis l'Amérique du Sud, les grandes Antilles et enfin les petites Antilles. La cercosporiose noire a été observée en Martinique pour la première fois en 2010 (Figure 1.5) (Ioos et al. 2011) et a, par la suite, colonisé toute l'île. Elle est aujourd'hui la principale problématique pour la production de banane export en Martinique. Les autres bioagresseurs présents sont les nématodes et les charançons noirs du bananier. La mise en place de jachères et l'utilisation de vitroplants (plants issus de la micro-propagation *in vitro*) permettent d'assainir les parcelles de ces bioagresseurs. Pour la cercosporiose noire, sa gestion est plus compliquée à cause de sa capacité de dispersion sur de plus longues distances, ce qui ne permet pas d'assainir une parcelle par une simple jachère.

A l'heure actuelle, la méthode de lutte principale est l'application de fongicides. Les quantités et types de fongicides autorisés varient entre les pays. Leur utilisation a des conséquences sur les populations humaines et animales vivant proches des champs de bananes (Castillo et al. 2000; van Wendel de Joode et al. 2014). Par exemple, au Costa Rica, environ 70 kilogrammes de substances actives par hectare et par an sont appliqués (De Lapeyre de Bellaire et al. 2010), contre 3 kilogrammes par hectare et par an en Martinique (données SICA Cercoban). En Martinique, le traitement était réalisé par voie aérienne (par avion puis par hélicoptère) jusqu'en 2014, il est maintenant réalisé par des moyens terrestres (principalement des canons remorqués par des tracteurs, Figure 1.8). Dans la plupart des autres zones de production de bananes pour l'exportation, ces traitements sont encore réalisés par moyens aériens (principalement par avion Figure 1.9). Les traitements réduisent la progression de la maladie et empêchent de nouvelles contaminations durant quelques semaines. En Martinique, les décisions de traitements sont prises selon un système d'avertissement biologique grâce un indicateur de vitesse d'évolution de la maladie. L'indicateur s'appelle l'état d'évolution (EE) et prend en compte plusieurs paramètres pour définir l'avancement de la maladie d'une semaine sur l'autre. Il est utilisé pour prendre la décision de l'application de fongicides. L'EE est une évaluation quantitative des symptômes de la MRN sur les 4 plus jeunes feuilles de bananier. Les feuilles touchées, le stade de la maladie, la densité des lésions et l'émission foliaire sont relevés sur 10 bananiers sélectionnés aléatoirement sur la parcelle (Fouré and Ganry 2008). Les densités de lésions permettent de renseigner sur la vitesse d'évolution des lésions et sur une coalescence plus ou moins rapide des stades pour former des plages nécrotiques. Pour chaque numéro de feuille/stade de la maladie, un score est attribué en tenant compte de la vitesse d'évolution de la maladie et de la densité de l'infection (Fouré and Ganry 2008). Ces scores sont agrégés ensemble et multipliés par l'émission foliaire pour donner une vitesse d'évolution moyenne sur la parcelle. D'autres paramètres sont relevés, la plus jeune feuille touchée (PJFT) et la plus jeune feuille nécrosée (PJFN) pour avoir une approximation de la durée d'incubation, ou latence conidienne, et de la durée de latence ascosporée (Figure 1.4) (Fouré and Ganry 2008).



***Figure 1.8.*** *Traitement terrestre par canon de la cercosporiose noire (Photo IT2)*

Une autre mesure de contrôle largement utilisée est l'effeuillage, il consiste à couper les feuilles (effeuillage classique) ou les parties des feuilles nécrosées (effeuillage chirurgical) et sert à diminuer la quantité d'inoculum au sein de la parcelle et de l'exploitation (Guillermet et al. 2018). L'effeuillage avant récolte permet d'éviter la réduction de la DVV d'environ 40 jours pour un bananier très infesté (Chillet et al. 2013). L'effeuillage doit être réalisé de manière hebdomadaire pour être efficace, engendrant des coûts de main d'œuvre non-négligeables, estimés à 25 jours/ha/an dans les zones à forte pression (données non publiées).



***Figure 1.9.*** *Traitement aérien par avion de la cercosporiose noire (Photo Luc De Lapeyre de Bellaire)*

L'effet du paysage sur les dynamiques de la cercosporiose noire n'a fait l'objet d'aucune étude. L'influence de certaines variables climatiques sur les spores a été déterminée en laboratoire (Jacome and Schuh 1992; Jacome et al. 1991), montrant notamment

l'importance d'une humidité relative très élevée pour l'infection de la feuille et pour la sporulation (eau libre pour les ascospores). En plein champ, il a été démontré que les sporulations sont fortement liées à l'évaporation et l'humidité relative (Fouré and Moreau 1992). Plusieurs études ont été menées sur l'effet d'association avec des arbres dans des systèmes agroforestiers sur la cercosporiose (Norgrove and Hauser 2013; Poeydebat et al. 2018). Ces travaux ont démontré que la présence d'arbres, notamment ceux de la même strate que les bananiers (1.5-5 mètres) diminuent l'abondance des spores, augmentent la durée d'incubation (latence conidienne) et diminuent l'efficience contaminatrice qui entraine une diminution de la vitesse d'évolution de la sévérité (Poeydebat et al. 2018). Une des hypothèses de mécanisme d'action sur cette réduction est la dilution du nombre d'hôtes (moins de bananiers) et donc la diminution des potentielles sources de maladies. La modification du microclimat apportée par l'ombrage peut permettre de diminuer la durée d'incubation et de latence. La dispersion est limitée par un effet barrière des arbres vers les bananiers, et l'interception des gouttes de pluie par la canopée permet de limiter la libération des ascospores (Meredith et al. 1973). La réduction des écarts de températures permet de réduire la condensation de l'eau sur les feuilles et donc de réduire la pénétration stomatique (Jacome and Schuh 1992; Jacome et al. 1991; Schroth et al. 2000). La réduction du vent grâce à l'effet brise-vent des arbres peut permettre de réduire la quantité de conidies libérées. La distance parcourue lors de la dispersion va aussi être contrainte par la modification aérologique, la direction et la force du vent grâce aux arbres. En revanche, la protection des UV fournie par une strate foliaire avantage les spores dans leur temps de survie, temps qui serait restreint par une exposition directe aux UV (Parnell et al. 1998). La présence d'arbres au sein de l'agrosystème a démontré un potentiel de régulation de la maladie, l'utilisation de haies autour de la parcelle ou à l'intérieur de la parcelle pourrait être un autre levier intéressant pour réguler la maladie.

## F. Problématique scientifique

L'objectif global de ce travail de thèse est d'identifier de nouveaux leviers de gestion de la cercosporiose noire à l'échelle du territoire afin de proposer des stratégies de gestion plus durables de cette maladie. Pour cela nous étudierons **l'influence de la composition et de la dynamique paysagère sur *la dynamique épidémique de la maladie à cette échelle de travail*.** L'hypothèse faite dans ce travail est que la structure du paysage (composition, organisation spatiale) influence la dynamique épidémique de la MRN. Au vu des capacités de dispersion du champignon, contrastées selon les deux types de propagules, il est nécessaire d'étudier l'influence du paysage à différentes échelles, de quelques mètres (échelle plante ou intra-parcellaire) à plusieurs kilomètres (échelle supra-parcellaire) (Figure 1.10).

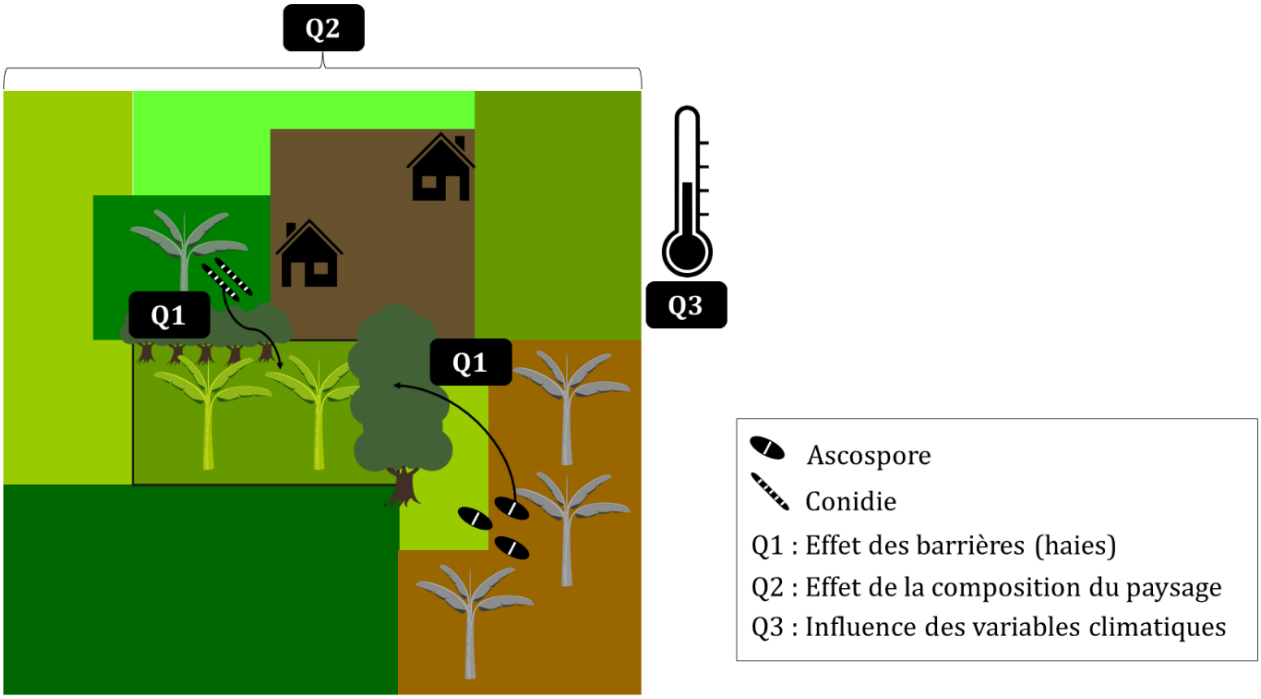



***Figure 1.10.*** *Schéma de la thèse et des questions de recherche au sein du paysage*

**A l'échelle intra-parcellaire**, il s'agit de comprendre **comment les haies influencent la dispersion des spores**. L'hypothèse faite est que les haies jouent un rôle de barrière à la dispersion des spores (***Question 1***, Figure 1.10). Il n'y a quasiment aucune étude sur le rôle des haies sur la dispersion des maladies aériennes, et aucune sur MRN (Schroth et al.

2000). Les seules connaissances existantes sont l'effet des arbres en agroforesterie. Afin de comprendre ce mécanisme de barrière à la dispersion, nous avons donc mis en œuvre une expérimentation avec des haies aux caractéristiques contrastées (hauteur, largeur et porosité optique). Nous avons mis en place des sources artificielles d'inoculum d'ascospores ou de conidies d'un côté de la haie afin de pouvoir déterminer l'impact de la haie sur la dispersion et sa capacité d'interception des spores. Nous avons placé des plantes pièges de chaque côté de la haie pour mesurer la quantité de spores dispersées selon la position par rapport à la haie.

**A une plus grande échelle**, il s'agit de comprendre **comment la structure du paysage influence la dynamique de la maladie** (***Question 2***, Figure 1.10). En particulier, il s'agit d'identifier les éléments du paysage favorisant ou limitant la dynamique épidémique de la MRN, ainsi que la distance d'influence de chaque élément. Une des difficultés dans l'analyse de l'effet du paysage sur une maladie est de séparer cet effet des autres effets influant la maladie (climat, pesticides, prophylaxie…). Afin de séparer ces différents effets, nous avons développé un modèle capable de prendre en compte l'ensemble des effets potentiels.

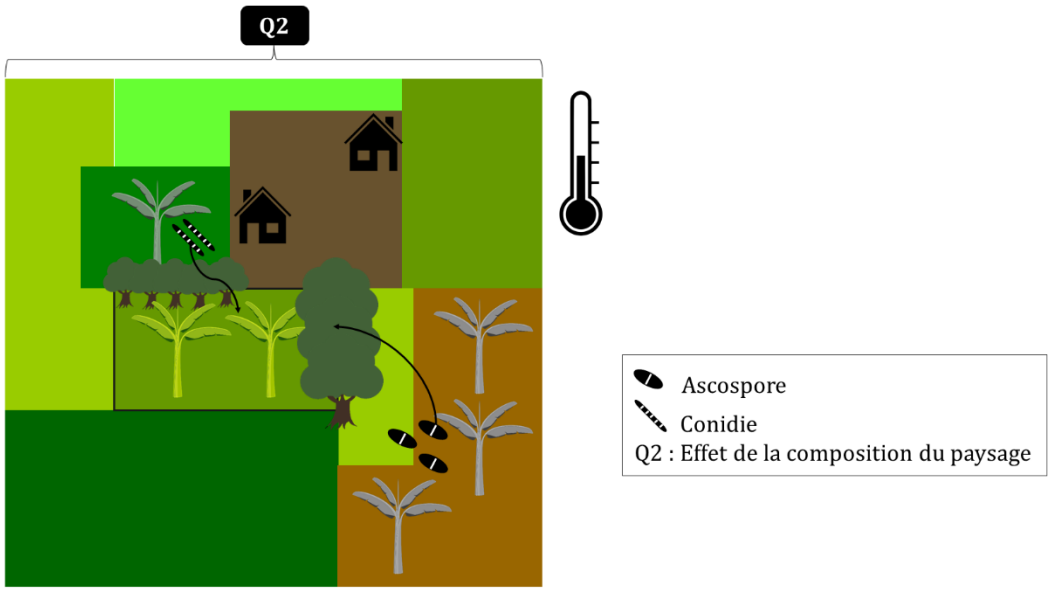
Enfin, à cette échelle supra-parcellaire, il est également important de bien comprendre quels facteurs abiotiques (climatiques) influencent la production d'allo-inoculum. En effet, contrairement aux maladies fongiques en climat tempéré, cet allo-inoculum est produit de manière continue et peut constituer un élément important des processus épidémiques de cette maladie polycyclique. Dans le cas de la MRN, il s'agit de comprendre **comment les facteurs climatiques influencent la production d'allo-inoculum** (***Question 3***, Figure 1.10). Afin de mieux caractériser ce facteur qui reste encore largement méconnu, nous avons mis en œuvre une approche expérimentale avec des plantes pièges dans des zones éloignées de sources potentielles d'inoculum. Ensuite, avec une approche statistique adaptée, nous avons i) testé si les différentes variables météorologiques influencent la quantité de spores capturées par les plantes pièges et ii) détecté la période à laquelle ces variables sont le plus influentes.

# CHAPITRE 2. Disentangling the factors affecting the dynamic of *Pseudocercospora fijiensis*: quantification of weather, fungicide and landscape effects



*Photo de Jérôme SAINTE-ROSE*

Dans ce chapitre, nous avons utilisé des données récoltées par la SICA-CERCOBAN (organisme de conseil pour les traitements contre cercosporiose noire en Martinique) lors de l'avertissement biologique. Le but de cette partie est de répondre à la **question 2 : comment la structure du paysage influence la dynamique de la maladie**. En paramétrant les différents facteurs impactant l'évolution de la maladie grâce aux données, nous avons modélisé l'état d'évolution de la maladie. Les résidus des prédictions obtenues (différence entre la valeur mesurée et la valeur simulée) ont été comparés statistiquement avec la composition du paysage autour de la parcelle pour déterminer les éléments paysagers influençant positivement ou négativement l'état d'évolution de la maladie. Ce travail a été publié dans le journal *Phytopathology*.



# Disentangling the factors affecting the dynamic of *Pseudocercospora fijiensis*: quantification of weather, fungicide and landscape effects

Lucile Delatouche, Luc de Lapeyre de Bellaire, Philippe Tixier

## A. Introduction

Landscape composition is an important feature for agroecological management. It refers to the proportion of each landscape element around cultivated fields. There is a wide literature on the effect of landscape composition on natural enemies and on pest regulation (Aviron et al. 2016; Chaplin-Kramer et al. 2011; Lykouressis et al. 2008; Tscharntke et al. 2007). Pests' development is modulated by landscape elements that provide favorable or unfavorable habitats, facilitate their dispersal, and modify microclimate. The landscape composition can differentially be conducive or suppressive to the dynamics of a pathogen (Veres et al. 2013). For example, Condeso and Meentemeyer (2007) demonstrated that a large host area from 50 meters around a disease spot increase severity of the disease (Condeso and Meentemeyer 2007). At the opposite, host density can also reduce disease severity (Finckh et al. 1999).

To date, few studies have been dedicated to a clear demonstration of landscape effects on plant diseases (Plantegenest et al. 2007). This is probably due to the complexity of disentangling landscape effects from other factors such as natural disease growth, cultural practices and weather. Tools to partition these different effects in a standardized way are required to better assess the effect of landscape composition on diseases and ultimately to better use this lever in integrated agroecological strategies.

Modelling the spatial dynamics of crop diseases is increasingly used to understand the factors involved in pathogen dispersal and landscape effects, such as landscape structure, the relative position of each landscape element (Papaïx et al. 2014), or the effect of the presence of resistant plants (Pacilly et al. 2018). However, existing models often remain theoretical approaches that are scarcely based on biological or agricultural data.

Moreover, most of these approaches neglect management practices (prophylaxis or pesticide treatment) unless they probably play an important role (Pacilly et al. 2018). On the other hand, purely statistical approaches including Bayesian computing (Martins et al. 2013) are appropriate for extracting climatic or environmental effects (Cendoya et al. 2020), but are limited in taking into account more complex cultural practices. Here, we propose an approach that combines dynamic modelling and statistical analysis in order to partition major effects involved in the dynamics of a fungal disease of bananas, including epidemiological traits of this disease, disease management practices, and the weather, in order to estimate landscape effects on an aerial tropical polycyclic disease.

Black Leaf Streak Disease (BLSD), also called Black Sigatoka, a foliar disease caused by the ascomycetous fungi *Pseudocercospora fijiensis,* is the main issue for banana production systems for exportation (De Lapeyre De Bellaire et al. 2009). This disease is an emerging disease whose intercontinental expansion can now be considered as almost complete (Guzmán et al. 2018). It was reported for the first time in Martinique in 2010(Ioos et al. 2011). This foliar disease provokes yield losses but also a reduction of fruit greenlife, which is essential for their exportation (Churchill 2011). The main control methods are chemical treatments which represent a significant economic production cost as well as environmental issues that are still largely unknown (De Lapeyre De Bellaire et al. 2009). Like most fungal diseases of plants, climatic factors (particularly temperature and humidity) influence the whole life cycle of the pathogen including infection, host colonization, sporulation but also dispersion and survival (Bebber 2019; Jacome et al. 1991). *Pseudocercospora fijiensis* can disperse by two types of propagules: ascospores resulting from sexual reproduction and conidia resulting from asexual reproduction (Meredith and Lawrence 1969). Conidia are produced at the youngest stages of the disease (1 to 4 on the 6 scale) (Fouré 1987) and can disperse over a distance of about ten meters, whereas ascospores are only produced in the oldest necrotic stage (stage 6) and can disperse over several hundred meters (Rieux et al. 2014). Landscape composition and structure are therefore likely to play a multiple role in this disease. Rieux et al. (2013) have shown using neutral clines markers that landscape composition did not affect genetic structure of pathogen populations at a local scale (50x80 km). However, this study does not preclude of landscape effects on disease epidemics since this genetic structure was mostly influenced by historical fungal expansion in this area through long distance dispersal events. At a plot scale, it has been shown that the presence of trees nearby

banana plants (within 10 m) can reduce the inoculum of *P. fijiensis* available for new infections(Poeydebat et al. 2018), but no study has been conducted at a larger scale to determinate how landscape structure or composition (as the presence of hedgerows) participate to disease control.

There are currently very few models dealing with BLSD. In their model, Landry et al. (Landry et al. 2017) simulated BLSD dynamics, taking into account the biology of the plant and its architecture as well as pathogen development (infection, lesion development, sporulation, spore dispersal). This model simulates the disease development at plant scale and does not allow an integration of potential landscape effects nor the effect of chemical control practices. Our model aims to work at a larger scale and take into account these effects.

In this paper, we have developed a model that simulate the BLSD dynamics accounting for its exponential growth, the effects of weather, fungicide applications, and landscape. It simulates the stage of evolution of the disease (SED) that is a disease monitoring descriptor (Fouré and Ganry 2008). This model, combines (i) an exponential growth rate of the SED that is altered by the effects of weather and fungicide applications, with (ii) a generalized linear model allowing to take into account the dynamics of the disease since its introduction in Martinique and the seasonality of BLSD in Martinique. After parameterization, we used the model to estimate landscape effect on SED. Finally, we investigated how landscape metrics influenced this landscape effect.

## B. **Materials and methods**

This study was conducted in Martinique (Latitude: 14° 36' 32 N, Longitude 61° 4' 24 W), a Caribbean island characterized by a tropical climate with highly contrasted climatic conditions according to altitude and windward exposition (between 1000 and 5000 mm annual rainfall depending on area). Landscape structure and composition are contrasted in Martinique according to topography, proximity to the coast, prevalence of cultivated bananas (about 5000 ha or 25% of the useful agricultural area of the island), human habitat or natural forest areas. Almost all banana production is exported and cultivated

with banana cultivars of the Cavendish subgroup (*Musa acuminata*, AAA group, Cavendish subgroup), which are highly susceptible to BLSD.

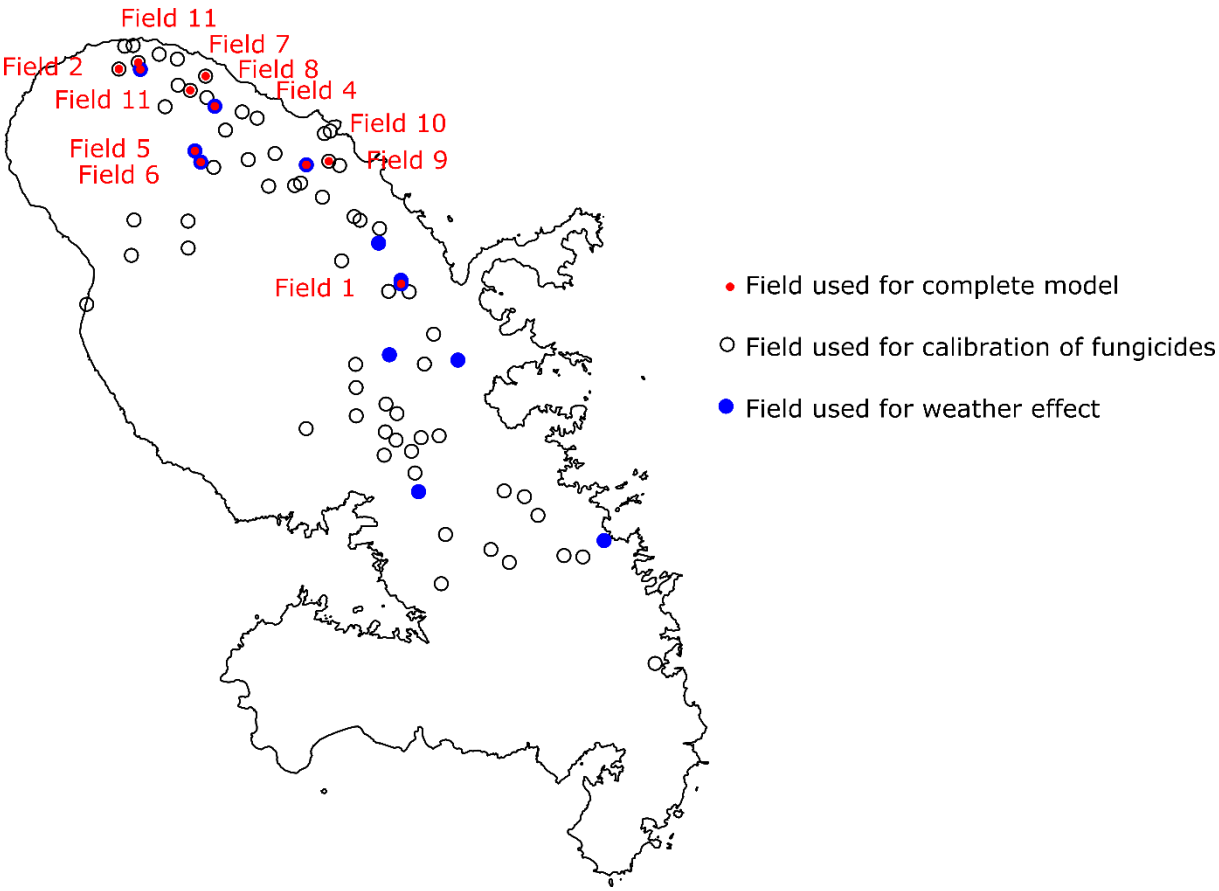



***Figure 2.1.*** *Fields location used for the study. Black spots are fields where only SED where measured and were used for Equation 2.2 & 2.4 calibration. Blue spots are fields where SED and Piche evaporation where measured. Red spots are fields used equation 2.1.a, 2.1.b and 2.1.c with the closest Piche evaporation data.*

### B.1 The stage of evolution of the disease as disease parameter

We have used a data set of regular weekly BLSD monitoring carried out in banana plantations over 83 banana plots representative of all island situations over a five-years period from 2015 to 2019 (Figure 2.1). The disease parameter measured weekly was the stage of evolution of the disease (SED), which is an indicator of the speed of development of the disease in a field that is used for taking the decision of the application of fungicides (Fouré and Ganry 2008). The SED is a quantitative evaluation of BLSD symptoms on the 4 youngest banana leaves where initial infections occur. For each leaf number/stage of the disease a coefficient is attributed taking into account the speed of evolution of the disease and the density of infection (Table 2.1).

***Table 2.1:*** *Coefficients used for calculating stage evolution of the disease (SED) for Black Leaf Streak Disease (BLSD) of bananas and plantains.*

| | | LEAVES | | |
|---|---|---|---|---|
| **STAGES** | | **II** | **III** | **IV** |
| **1** | **-** | 60 | 40 | 20 |
| | **+** | 100 | 80 | 60 |
| **2** | **-** | 100 | 80 | 60 |
| | **+** | 140 | 120 | 100 |
| **3** | **-** | 140 | 120 | 100 |
| | **+** | 180 | 160 | 140 |
| **4** | **-** | 180 | 160 | 140 |
| | **+** | 200 | 200 | 180 |
| **5** | **-** | 220 | 200 | 180 |
| | **+** | 260 | 240 | 220 |
| **6** | **-** | 260 | 240 | 220 |
| | **+** | 300 | 280 | 260 |

Technically, the observation is made weekly on the same 10 banana plants and the SED is the sum of all the coefficients multiplied by the mean foliar emission rate (Fouré and Ganry 2008). Indeed, the SED reflects the presence of new infections detected in the youngest banana leaves taking into account their stage and their abundance. Since a banana plant has a regular weekly foliar emission and that new infections occur mainly on these young leaves, SED is a good indicator of new epidemic waves of this polycyclic tropical disease (De Lapeyre de Bellaire et al. 2010). This indicator is impacted by all the

variables that alter disease progress and is continuous, 10 new banana plants being selected after flowering.

We used data collected from 2015 to 2019; after 2015, it is possible to consider that BLSD had already invaded all banana plantations of Martinique and showed a significant level in all regions. In total, our database contains 17628 rows (one week of measure in one given field). All fungicide treatments were collected weekly on the various plots from 2017 to 2019, for a total of 2020 treatments with 5 types of fungicides (SICO: Difenoconazole, 250 g $L^{-1}$, SYNGENTA France SAS; CONSIST: Trifloxystrobin, 500 g $kg^{-1}$, BAYER SAS; LUNA: fluopyram, 250 g $L^{-1}$, BAYER SAS; SERENADE: Bacillus subtilis str. QST 713, 15.67% m/m, BAYER SAS; TILT: Propiconazole, 250 g $L^{-1}$, SYNGENTA France SAS).

### B.2. Weather data

Piche evaporation is a meteorological data that integrates various weather factors such as humidity, rainfall, wind and temperature (Jacobs and Arriëns- Bekker 1983). Piche evaporation measured in a modified shelter is a very good indicator of hydric status at the leaf surface and is correlated with BLSD development and particularly SED (Ganry and Laville 1983; Ganry and Meyer 1972). Our dataset contains 12 Piche evaporation measurement sites on 12 plots (blue points on Figure 2.1) where SED was assessed weekly from 2015 to 2019 (1633 data in total for the 12 fields).

### B.3. Landscape metrics

We described the Landscape composition for several plots (red points in Figure 2.1, selected in a high pressure area of BLSD with evaporation data closed to the plot) within 200, 500, 800, and 1000 m radius buffer zones from the center of the plot (Figure 2.2) because such areas are potentially influenced by ascospore dispersal (Rieux et al. 2014). As the landscape composition (especially the crops and their surfaces) is changing over the years, we mapped and established the proportion of each landscape element for each year between 2017 and 2019. The composition of landscape was established thanks to several GIS (Geographic Information Systems) databases:

- The Graphic Land Registers edited by the French Ministry of Agriculture (DAAF, Direction de l'Agriculture, de l'Alimentation et de la Forêt) for the three years 2017, 2018 and 2019) (contains data for all crops)
- Vegetation formations drawn by the French ministry of environment (DEAL, Direction de l'Environnement, de l'Aménagement et du Logement) (contains data for forest elements)
- Land use drawn by the DEAL also (contains data of all artificial structures).

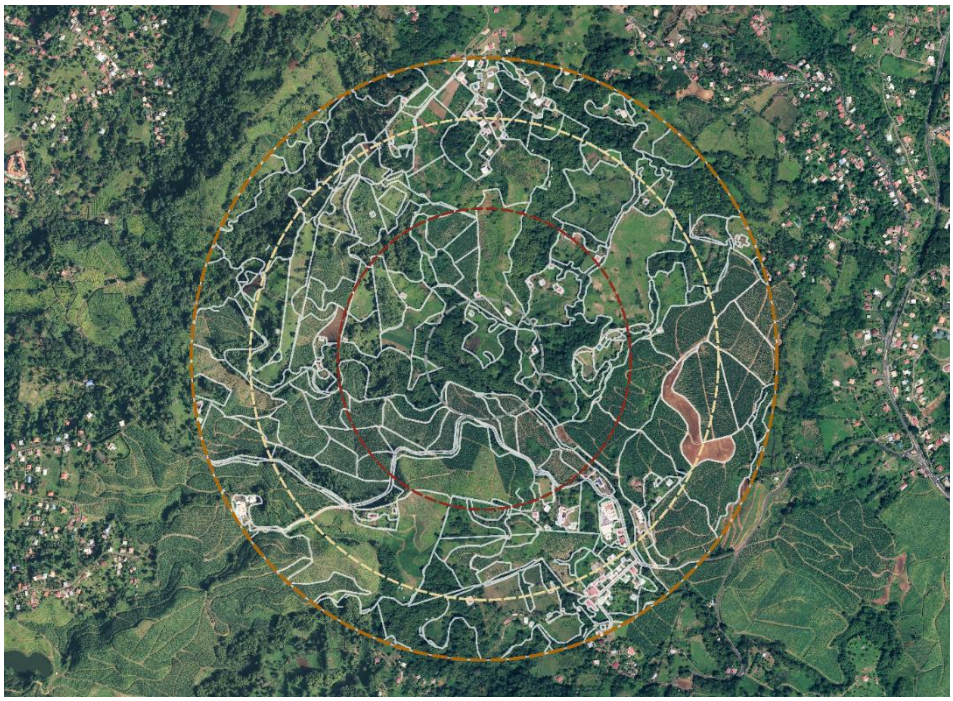


***Figure 2.2.*** *Illustration of the four buffer zones (200 m, 500 m, 800 m, 1000 m) around the plot where SED was measured.*

Following this mapping, the landscape composition of each buffer zone was classified into five categories of landscape elements that may have an effect on the epidemiology of BLSD:

- Percentage of cultivated host crops (**%Managed-banana-plants**) including fields of Cavendish export bananas and plantain: maintained and treated for most of the surface (98.55 % of this surface is regularly treated with fungicides).
- Percentage of forest (**%Forest**): it is an element of the landscape that can alter the microclimate, the dispersion of the pathogen with high strata vegetation, and that can also contain scarce untreated banana plants.

- Percentage of hedgerows (**%Hedgerow**): positioned around fields, of various width and height. Such features could potentially play a role of barrier limiting the dispersal of spores. We took into account the surface of hedgerows in order to take into account width and length and to compare with other landscape elements.
- Percentage of non-host elements (**%Non-banana-culture-and-artificial-structures**) including (grassland, cane, Road, building) with assumed neutral effect on the epidemiology of the disease except through fragmentation of host areas among the landscape.
- Potential sources of inoculum (**%Unmanaged-banana-plants**): it includes fallows after banana plantation and home gardens that can both include banana plants without fungicide treatments.

***Table 2.2.*** *Description of the state and input variables of the model.*

| **Variables** | **Unit** | **Description** |
|---|---|---|
| *State variables* | | |
| $SED_t$ | - | Stage of evolution of the disease at step t |
| $SEDst_t$ | - | Standardized stage of evolution of the disease at step t |
| $BG_t$ | - | Biological growth of the disease at step t |
| $K_t$ | - | Carrying capacity of the disease (maximal value of SED achievable) at step t |
| $Efungicide_t$ | - | Effect of fungicides on the SED at step t |
| $Eiia_t$ | - | Intra&Inter-annual effect on the SED at step t |
| $Elandscape_t$ | - | Effect of the landscape on the SED at step t |
| *Input variables* | | |
| $Evap_t$ | mm | Evaporation measured at step t |
| $tat_{p,t}$ | week | Time after application of fungicide p at step t |
| $tae_t$ | week | Time after the beginning of the measures at step t |
| $woy_t$ | week | Week of the year at step t |

## B.4. Model description

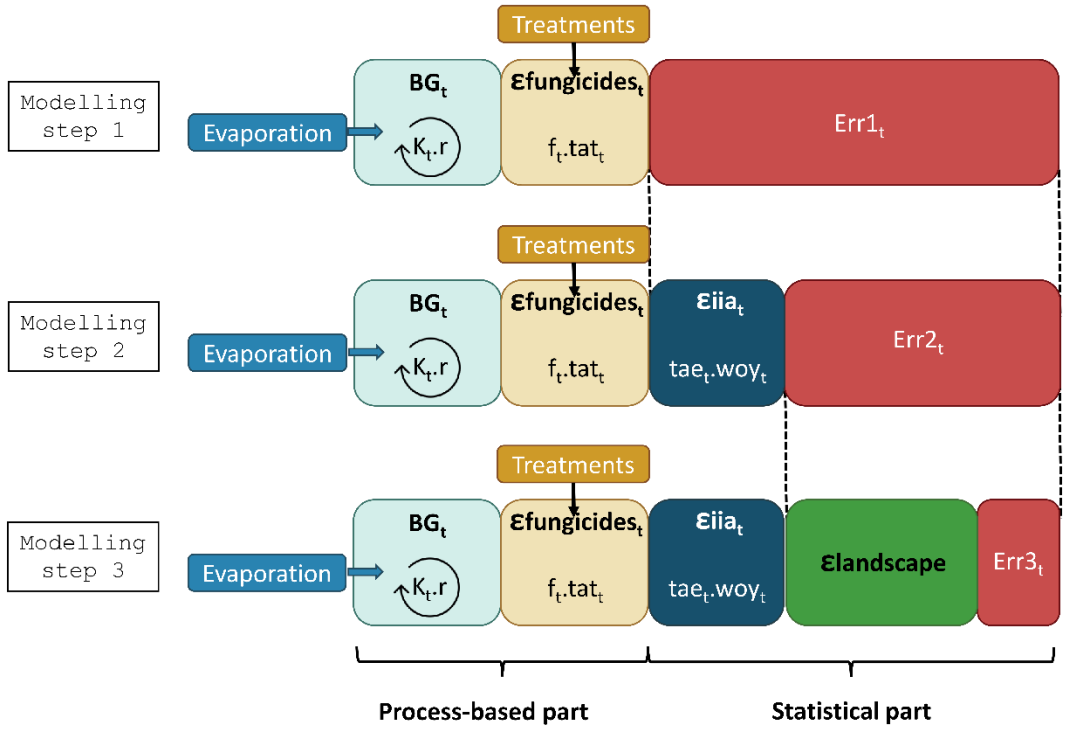



***Figure 2.3.*** *Model diagram illustrating the partitioning of $SED_t$ as performed in the three modelling steps, including process-based and statistical parts. All variables are described in Table 2.1.*

The whole model was coded with R 4.1.1 (R Core Team 2021). All variables and model parameters are presented in Tables 2.2 and 2.3. This model does not aim at predicting long-term disease levels but at partitioning biotic and abiotic factors influencing BLSD dynamics. This model was used at each weekly time step to simulate the SED from the measured value of SED at the previous time step by calculating each factor that could be quantified and isolate the part associated to landscape effect. The model was parameterized in three modelling steps (Figure 2.3). First, we assumed that the variation in SED depended on the biological growth of the disease (exponential growth rate and weather effect) and the effect of fungicide applications. In a second step, we evaluated the intra- and inter-annual effect based on the residuals of the model of step 1. Finally, we assessed the effect of the landscape based of the residuals of the model of step 2. The three following sections present these modelling steps.

***Table 2.3:*** *Description and calibrated values of the parameters of the model.*

| Parameters | Calibrated values | Unit | Description |
|---|---|---|---|
| r | 0.415 | - | Exponential growth rate of SED |
| Ka | 2309.1666 | - | Maximal value of Kt |
| Kb | -0.1250 | - | Slope of the exponential function that link $K_t$ and $Evap_t$ |
| Kc | 30.6787 | mm | Value of $Evap_t$ at inflexion in the exponential function that link $K_t$ and $Evap_t$ |
| $\alpha_f$ | 0.8601<br>1.4027<br>0.7480<br>0.8663<br>0.8103 | - | Asymptote values of the logistic function that link $Efungicide_t$ and $tat_{p,t}$ for CONSIST, LUNA, SERENADE, SICO, TILT, respectively |
| $\beta_f$ | 3.4585<br>1.2584<br>2.5512<br>3.4660<br>3.2769 | week | The values of $tat_{p,t}$ at inflexion in the logistic function that link $Efungicide_t$ and $tat_{p,t}$ for CONSIST, LUNA, SERENADE, SICO, TILT, respectively |
| $\gamma_f$ | -0.6109<br>-1.8806<br>-0.4702<br>-1.2331<br>-0.7032 | - | Slopes of the logistic function that link $Efungicide_t$ and $tat_{p,t}$ for CONSIST, LUNA, SERENADE, SICO, TILT, respectively |
| $int_{Eiia}$ | -54.1486 | - | Intercept of the linear model that predict $Eiia_t$ |
| $coef_{tae}$ | 0.09978 | - | Coefficient of the effect of $tae_t$ on the prediction of $Eiia_t$ |
| $coef_{woy}$ | 4.1265 | - | Coefficient of the effect of $woy_t$ on the prediction of $Eiia_t$ |

### B.4.1. Modelling step 1 – Biological growth and fungicide effect

In this first step, we used a dynamic model to simulate the evolution of SED thanks to a GLM (Generalized linear model) including the biological growth ($BG_t$) that was modelled according a logistic growth that is altered by weather and by fungicide applications (Figure 2.3-1, Equation 2.1.a).

$$\delta SED_t = BG_t \,.\, (1 - Efungicide_t) + Err1_t \qquad (2.1.a)$$

With $\delta SED_t$ the simulated variation of SED at time step t, $BG_t$ the biological growth of the SED at time step t, and $\mathcal{E}fungicide_t$ the effect of fungicide application at time step t, and $Err1_t$ the residues of the model at time step t.

The biological growth of the SED ($BG_t$) is represented by a logistic equation (Equation 2.2) (Donzelli and Churchill 2007). This formalism is suitable to simulate a growth that can be very fast (exponential growth).

$$BG_t = r\,.\,SED_{t-1}\,.\left(\frac{K_t - SED_{t-1}}{K_t}\right) \qquad (2.2)$$

With r and $K_t$ the exponential growth rate and the carrying capacity of the logistic growth of the SED at step t, respectively.

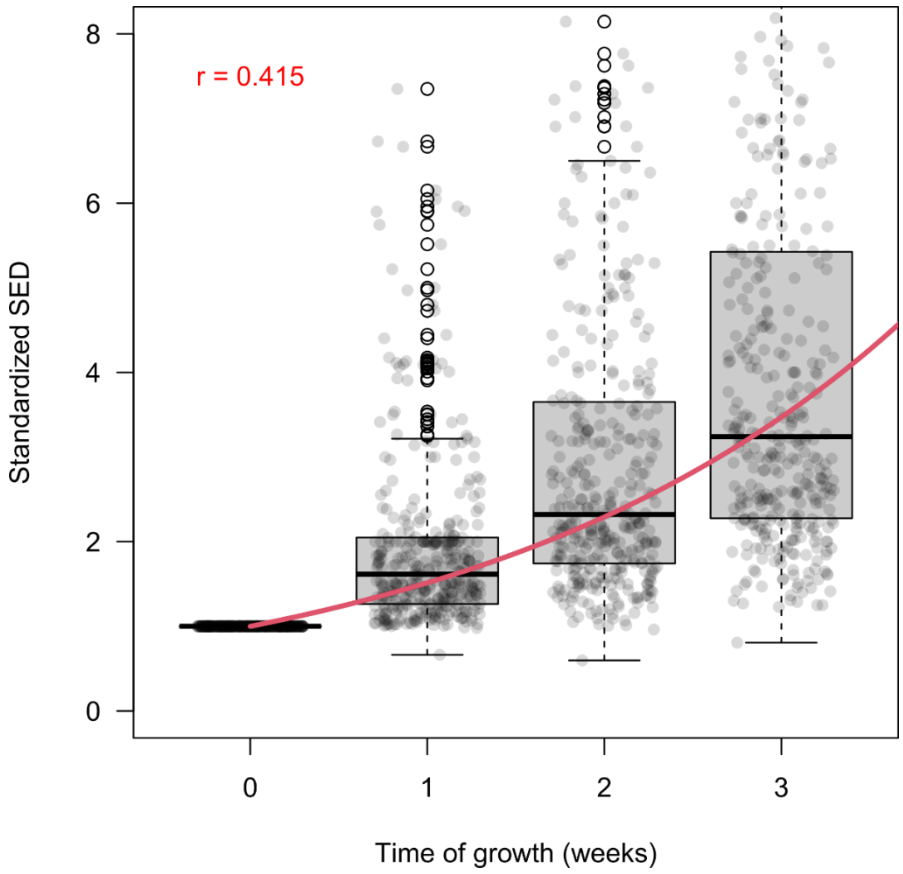



***Figure 2.4.*** *Exponential growth modelling of SED based on growth exponential sequences of SED data over 4 weeks periods without fungicide treatment from data from 2015 to 2019. The intrinsic growth rate r was calculated on standardized SED (1 as the value of SED on the first week from the sequences).*

The exponential growth rate of SED (r), was evaluated on sequences of exponential growth over a period of at least 4 weeks and without fungicide treatment. The estimation of the exponential growth rate of SED was achieved on 372 sequences of exponential growth, selected from 71 plots and corresponding to 1830 SED measurements (Figure 2.4 Table 2.4). We standardized these data to the first value of each sequence. Then, we determined the exponential growth r by fitting (with the nls function of R) an exponential model $y = e^{(r.x)}$ where y is the standardized SED and x is the number of weeks after the beginning of each selected sequence.

***Table 2.4.*** *Datasets used for the parameterization of each part of the model.*

| **Use (parameters, equation)** | **Date/Time** | **Number of data or sequences** |
|---|---|---|
| Growth rate (r, equation 2.1.a, 2.1.b, 2.1.c, 2.2) | 2015 - 2019 | 372 sequences or 1830 data selected manually on 83 plots |
| Weather effect (ka kb kc, equation 2.3) | 2015 - 2019 | 1633 data on 12 sites |
| Fungicides effect ($\alpha_p$, $\beta_p$, $\gamma_p$, equation 2.4) | 2017 - 2019 | 2550 data from 1350 sequences from 83 plots shared in<br>- 329 data in 135 sequences for CONSIST<br>- 332 data in 146 sequences for LUNA<br>- 703 data in 322 sequences for SERENADE<br>- 1019 data in 425 sequences for SICO<br>- 767 data in 322 sequences for TILT |
| Intra&Inter-annual effect (Ɛiia, equation 2.1.c, 2.1.b) | 2017 - 2019 | 995 rows on 11 plots |

The weather is an important factor that alter the potential of development of the disease. Air humidity allows the disease to develop (Guzmán et al. 2018), and saturation of air humidity and the presence of free water on the leaf surface allows the germination and sporulation of ascospora and conidia (Meredith and Lawrence 1969). We assumed that $K_t$, the maximum value attainable by the SED at time step t, follows a logistic curve with the evaporation measured on the field (Equation 2.3).

$$K_t = \frac{ka}{1+e^{-kb.(Evap_t-kc)}} \qquad (2.3)$$

With $Evap_t$ the evaporation measured in the plot at step t. ka, kb, kc are the parameters of the exponential function that links $K_t$ and the evaporation, corresponding to asymptote of the function i.e. the maximal value of $K_t$, the slope of the curve, and the value of $Evap_t$ at inflexion, respectively.

We calibrated the relationship between evaporation and maximum SED values using data from 12 plots (blue points on Figure 2.1) for which evaporation measurements were available (1633 measurements in total, Table 2.4). We defined evaporation classes by 5 mm (and > 10 mm because there was not enough data below 10 mm) and selected the SED values of the last quartile of each class. Next, we fitted Equation 2.3 to these values which we assumed to be the maximum achievable SED in each evaporation class.

Fungicides are clearly a major driver of the dynamic of plant diseases while it is rarely taken into account. Here, the effect of fungicides on SED was considered as a logistic function decreasing with the time after application (Equation 2.4). Based on the whole dataset (all points of Figure 2.1). We isolated 1350 treatment sequences (Table 2.4) composed of the value of the SED each week from the week of the treatment and the following 5 weeks (beyond 5 weeks, too few data were available for the parameterization). The decay of this three-parameter logistic function (α, β, γ) allows representing the maximum effect of fungicides and its decay after application.

$$\text{Efungicide}_t = \frac{\alpha_f}{1+e^{\left(\frac{\beta_f - tat_{f,t}}{\gamma_f}\right)}} \qquad (2.4)$$

With f the fungicide, $tat_{f,t}$ the time (in weeks) after treatment of the fungicide f at step t. $\alpha_f$, $\beta_f$ and $\gamma_f$ are the parameters of the logistic function that link the effect of fungicide f and the $tat_{f,t}$, corresponding to the asymptote of the function, the value of $tat_{f,t}$ at inflexion, and the slope of the function, respectively.

For that $Efungicide_t$ could be applied directly as the fraction of SED lost at time t because of pesticide application, we performed a standardization of the data to assess the effect of fungicides by subtracting the biological growth of the disease, following the formula: $SEDst_t = \frac{SED_t}{SED_{t-1}} - r - 1$ ; with $SEDst_t$ the standardized value of SED at time step t and r the exponential growth. In this equation, the subtraction of 1 allowed the calculated ratio to be directly applicable in the model.

After calibration of Equations 2.2, 2.3, and 2.4, the model described in Equation 2.1.a (with data from sites shown in red in Figure 2.1) led to a prediction of the $SED_t$ as illustrated by yellow points in Figure 2.5, and to residues $Err1_t$.

### B.4.2. Modelling step 2 – Intra&inter-annual effect

The second modelling step aimed at explaining the part of the residual variance from modelling step 1 ($Err1_t$) that can be attributed to the disease dynamics at the island scale taking into account the disease progress linked to progressive *P. fijiensis* expansion over the years and the seasonal variations (intra&inter-annual effect, Ɛiia). The equation of prediction of SED in the modelling step is presented in Equation 2.1.b.

$$\delta SED_t = BG_t \,.\, (1 - Ɛfungicide_t) + Ɛiia_t + Err2_t \qquad (2.1.b)$$

With $Ɛiia_t$, the intra&inter-annual effect at time step t and $Err2_t$ the residues of the model at time step t.

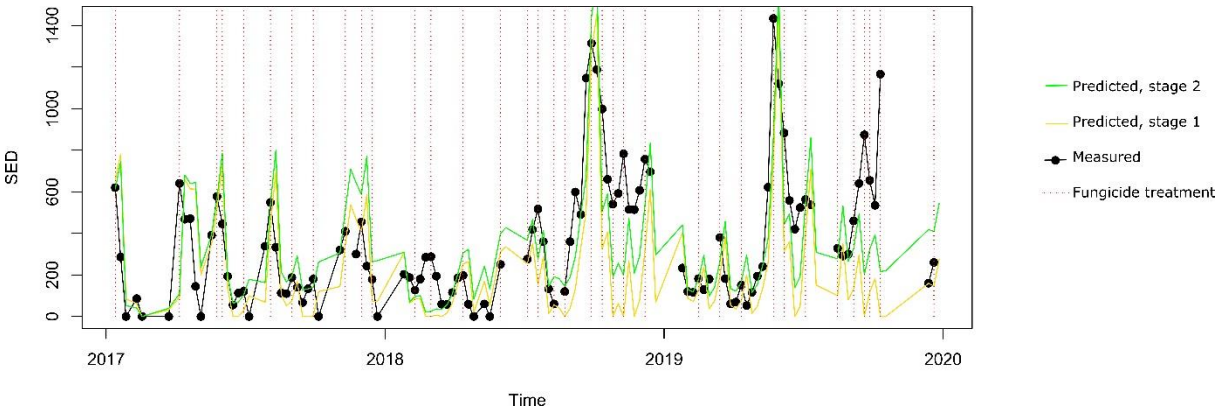



***Figure 2.5.*** *Illustration of the weekly dynamic of SED (Field 6) between 2017 and 2019, measures are in black, predicted SED in modelling step 1 with Equation 2.1.a in yellow (SED prediction with weather and fungicide effect), and predicted SED in modelling step 2 with Equation 2.1.b in green (SED prediction with weather, fungicide and intra&inter-annual effects). Vertical red dotted lines show the fungicide applications.*

The $Ɛiia_t$ was estimated with a linear model of the residuals from modelling step 1 ($Err1_t$) as response variable and with two predictors: (i) the time since the beginning of BLSD assessment in Martinique to take into account the progression of the disease since its introduction, and (ii) the week of the year to take into account the seasonality of inoculum levels that are clearly more important at the end the year (green line in Figure 2.5). The calculation of Ɛiia can thus be described as a function of $tae_t$ the time in weeks after the start of the measurements (01/01/2015) and $woy_t$ the week of the year (Equation 2.5).

$$Ɛiia_t = int_{Ɛiia} + coef_{tae} . tae_t + coef_{woy} . woy_t \quad (2.5)$$

With $int_{Ɛiia}$, the intercept of the model, $coef_{tae}$ the coefficient of increase of SED inter-annual and $coef_{woy}$ the coefficient of increase of SED intra-annual.

After calibration of the linear model presented in Equations 2.5, the model described in Equation 2.1.b (with data from the sites shown in red in Figure 2.1) led to a prediction of the $SED_t$ as illustrated by green points in Figure 2.5 and to residues $Err2_t$.

### B.4.3. Modelling step 3 – Landscape effect

The third modelling step aimed at explaining the part of the residual variance from modelling step 2 ($Err2_t$) that can be attributed to landscape effects. Finally, we used linear models to analyze how the previously described landscape metrics (hedgerow, Forest, managed-banana-plants, non-banana-cultures-and-artificial-structures and unmanaged-banana-plants) were good predictors of $Err2_t$. At the end, the model that partition the variance of SEDt can be summarized in Equation 2.1.c.

$$δSED_t = BG_t . (1 - Ɛfungicide_t) + Ɛiia_t + Ɛlandscape_t + Err3_t \quad (2.1.c)$$

With $Ɛlandscape_t$ the landscape effects and $Err3_t$ the residuals of the model at step t, respectively.

## C. Results

### C.1. Estimation of the exponential growth rate of SED and the effect of weather

The estimation of the exponential growth rate of SED fitted is r = 0.415 (equation 2.2) (Figure 2.4). Then, the calibration of weather effect on the growth of SED allowed us to estimate the parameters ka = 2309.167, kb = -0.125 and kc = 30.679 of Equation 2.3 using the 'nls' function of R (Figure 2.6, Table 2.3).

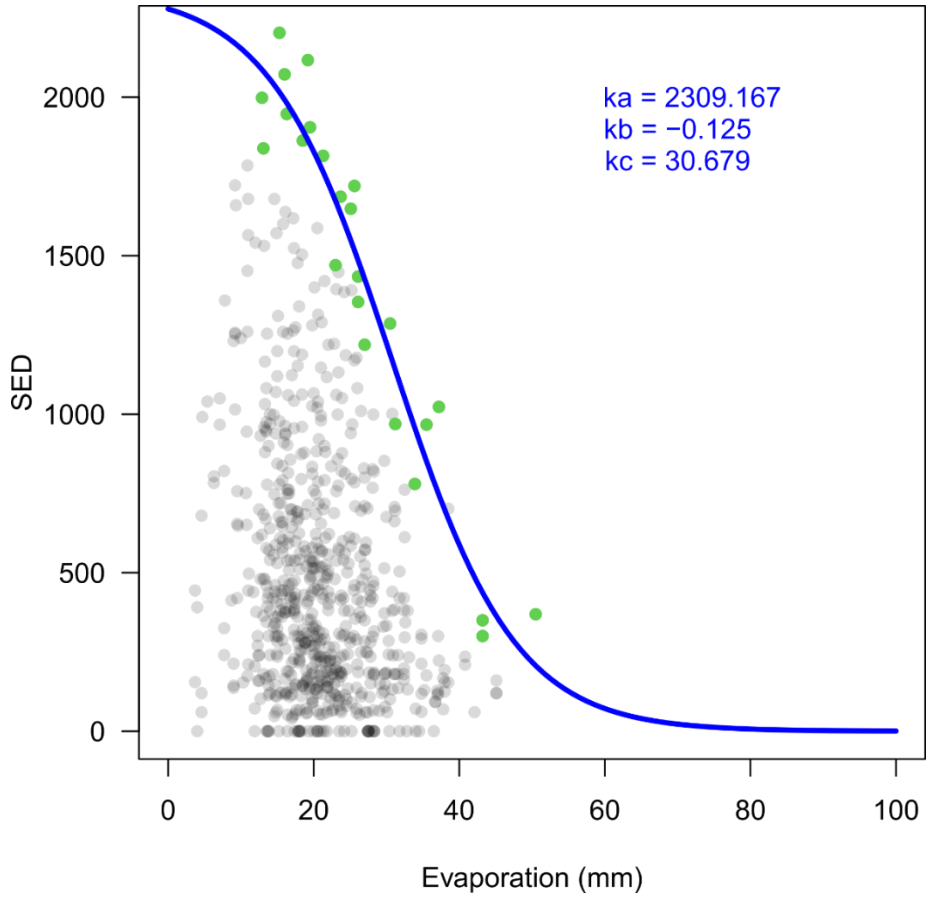



***Figure 2.6.*** *Representation of SED as a function of evaporation (millimeters). The blue curve represents the achievable SED (K) for each evaporation value (see Equation 2.2). Green points are the ones used to calibrated the line.*

### C.2. Effect of fungicides

The calibration of fungicide effects on all SED data since 2017 provided the fit of $\alpha_f$, $\beta_f$, $\gamma_f$, which shows contrasting pesticide effects for each of the five fungicides used in the study (Figure 2.7, Table 2.3). Time of effect and efficiency vary between the fungicides. Beyond the parameterization of the model, this approach provides a standardized comparison of the effect of each fungicide type. The most effective fungicides 3 weeks after the application have the highest values of $\alpha_f$ and $\beta_f$ (that were the systemic products *CONSIST*, *SICO*, and *TILT*). SERENADE efficiency decreased faster than the other fungicides after two weeks and had a negligible effect after 3 weeks. CONSIST has a better efficiency within 3 weeks, and *SICO* and *LUNA* remain the most effective after 4 weeks.

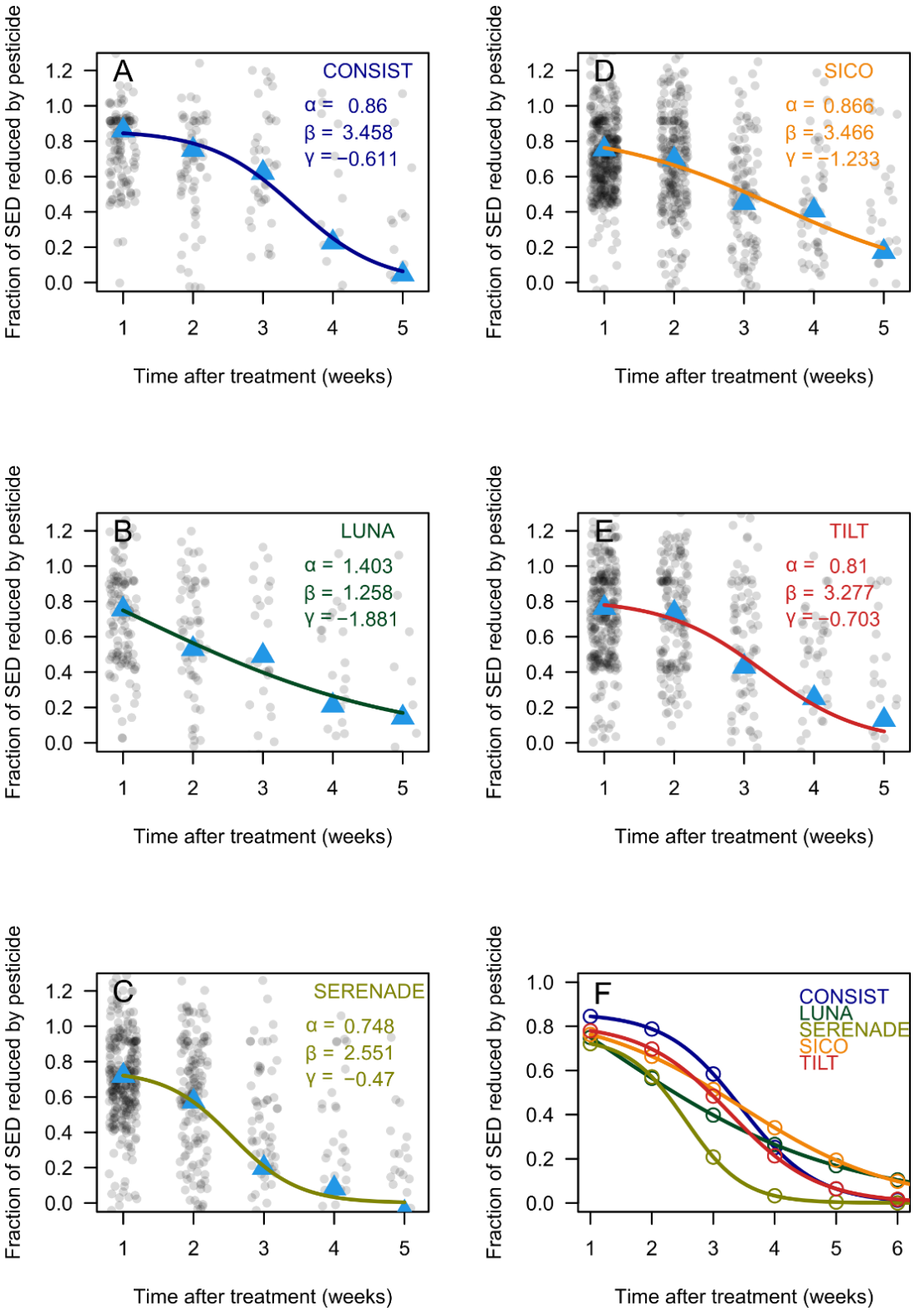



***Figure 2.7.*** *Estimation of the pesticide effects fitted on the standardized SED (SEDst) as a function of the time after treatment ($tat_t$) following the Equation 2.4 for the five pesticides used in our study (A-E). Comparison of the fitted curves for the five pesticides (F). Parameters for each pesticide are presented in Table 2.2.*

### C.3. Intra & inter-annual effects

The $\text{Ɛiia}_t$ was assessed by analyzing the model residuals of Equation 2.1.a (red points in Figure 2.1) with a linear model including the time since measurements beginning ($\text{tae}_t$) and the week of the year ($\text{woy}_t$) as predictors (modelling step 2). These two predictors were significant ($p = 0.004$ and $p < 0.001$, respectively) with positive estimates ($\text{coef}_{tae}$ and $\text{coef}_{woy}$) 0.09 ± 0.03(SE) and 2.86 ± 0.75(SE), respectively. Both coefficients correspond to (i) an increase in disease pressure over time (explained by the fact that island colonization of the disease has been ongoing since its introduction in 2010), and (ii) to the gradual increase of the disease over the year before a decrease at the beginning of the next year with the beginning of the dry season (Figure 2.8).

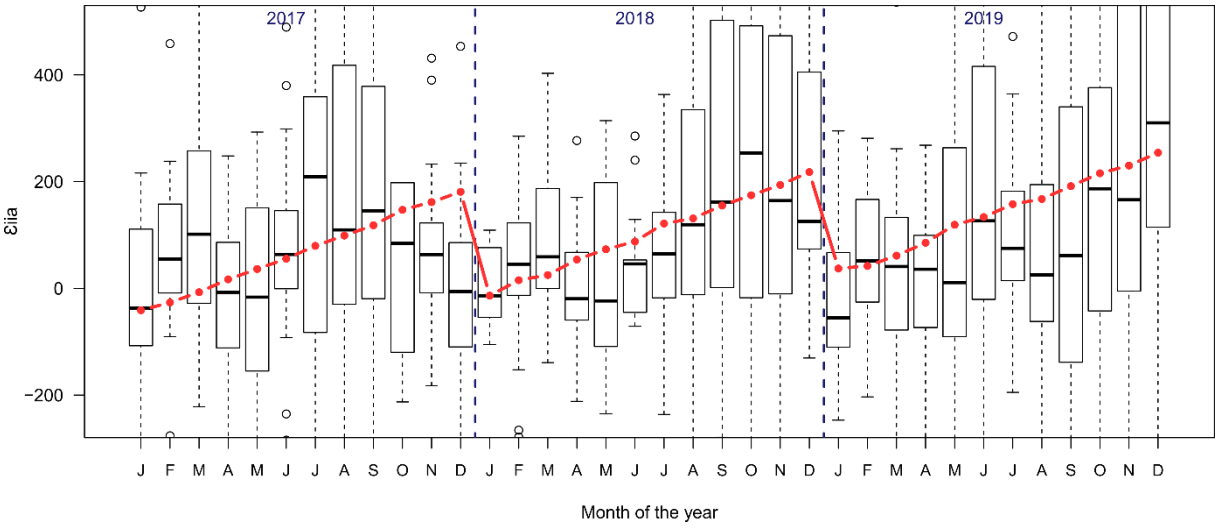



***Figure 2.8.*** *Variability of the intra&inter-annual effect (Ɛiia) weekly estimated, based on the residual of the model (Equation 2.1.a) between 2017 and 2019. Each box show the first and third quartiles, black lines in the middle of each box shows the median of the Ɛiia. The red dotted line shows the fit of the linear model with number of the week of the year and the time since the first measurement as predictors (Equation 2.5).*

### C.4. Evaluation and analysis of the landscape effects

We have estimated the landscape effect and a residual variation in BLSD dynamics (Ɛlandscape + Err) for each of the 11 plots selected (red points on Figure 2.1) by analysing the model residuals from Equation 2.1.b. The mean landscape effect on the disease of each plot and each year (Ɛlandscape + Err) varied between -152.17 and 135.95 (Figure 2.9). Next, we analyzed, for each field, for each year and in each buffer zone, how landscape

metrics influenced Ɛlandscape. We tested landscape metrics separately in each buffer zone in order to not suppressing an effect because of the abundance of another element. For each landscape feature, we selected at which buffer zone it was a better predictor of Ɛlandscape (with the highest significance):

- The presence of Managed-banana-plants with BLSD control had a depressive effect on BLSD at all distances (Figure 2.10). However, the most significant effect was within the 1000 m radius buffer zone (Figure 2.10). Ɛlandscape values decreased with host crop area in a 1000 m radius buffer zone effect (-5.825, $p < 0.001$) and beyond 30% of managed banana area landscape effects values are nearly all negative (Figure 2.11-A).

- The presence of Forest significantly promoted BLSD at all buffer zone sizes (Figure 2.10), stronger effects being at longer distances within the 1000 m radius buffer zone. At that distance, a positive linear coefficient (4.019, $p < 0.001$) indicates that Ɛlandscape tends to increase with the amount of forest (Figure 2.11-B). When the percentage of forest exceeds 33.8 %, nearly all landscape effects are positive.

- Non-banana-cultures-and-artificial-structures characterized by the absence of host plants had a depressive effect on BLSD only significant for larger distances (800 and 1000 m, Figure 2.10). Ɛlandscape values decreased when the percentage of such features increased with negative coefficients -4.105 ($p < 0.05$) and -5.384 ($p < 0.01$), for 800 and 1000 m radius buffer zones, respectively (Figure 2.11-C).

- The effect of Hedgerow was significant and maximal in the shorter radius buffer zone of 200 m (Figure 2.10) and was depressive on BLSD (linear coefficients: -23.089, $p < 0.05$). Interestingly, when the percentage of hedgerows was just over zero, the landscape effect was always below (or near) zero (Figure 2.11-D). Largest effects were observed for percentage of hedgerows between 1% and 3%.

- The presence of unmanaged-banana-plants and therefore potential sources of inoculum had promoted BLSD only at the longest distance within the 1000 m radius buffer zone (Figure 2.10) and has a positive coefficient that increase the Ɛlandscape (6.704) (Figure 2.11-E).

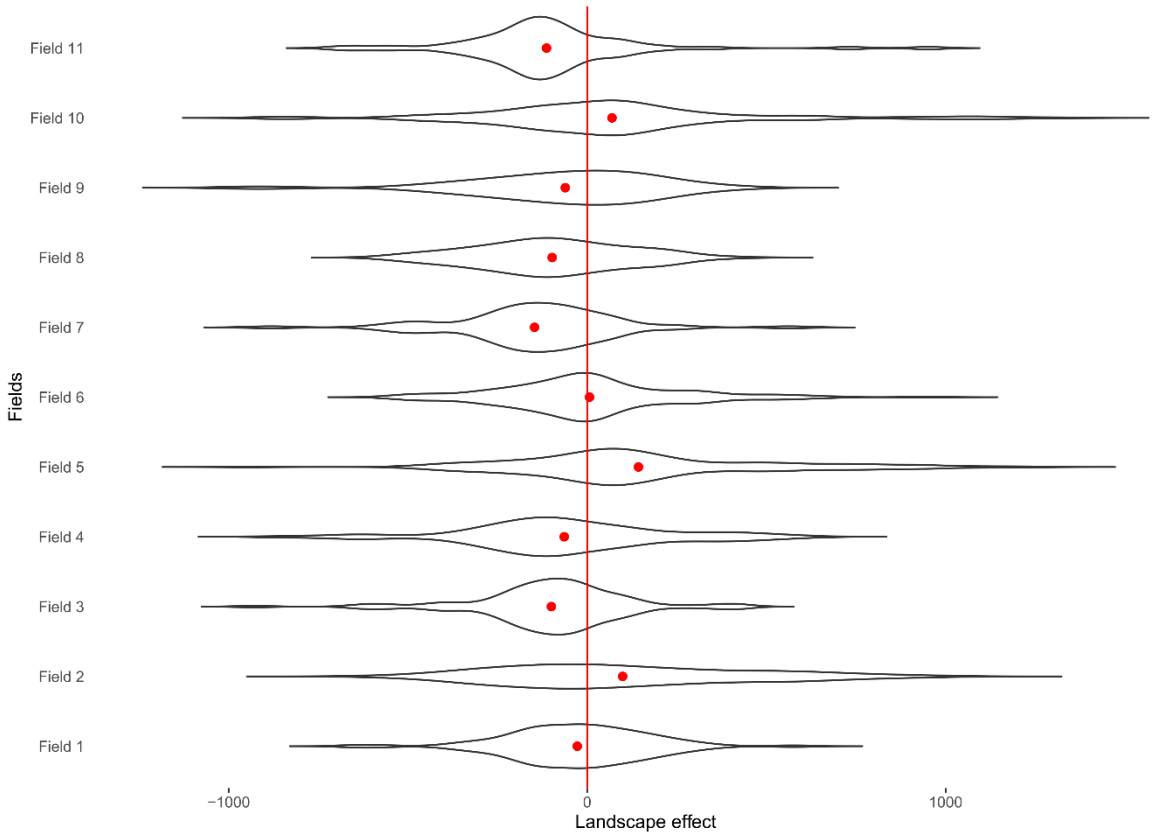



***Figure 2.9.*** *Distribution of landscape effects estimated weekly on the 11 fields studied. Landscape effect are the residues of the model (equation 2.1.b). Each distribution of landscape effects is corresponding to data analyze of a given field (33 to 135 weeks). Red points show the mean value the landscape effect for a given field. Negative and positive landscape effects are corresponding to suppressive and conductive landscapes, respectively.*

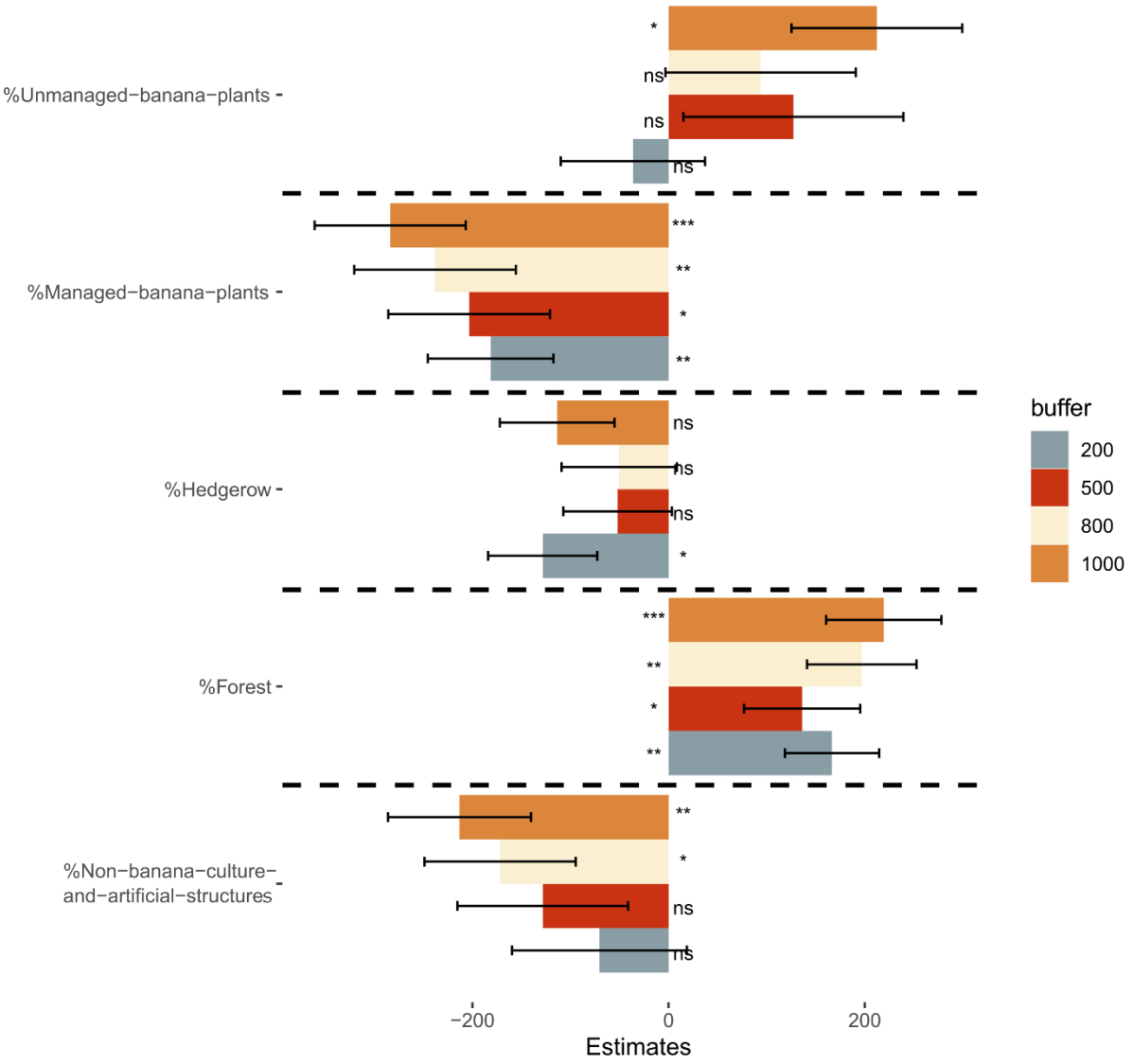



***Figure 2.10.*** *Estimates (on the x-axis) and significance of the estimates (on each bar) of the standardized landscape metrics (in the four defined buffer zones) (on the y-axis) on the landscape effect.*

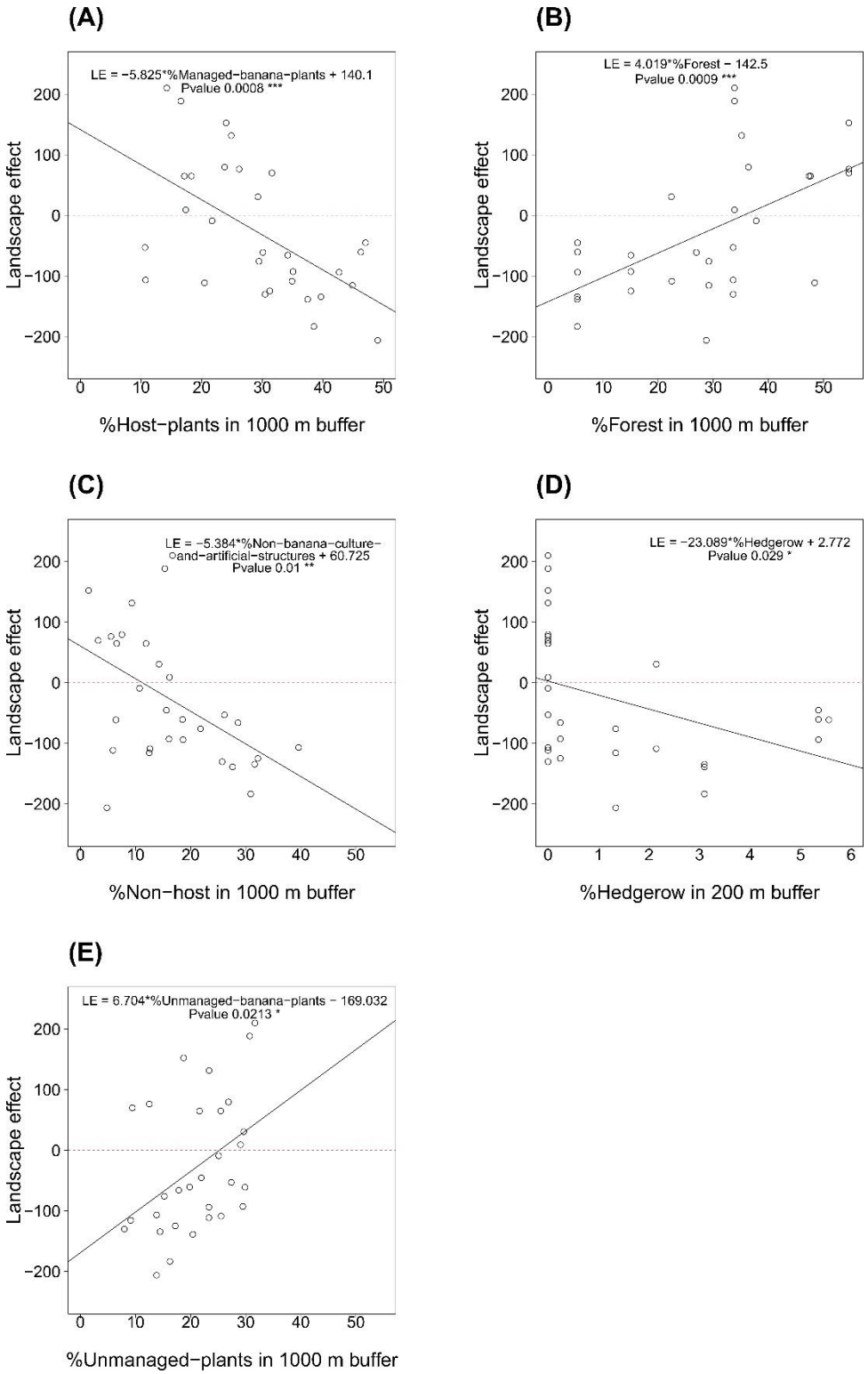



***Figure 2.11.*** *Relationships between the landscape effect (mean of residues of equation 2.1.b per field) and landscape metrics: (A) Percentage of hedgerow in 200 m radius buffer zone, (B) Percentage of Forest in 1000 m radius buffer zone, (C) Percentage of Managed-banana-plants in 1000 m radius buffer zone, (D) Percentage of Unmanaged-banana-plants in 1000 m radius buffer zone, (E) Percentage of Non-banana-cultures-and-artificial-structures in 1000 m radius buffer zone. The black solid lines show the fit of the linear model. The red dotted lines show the limit between conductive (positive values) and suppressive (negative values) landscapes.*

## D. Discussion

Our approach proposes a method that aims at disentangling, in the most process-based way possible, main factors influencing the epidemiological dynamics of an aerial foliar disease, at different spatio-temporal scales (from local fungicide application on banana plots, to seasonal dynamics of the disease and landscape effects at different scales). The originality of the approach is to have a dynamic model, with a process-based part and a statistical part. In the process-based part, we took into account the exponential growth rate of the disease and the direct effects of weather and fungicide applications, and in the statistical approaches we took into account the effects linked to larger temporal scales (colonization of the disease), to finally deduce the effect of the landscape. This strategy allowed a parsimonious approach in terms of the number of parameters and a biological significance of most of these parameters.

### D.1. Modelling the dynamic of BLSD

Our model allowed estimating factors that were never quantified before and can be used in other modelling studies. As we studied them separately, we have a good biologic appreciation of the contribution of each factor. The exponential growth rate (r) of the logistic growth (equation 2.2) is consistent with the fast growth of the disease (about 30% per week) under favorable conditions. In our model, the effect of weather is taken into account through the carrying capacity K of the logistic growth. The Piche evaporation is an integrative measure of weather that simulates leaf wetness and aggregates the temperature, wind speed, air humidity, solar radiation (Ganry and Laville 1983). Our data set cover well most conditions typical of humid tropic climate. The calibration of K as a response to Piche evaporation shows that it strongly decreased for evaporation above 20 mm and was extremely low for evaporation above 40 mm (Figure 2.6). These conclusions are in-line with Piche evaporation relationship with Sigatoka Disease another leaf spot disease of bananas (Ganry and Laville 1983). A maximal potential of growth of the disease for evaporation below 20 mm is consistent with existing literature that established an optimum growth for high humidity and air temperature between 25-28 °C (Jacome and Schuh 1992). Moreover, sporulation of conidia and ascospores are initiated by humidity (92-100%) or free water, respectively(Jacome et al. 1991).

The effect of fungicides is a major limit to understand how the landscape structure and composition is involved in ecological processes because it hides ecological regulations and it is often difficult to disentangle ecological and pesticide effects (Ricci et al. 2019). While crucial, this effect is rarely addressed since it requires having dynamic data of the disease and the exact information on the date and nature of pesticide applications. Other experiments determined the global efficiency of fungicides on the disease (Samuelian et al. 2016; Vawdrey et al. 2005) but not their dynamic effect in field conditions. Our approach allowed the estimation of the effect of each fungicide on the reduction of the SED during the five weeks after their application. Our estimation of this effectiveness was consistent with former knowledge of experimental evaluation of the efficiency of these products and with the appreciation of farmers on their farms. Specifically, the three systemic products with the strongest curative effect (CONSIST, SICO and TILT) showed a stronger and a more persistent effect than other products. This is the first time that such a precise and dynamical estimation of fungicide effect was achieved on BLSD, and was possible thanks to the precise dataset and to the modelling approach.

### D.2. Estimation of the effect of landscape

Taking into account the effects of the landscape in the control of crop pests is increasingly mentioned as a lever to be mobilized in alternative strategies to chemical treatments (Delaune et al. 2021; Fabre et al. 2015), but few studies are available for fungal diseases. The quantification and modelling of the landscape effect on a disease progress remains rare and difficult because this effect is associated with many other factors. Our approach allowed an estimation of this effect by subtracting, in the most process-based way possible, factors related to the exponential growth rate of the disease, the effect of weather, pesticides and seasonal dynamics. For each plot studied, we estimated an annual average landscape effect that covered values corresponding to different levels of suppressiveness or conduciveness of the disease (Figure 2.11).

At short distance (200 m radius buffer zone), the presence of Hedgerow showed a significant suppressive effect on BLSD. This suggest that the effect of hedgerows might be effective once a hedgerow is present and only at short distances to the plot. This seems consistent with the potential effect of hedgerows in limiting the dispersal of diseases, i.e. a barrier effect including the interception of spores, the modification of airflow patterns

and potentially of microclimate (Forman and Baudry 1984). Overall, presence of hedgerow increases the suppressiveness of the landscape, even at small percentages of hedgerow area. In future studies, it could be interesting to evaluate experimentally the effect of different types of hedgerows (size, width, mature) on inoculum dispersal.

As expected, landscape features without host plants (%Non-banana-cultures-and-artificial-structures) were suppressive (forest excluded), confirming that the fragmentation of landscape with non-host area limit the epidemic progression of BLSD through two potential ways: (i) a reduction of inoculum level per unit area and (ii) an increase of distance between susceptible hosts (Mundt 2002). This effect was observed at all distances but significant and maximal for 800 and 1000 m radius buffer zones. Beyond 15% of Non-host plants in 800 m radius buffer zone, Ɛlandscape values were all negative and landscape effect always suppressive. These discontinuity areas did not had significant effect at small scale because the distance between host areas were not large enough to reduce dispersion (Condeso and Meentemeyer 2007). A similar effect was expected for Forest features, but surprisingly forests promoted BLSD at all radius buffer zone sizes (most significant and higher effect in the 1000 m radius buffer zone). Forests might alter the epidemiology of BLSD through contrasted effects: (i) increasing host discontinuity that should be suppressive, and (ii) modifying microclimate that should be conducive. Indeed, forests tend to increase the air relative humidity, which is favorable to most fungal diseases (Condeso and Meentemeyer 2007). Here we cannot exclude that banana plants could be present in forest as commonly observed in various occasions (personal observations). At small values of %Forest, fragmentation effect compensates potential inoculum sources and are not able to modify microclimate. On the contrary, when %Forest exceeds 30%, the risk of inoculum source and the negative effect on the microclimate is probably more important than the benefit of fragmentation.

The Managed-banana-plants area, had a significant suppressive effect on BLSD at all distances, with a stronger significance at 1000 m. The Managed-banana-plants area and the suppressive effect increased proportionally. Beyond 31% of Managed-banana-plants area, landscape effects assessed were always suppressive. This result is counterintuitive because we expected a conducive effect of this landscape feature. However, this suppressive effect might traduce that BLSD control is more efficient in large banana plantations than in small banana plantations. Indeed, the suppressive effect increased

with the percentage of host crop area. In most commercial banana plantations, because of fungicide applications and regular deleafing of necrotic areas, ascospores, that are dispersed at large distance, are generally absent and epidemics are only driven by conidia that disperse at very short distance. Rieux et al. (2013) By another hand, BLSD control is more efficient in bigger farms than in small farms (de Lapeyre de Bellaire, personal communication) which could explain the greatest significance of this feature at the largest scale.

The presence of potential inoculum sources (unmanaged banana plants) in a 1000 m radius buffer zone promoted BLSD, suggesting that these features could be important sources of BLSD ascospora. While this relation is poorly significant, it suggests that a better management of these areas would help decreasing the sources of BLSD inoculum (especially in fallows after banana production and home gardens where untreated bananas might be present).

We have tried to explain the landscape effect via its composition. However, the landscape effect can also come from the organization of the landscape around the plot and the connectivity between the host areas. Although hedgerows are significantly a constraint to disease dispersion, their arrangement may be a key solution to spore interception around plots. The distance between the plot and the hedge, the height of the hedge and the angle to the prevailing winds are characteristics that we did not take into account and that may interfere with the amount of spore interception. The importance of the orientation of the barrier further to the wind has been shown in the study of Bouws et al. (Bouws and Finckh 2008) on potato blight, where the alternation of host and non-host zones perpendicular to the wind shows a barrier effect.

## E. **Conclusion**

In this study, we modelled step by step each factor that have an impact on the SED and used the residuals to quantify landscape effect on SED. This modelling approach has enabled the acquisition of new knowledge on the evolution of BLSD in Martinique on the growth parameters, the effect of meteorological conditions (Piche evaporation), the effects of fungicides, and finally on the effects of landscape elements. Our model separates

effects and allows a better understanding of disease dynamics and the factors that affect this dynamic. This knowledge can be used as a basis for future disease management studies through levers related to the organization of the landscape, such as the presence of hedgerows close to the plot, in order to achieve collective management and a more reasoned use of pesticides. The efficiency of each fungicide over time could lead to a better use of such fungicides. Interestingly, the hedgerow effect seems to be important and it will be necessary to carry out field experiments to better understand their effect on the dispersal of spores.

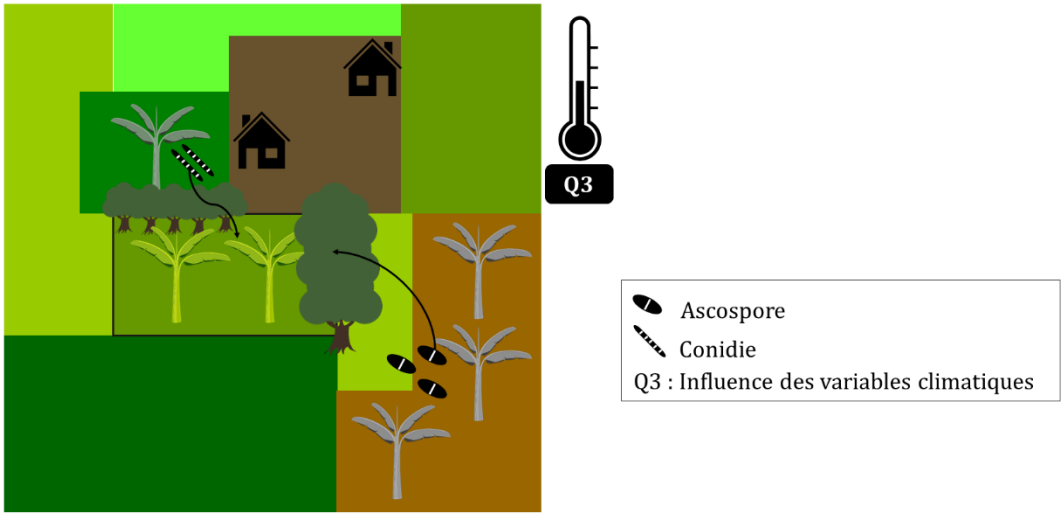
## F. Acknowledgements

We thank Mr Emmanuel Husson from SICA-CERCOBAN (BANAMART) for the fruitful collaboration. We also thank all the technicians from SICA-CERCOBAN for the collection of data, especially Mr Frantz Agricole, Mr Moïse Jarrin, Mr David Audinay, Mr Grégory Coldold, Mme Émilie Charles. We would like to thanks Mme Karine Vincent from BANAMART.

# CHAPITRE 3. Influence des facteurs météorologiques sur la dynamique de l'allo-inoculum



Ce chapitre est un travail expérimental pour répondre à la **question 3 : comment les facteurs climatiques influencent la production d'allo-inoculum.** Des mesures d'inoculum ont été menées entre juin 2020 et décembre 2021 sur 6 lieux de Martinique, éloignés des bananiers, dans le but d'observer la dynamique de présence d'allo-inoculum. A partir de la littérature, nous avons fait l'hypothèse que l'allo-inoculum était composé uniquement d'ascospores. Les résultats de ses mesures ont ensuite été analysés au regard des variables météorologiques au moment et avant chaque mesure pour comprendre la dynamique des spores longues distances au cours du temps.



# Effect of weather variables on long distance dispersal of Black Leaf Streak Disease in Martinique

Lucile Delatouche, Philippe Tixier, Marie-Odette DARIBO, Jérôme SAINTE-ROSE, Luc de Lapeyre de Bellaire

## A. Introduction

Dispersal is a key component of windborne fungal disease epidemics (Burt et al. 1998). In a given plot, there are a two types of inoculum: auto-inoculum that is produced in the plot itself, and allo-inoculum that comes from exogenous plots through long distance dispersal. Long-distance dispersal (LDD) allows the disease to expand on the territory and to infect new regions. It is important to know dispersal mechanisms in order to improve disease control. The distance travelled by allo-inoculum of a given disease depends on biotic and abiotic factors. For instance, the biology of the spores will condition its capacity of dispersal. The topography of landscape leads to highly heterogeneous ascospores deposition (García-Mozo et al. 2004). These authors showed that corridors can facilitate the dispersal of spores. Similarly, roads can be preferred dispersal routes for fungal disease dispersal (Laine and Hanski 2006). Production of spores and their LDD are clearly depending on weather variables (Crandall and Gilbert 2017; Crandall et al. 2020; Delaune et al. 2021; Pakpour et al. 2015). Acquiring knowledge on allo-inoculum is thus important to develop new tools to better predict the development of diseases. For example Skelsey et al. (2009) showed the importance of using weather data to determine the periods at risk for tomato and potato late blight disease and therefore improve its control by preventing contamination. This knowledge is essential for developing large scale strategies to reduce allo-inoculum, it can be based on modelling spore fluxes across the landscape (Aylor 2003).

Black Leaf Streak Disease (BLSD) is a foliar disease of *bananas,* caused by *Pseudocercospora fijiensis*, an ascomycetous fungus. BLSD has i) an asexual reproduction, through the production of conidia that are dispersed by the wind at short distance around the banana tree (about 10 meters) and ii) a sexual reproduction, through the production

of ascospores that are dispersed by the wind at long distances, up to more than one kilometre (Meredith and Lawrence 1969; Rieux et al. 2014). Based on previous study, inside the plot, most of the spores captured are conidia (Burt et al. 1998). Ascospores are in greater quantities in the allo-inoculum (Burt et al. 1998) and play an important role on LDD of the disease (Churchill 2011). The release of ascospores and infection efficiency was reported to depend on several weather factors. Higher quantity of spores are released during rainfall season than during dry season, as perithecia have to be impregnated with water for sporulation (Gaulh 1994). Optimal temperature for disease growth and sporulation is around 27°C (Churchill 2011). Free water or nearly saturated environment is required for germination and germ tube growth of ascospore, conidia can germinated until 92% of relative humidity (Jacome et al. 1991). Leaf wetness is required for the penetration in stomata and the infection of the leaf (Jacome and Schuh 1992). Weather factors influence BLSD at all the stages and its dispersal (Jacome and Schuh 1992, 1993; Jacome et al. 1991; Meredith and Lawrence 1969; Meredith et al. 1973; Parnell et al. 1998). These factors impact also the level of allo-inoculum and so the LDD. The study of allo-inoculum dynamics and of the effect of weather variables on it could help predicting the risks of BLSD contamination.

Previous works on *P. fijiensis* dispersal, as Burt aerobiology studies in Costa Rica, have used spore trap as Burkard or Rotorod to measure spore density in the air (Burt et al. 1998). With this method we cannot distinguish infectious spores from dead spores. Yet, spores are very sensitive to UV radiation and have a life expectancy of 6 hours after release (Parnell et al. 1998). Using trap plant method allows to detect only infectious spores that play a role in LDD and epidemiology (Poeydebat et al. 2018).

Banana export production is the most important culture in Martinique (27% of agricultural surface) and is threaten by BLSD, which can cause up to 25% yield loss (Stover 1972) and especially reduce in quality of the fruits especially their green-life (De Lapeyre de Bellaire et al. 2010). BLSD was first reported in Martinique island (West French Indies) in 2010 (Ioos et al. 2011). Since this first report BLSD expansion is now complete and BLSD control represents the main use of pesticides in this island, but far from the intensive use in other countries (Costa Rica up to 70 kilos active substance.ha$^{-1}$.year$^{-1}$). The use of these fungicides impact biodiversity, environment and human health.

This massive of fungicides also increases the risk of emergence of fungicide-resistant strains of *P. fijiensis* (De Lapeyre de Bellaire et al. 2010), which makes much complicated the management of BLSD. Developing new strategies against BLSD is necessary to reduce pesticides use and to have a more sustainable export banana production. Studying the effect of weather variables on allo-inoculum and LDD is important to develop accurate strategies to control BLSD at the landscape scale.

The aim of this study carried out in Martinique Island was to estimate the effect of weather variables on the abundance of long-distance inoculum of BLSD. We evaluated the dispersal capacity of *Pseudocercospora fijiensis* on a large-scale using trap plant located far from potential sources of *P. fijiensis* spores. We measured the density of spores intercepted by trap plants ten-times between June 2020 and December 2021 at 6 spots in contrasted conditions in Martinique Island. Then, we used an original statistical approach to determine which weather variables affected the density of spores captured by trap plants and at what period before spore deposition it was at play.

## B. Material & Methods

In this experiment, we evaluated the abundance of *P. fijiensis* spores in the air thanks to trap plants in six contrasted locations in Martinique Island (Figure 3.1). Trap plants were exposed during 10 periods between June 2020 and December 2021 (Table 3.1). At each time of measure and at each location, we installed six trap plants during seven days and counted the density of lesions on each plant after an incubation time in green house. Then, we analysed how weather and disease data maybe predictors of the BLSD lesion densities.

***Table 3.1.*** *Date and place of experiments of measurement of allo-inoculum presence in the air with trap plants*

| Location | Altitude (m) | Date of exposure | Mean lesion density (number of lesion.cm$^{-2}$ of leaf) (2021 only) |
|---|---|---|---|
| Place 1 | 226 | 18/06/2020, 13/11/2020, 26/01/2021, 26/04/2021, 10/06/2021, 15/07/2021, 18/08/2021, 23/09/2021, 28/10/2021, 09/12/2021 | 0.016 |
| Place 2 | 364 | 26/01/2021, 26/04/2021, 10/06/2021, 15/07/2021, 18/08/2021, 23/09/2021, 28/10/2021, 09/12/2021 | 0.030 |
| Place 3 | 23 | 26/01/2021, 26/04/2021, 10/06/2021, 15/07/2021, 18/08/2021, 23/09/2021, 28/10/2021, 09/12/2021 | 0.016 |
| Place 4 | 203 | 26/01/2021, 26/04/2021, 10/06/2021, 15/07/2021, 18/08/2021, 23/09/2021, 28/10/2021, 09/12/2021 | 0.030 |
| Place 5 | 71 | 18/06/2020, 13/11/2020, 26/01/2021, 26/04/2021, 10/06/2021, 15/07/2021, 18/08/2021, 23/09/2021, 28/10/2021, 09/12/2021 | 0.011 |
| Place 6 | 11 | 18/06/2020, 13/11/2020, 26/01/2021, 26/04/2021, 10/06/2021, 15/07/2021, 18/08/2021, 23/09/2021, 28/10/2021, 09/12/2021 | 0.035 |

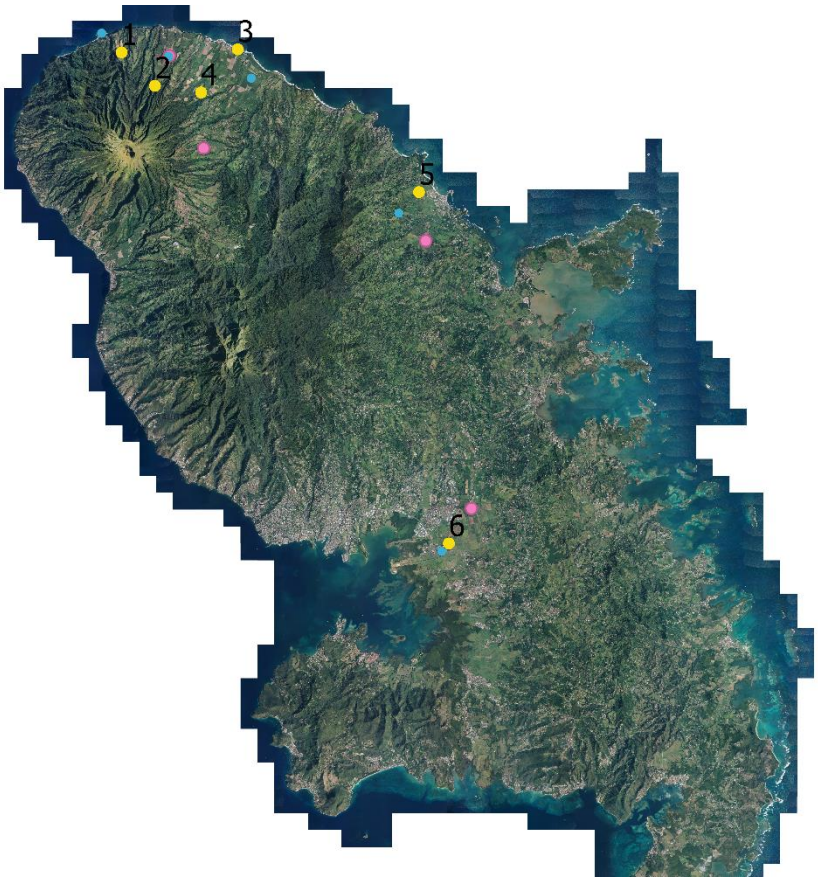



***Figure 3.1.*** *Different locations for allo-inoculum measurements (yellow points), weather station (blue points) and PICHE evaporation measurements (pink points) (background image from GéoMartinique, Provider Institut national de l'information géographique et forestière (IGN)).*

### B.1. Selection of location for allo-inoculum estimation

To evaluate the abundance of *P. fijiensis* allo-inoculum in the air resulting from LDD, we selected six locations in Martinique. Each location was selected in a banana production area, at least 300 m away from any banana trees that could be a potential source of spores (Figure 3.2). According to Rieux et al (2014), 300 m is clearly sufficient to prevent the contamination by conidia that hardly disperse more than 10 m. By another hand, most ascospores disperse 200 m from an inoculum source. We selected locations with constrated conditions on banana production in Martinique Island at contrasted altitudes (Table 3.1 and Figure 3.1, yellow points).

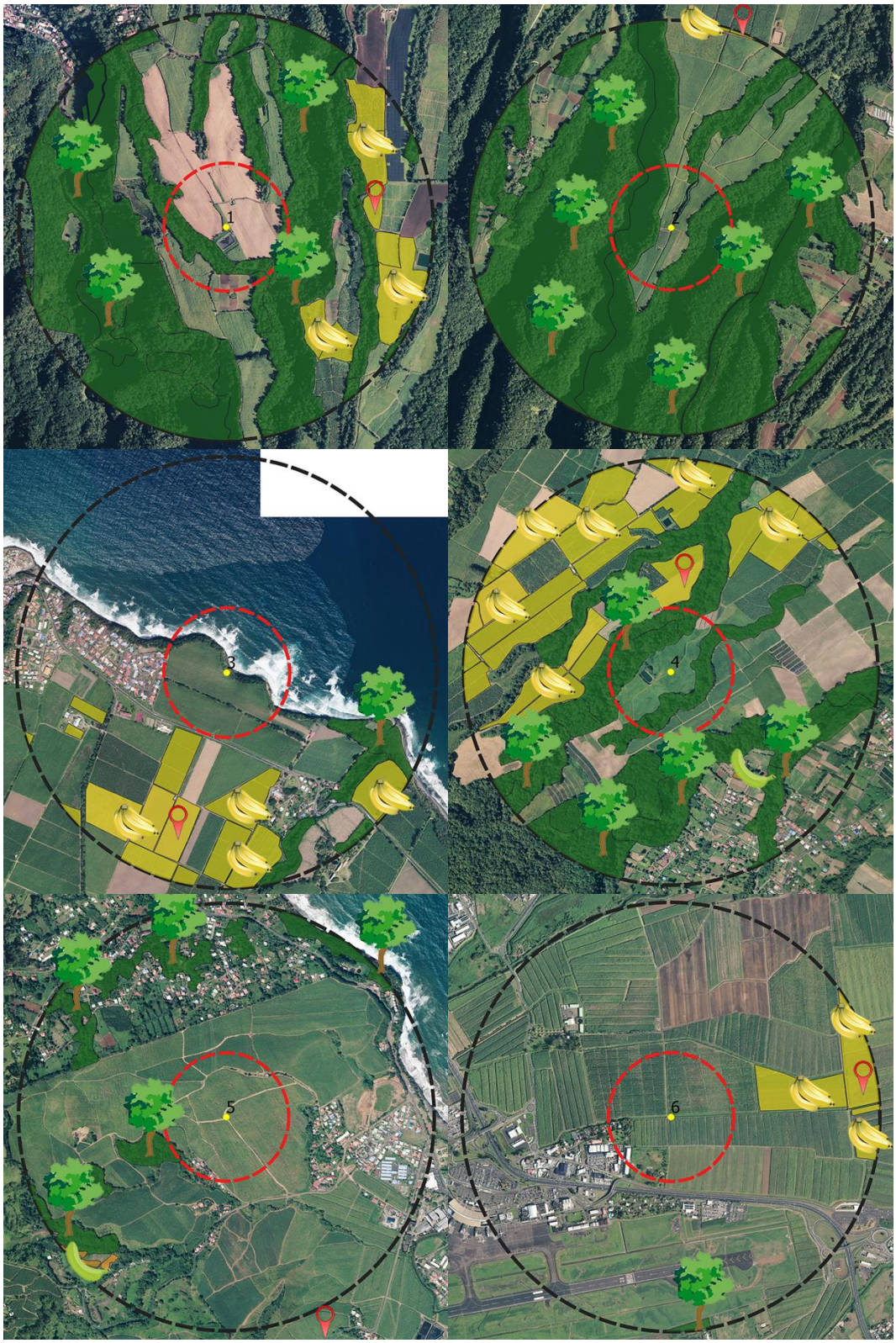



***Figure 3.2.*** *Environment description in 1 kilometre radius (dotted black line) around trap plant spot (presence of Cavendish production, yellow bananas; presence of plantain, green banana; presence of natural forest, tree) and stage evolution of the disease (SED) measurement spot (Red pin). The dotted red line represent de 300 meters radius without banana plant around the spot. (background image from GéoMartinique, Provider Institut national de l'information géographique et forestière (IGN)).*

### B.2. Trap plants

We used trap plants (young banana plants from the Cavendish group (cultivar GALL, use in Martinique) issued from *in vitro* micropropagation) as an indicator of allo-inoculum abundance. Using trap plants, instead of spore trap, allows taking into account only spore that can play a role in the epidemiology, i.e. with the capacity to germinate. We installed six trap plants with new leaf unfurled at stage B at each location during seven days (Poeydebat et al. 2018). After exposition, trap plants were moved in a greenhouse under optimal conditions for symptom expression. Indeed plants were placed under plastic bag to obtain a humidity of 100% and an average temperature between 25 and 29 °C (Jacome and Schuh 1992; Jacome et al. 1991), allowing to optimise number of lesions revealed on the trap plant. Incubation period varied from 17 to 24 days. Lesions were counted after twice the duration of incubation period minus two days (Poeydebat et al. 2018) and the lesion density (D) of lesions was calculated (equation 3.1) with the number of lesions divided by leaf area that was calculated based on an algometric relation (equation 3.2).

$$D = \frac{\text{number of lesions}}{\text{Leaf area}} \quad (3.1)$$

$$\text{Leaf area} = \text{Leaf length} * \text{Leaf width} * 0.83 \quad (3.2)$$

### B.3. Weather data

Weather data were obtained from Météo-France weather stations. We collected data of the closest weather station for each location (Figure 3.1, blue points). Daily rainfall, daily mean temperature, and daily UV radiation were used to explain lesion density as well as weekly evaporation provided by SICA-CERCOBAN (Figure 3.1, pink points).

### B.4. Disease data

The stage of evolution of disease (SED) is an indicator of the speed of development of BLSD, used to take the decision of the application of fungicides, calculated with the stage of the disease, range of leaf and leaf emission on 10 trees by field (Fouré and Ganry 2008). SED was provided weekly by SICA-CERCOBAN. Each allo-inoculum measurement site was associated to its closest plot where SED was collected in banana production plots (Figure 3.2, red pin).

### B.5. Statistical analysis

We used a model to determine if and when weather and SED influenced the lesion densities on trap plants. We modelled each factor for all possible combination time period defined by a starting and an ending date before exposure of the trap plant in the field. Studies of BLSD development have shown that the time between infection and first symptoms is about 10 to 14 days and time between first symptoms and necrotic stage are about 22 days in optimal conditions (Jones 2018). Thus, we chose to study the meteorological conditions during this period. For weather daily data, periods of time tested begin from 21 to 0 days and end 20 to 0 days before exposure of each trap plant. For the evaporation, we took the same length of time than other weather variables, so periods of time tested begin from 3 to 1 and 2 to 0 weeks, before exposure of each trap plant. Finally, for the disease data, periods of time tested begin from 6 to 1 and 5 to 0 weeks, before exposure of the trap plant to have a large range of analyses. Then, we calculated the likelihood of each model corresponding to each time period. We selected the periods with the highest likelihood as the best potential predictors of the lesion density measured on trap plants. Finally, we built a GLM to test the response of the lesion density (D) to the selected predictors defined in previous step. When necessary, we log-transformed the predictors and also tested the quadratic values of predictors to take into account potential non-linear relation between the predictor and the response. We used a backward approach to select a complete model (Bolker 2008). As the intercept was not significant, we forced it at 0. All tested predictors are summarized in Table 3.2. All statistical analyses were performed with R 4.1.1 (R Core Team 2021) and with an alpha level of 0.05.

## C. Results

The temporal dynamic of the lesion density measured at each site was characterized by two peaks, a first peak between November 2020 and February 2021 and a second peak between May and July 2021 (Figure 3.3). Inoculum collected on sites 2, 3, 4, and 6 was almost always higher than sites 1 and 5. However, we observed the same dynamics

between all sites on the island with the same peaks of allo-inoculum (Figure 3.3). The mean lesion densities during the 2021 measurements shown that there are differences between sites.

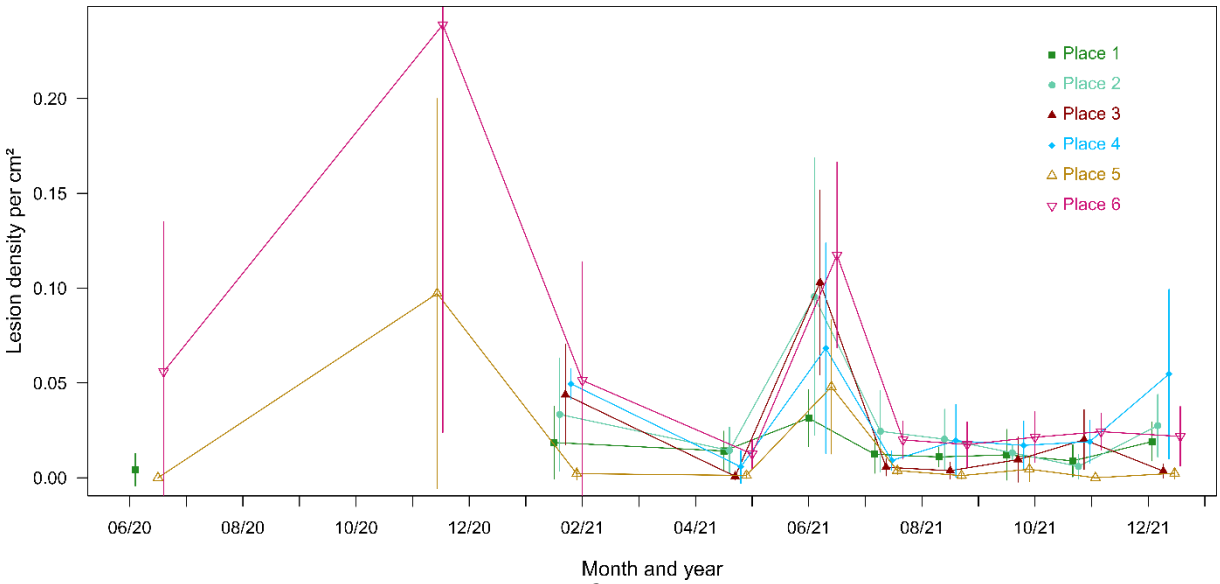



***Figure 3.3.*** *Mean lesion density (lesion.cm$^{-2}$ of leaf) and standard deviation of BLSD from long distance dispersal in 2021 in 6 spots in Martinique Island.*

We represented the likelihood of each model of lesion density with each weather variables at each time period with heatmaps (Figure 3.4). For each variable, we selected the time-periods with the highest likelihood, which were potentially the best predictors of the density of lesions measured in trap plants. Selected predictors were:

- the sum of rainfall between 7 and 4 days before exposure (Figure 3.4.A),
- the average temperature between 12 and 11 days before exposure and between 8 and 7 days before exposure (Figure 3.4.B),
- the average evaporation between the week before exposure (Figure 3.4.C),
- the average UV radiation between 17 and 16 days and between 2 and 1 days before exposure (Figure 3.4.E).

In the case of SED, it was not possible to determine a clear hot spot of likelihood (Figure 3.4.D). We selected the time period with the model with highest likelihood anyway to test its influence on lesion densities, which was between 3 and 2 weeks before exposure of the trap plant.

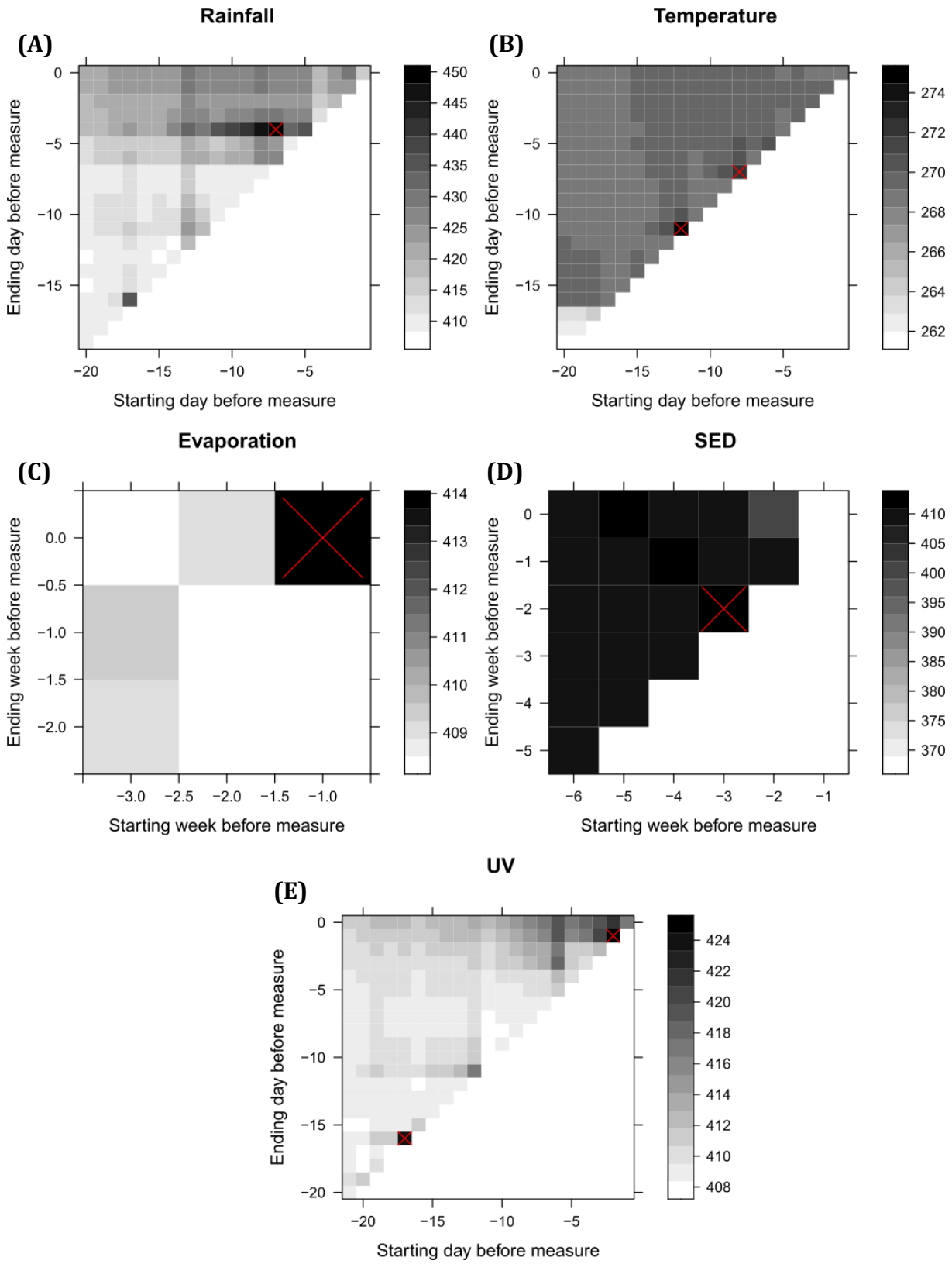



***Figure 3.4.*** *Heatmap of likelihood of linear models between rainfall (A), temperature (B), evaporation (C), stage evolution of the disease (SED) (D) and UV (E) during different time period and lesion density. Red cross representing time period with the higher likelihood.*

We used predictors selected in the previous step to build a complete linear model to predict the lesion density (D) and kept only significant ones (Table 3.2, equation 3.3).

$$D = 0 + \log(Rain_{7-4}) + (\log(Rain_{7-4}))^2 + Temp_{12-11} + Temp_{8-7} + UV_{2-1} \quad (3.3)$$

With $Rain_{7-4}$ the rainfall sum between 7 and 4 days before exposure, $Temp_{12-11}$ the average temperature between 12 and 11 days before exposure, $Temp_{8-7}$ the average temperature between 8 and 7 days before exposure, and $UV_{2-1}$ the average UV radiation between 2 and 1 days before exposure.

***Table 3.2.*** *Equation of modelling of lesion density (D) on trap plants with weather factors (during their main influence time period before trap plants exposure), description of the variables and parameters of model fitted on results of lesion density*

| **Equation** | $D = 0 + \log(Rain_{7-4}) + (\log(Rain_{7-4}))^2 + Temp_{12-11} + Temp_{8-7} + UV_{2-1}$ | | | | | | |
|---|---|---|---|---|---|---|---|
| **Variables** | **Unit** | **Description** | **Df** | **Estimates** | **AIC** | **δAIC** | **Pr(>F)** |
| **$Log(Rain_{7-4})$** | log(mm) | Logarithm of rainfall sum between 7 and 4 days before exposure of trap plants | 1 | -0.057135 | -1120.4 | 25.3 | $2.71 \times 10^{-07}$ ** |
| **$(Log(Rain_{7-4}))^2$** | $log(mm)^2$ | Square logarithm of rainfall sum between 7 and 4 days before exposure of trap plants | 1 | 0.018180 | -1094.5 | 51.2 | $6.94 \times 10^{-13}$ *** |
| **$Temp_{12-11}$** | °C | Mean temperature between 12 to 11 days before exposure of trap plants | 1 | -0.009366 | -1143.6 | 2.1 | 0.04608 * |
| **$Temp_{8-7}$** | °C | Mean temperature between 8 to 7 days before exposure of trap plants | 1 | 0.012380 | -1139.8 | 5.9 | 0.00582 ** |
| **$UV_{2-1}$** | $J.cm^{-2}$ | Mean ultra-violets radiation between 2 to 1 days before exposure of trap plants | 1 | -0.236918 | -1143.4 | 2.3 | 0.04262 * |

SED, evaporation and UV between 17 and 16 days before exposure did not significantly influence lesion densities (respectively, $P > 0.89$, $P > 0.17$, $P > 0.17$). Cumulated rainfall between 7 and 4 days before exposure appears to be the strongest factor to explain lesion densities, together $log(Rain_{7-4})$ and $log(Rain_{7-4})^2$ led to a variation of AIC above 76 compared, Table 3.2). $Temp_{8-7}$ was a stronger predictor than $Temp_{12-11}$, with variation of AIC of 5.9 and 2.1, respectively. $Temp_{12-11}$ and UV 2-1 were predictors with similar importance (Table 3.2).

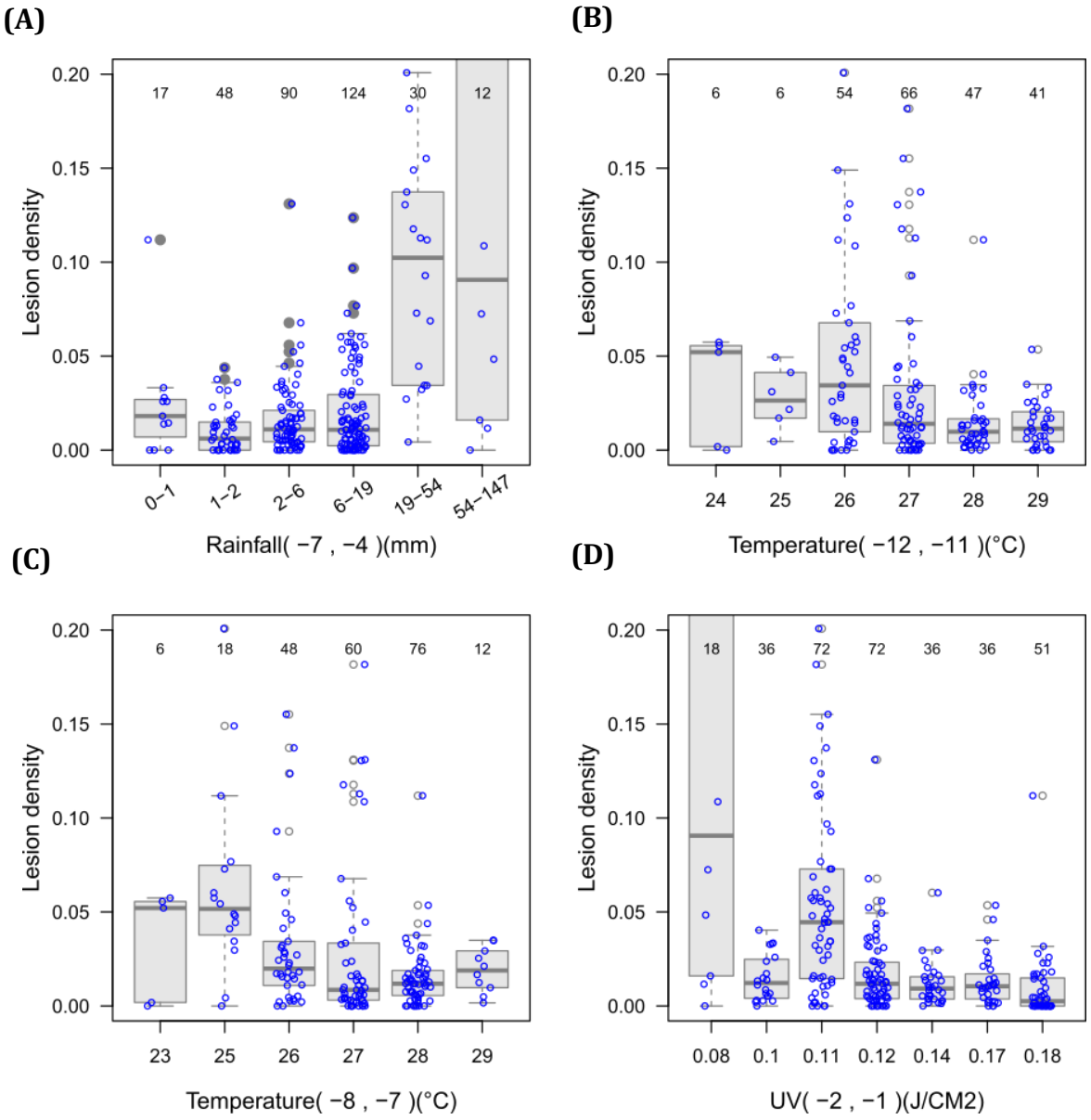



***Figure 3.5.*** *Evolution of lesion density on trap plant in function of weather variables at the time period the most significant: (A) lesion density in function of the sum of rainfall from 7 to 4 days before exposure of the trap plant, (B) lesion density in function of the average of temperature from 12 to 11 days before exposure of the trap plant, (C) lesion density in function of the average of temperature from 8 to 7 days before exposure of the trap plant, (D) lesion density in function of the average of UV from 2 to 1 days before exposure of the trap plant. Boxplot represent lesion density measured by classes of weather variable, the blue points represent each measure of lesion on the weather variable class.*

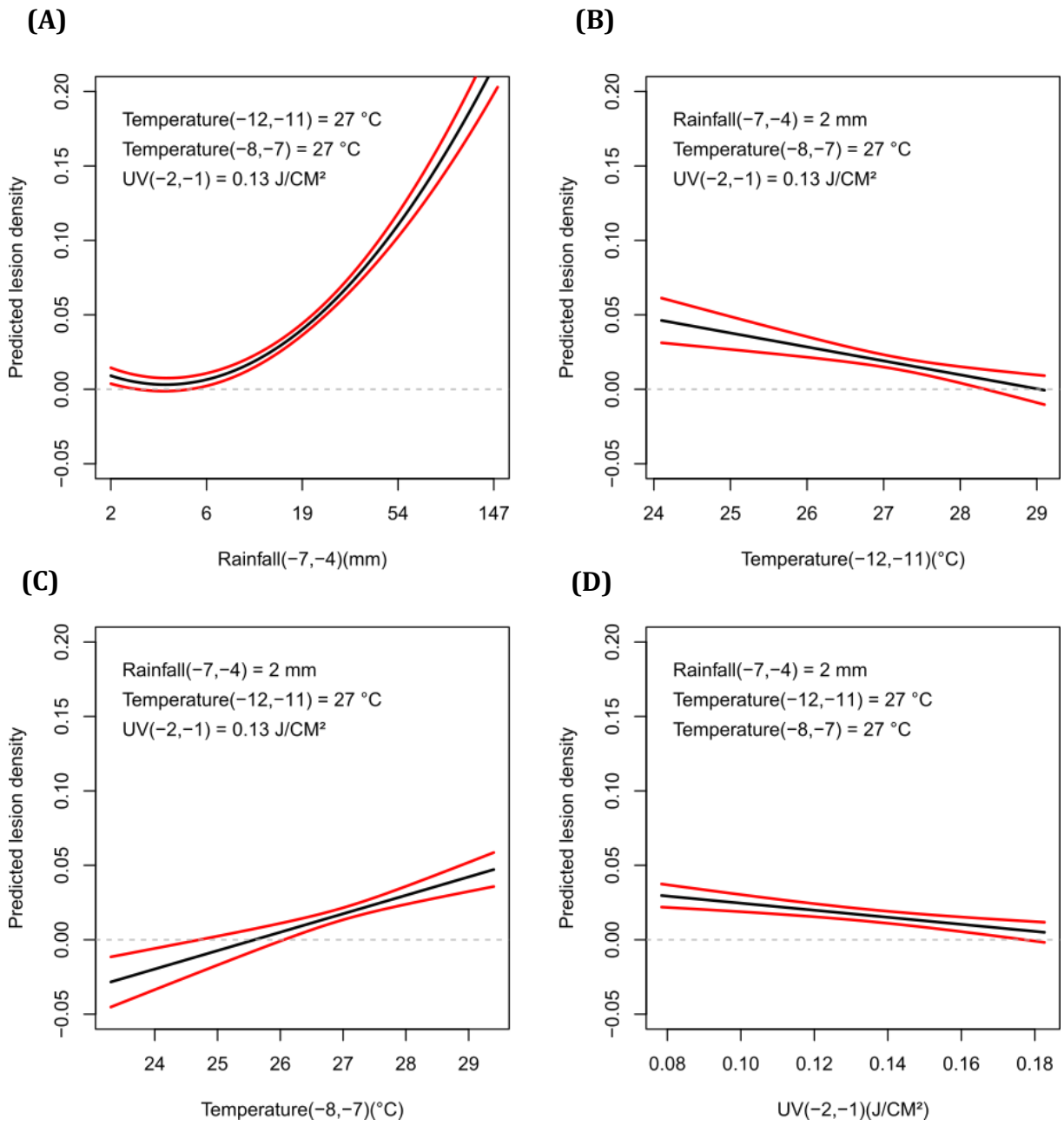



***Figure 3.6.*** *Predicted lesion density by the model varying each climate factor (black lines) with other factors fixed at their average: (A) variation of lesion density with rainfall sum between 7 and 4 days before exposure of trap plants, (B) variation of lesion density with average temperature between 12 and 11 days before exposure of trap plants, (C) variation of lesion density with average temperature between 8 and 7 days before exposure of trap plants, and (D) variation of lesion density with average UV between 2 and 1 days before exposure of trap plants. Red lines represent standard error of the prediction.*

Figure 3.5 shows the evolution of the lesion densities measured in our experiment for each selected predictor in the complete model. The mean predictions of lesion density by the complete model, for each predictor while fixing the other predictors at their mean

values, are presented in Figure 3.6. The lesion density dramatically increased with total $Rain_{7-4}$ when it was above 6 mm while it was predicted as stable below (Figure 3.6.A). The lesion density also increased with $Temp_{8-7}$ (Figure 3.6.C). Inversely, the lesion density decreased with the $Temp_{12-11}$ (Figure 3.6.B) and $UV_{2-1}$ (Figure 3.6.D).

## D. Discussion

Our study allowed to determine the period of effect of weather variables and how they influenced the BLSD lesion density caused by allo-inoculum contaminations. This work on the dispersion of inoculum at this scale is still a pioneer study. The allo-inoculum measured in our study is probably exclusively composed of ascospores since we selected sites located at least 300 m from banana plants and the conidia have very low dispersal capacities (about 10 m) (Burt et al. 1998; Rieux et al. 2014). We collected only alive and infectious spores thanks to the use of trap plants.

### D.1. Allo-inoculum dynamics

There was similar dynamics of the lesion density for all sites with two main peaks in November 2020 and June 2021. The production of allo-inoculum seems to be affected by factors at island scale rather than processes at small scale (< 1000 meters). Weather effects have shown a stronger effect than landscape use on airborne fungal spore in other studies (Crandall and Gilbert 2017). We probably had similar results with BLSD since there were similar variations of lesion density for the six sites. Although there were contrasted landscape composition around each measurement site (Figure 3.2), the dynamics of allo-inoculum in trap plants were following the same trend. However, the variability of quantity of lesion densities between sites could be explain by the availability of source of inoculum and their expositions to winds. The evolution of lesion density during the year that we obtained did not followed the pattern usually observed in Martinique with higher lesion density at the end of the year (November and December) and not during June as in our experiment. The year of 2021 was unusual in Martinique with few rainfall at the end of the year.

**D.2. No SED effect**

We did not find any correlation between SED collected in banana plantation and lesion densities measured on our trap plant during the year. This general trend confirms the hypothesis that the allo-inoculum is not produced in banana plantations. As said before, the allo-inoculum is exclusively composed of ascospores because of their large capacity of dispersion compared to conidia (Rieux et al. 2014). This result is consistent with the fact that farmers remove necrotic tissues which are the only ones producing ascospores. The allo-inoculum of BLSD is thus probably coming from other sources as unmanaged banana plant in private garden or abandoned areas. This result is in-line with the results of Delatouche et al. (in press) that showed that BLSD tends to decrease with the proportion of managed banana farms in the landscape surrounding banana plots.

**D.3. Rain effect**

The rain had a maximal impact on lesion density measured on trap plants between 7 and 4 days before exposure of the trap plant. It was the main factor explaining lesion densities measured. Rainfall events allow the growth of perithecia and the capacity of production of ascospores. Ascospores release is known to be induced by free water and especially by rainfall (Brun 1964; Gaulh 1994; Meredith et al. 1973). Our results also support that rainfall rate, higher than 6 mm from 7 to 4 days before exposure of trap plants, increased lesion density measured on trap plants (Figure 3.6.A). As Gauhl (1994) shown in his study, very small rate of rain can induce the release of ascospores. The increase of lesion densities is exponential with the rain rate. As rainfall between 7 and 4 days before exposure was clearly the best predictor of the lesion density on trap plants, we can hypothesize that this moment is crucial for the production of ascospores and their release. Since the life time of ascospore is usually assumed to be around few hours only (Parnell et al. 1998), we can hypothesize that 7 to 4 days before exposure of trap plant is corresponding to time of production of ascospores rather than to the release of the spores that contaminate our trap plants.

**D.4. Temperature effect**

The temperature influenced lesion densities measured on trap plants during two periods: between 12 and 11 days and between 8 and 7 days before exposure. We measured the highest lesion densities at average temperatures between 25°C and 27°C for both time

periods (Figure 3.5). This range of temperature (between 25°C and 27°C) is considered as an optimal temperature for the growth of necrotic lesions (Jacome and Schuh 1992, 1993). On the first time period (for 12 to 11 days), lesion densities increase with $Temp_{12\text{-}11}$. On the contrary, lesion density decreased with the temperature for $Temp_{8\text{-}7}$. This is consistent with the fact that spore production is expected to decrease with high temperatures (Burt et al. 1999; Jacome and Schuh 1993). The temperature have generally an optimal and an influence bell-shaped, but our case there were too few data under the optimal (at 25°C) to model this influence. In future experiments, it could be interesting to have a larger gradient of temperature, e.g. selecting more sites at higher altitude.

**D.5. UV radiation effect**

Lesion density decreased with UV radiation between 2 to 1 days before exposure of the plant, with a nearly null predicted lesion density for UV above 0.17 $J.cm^{-2}$ (Figure 3.6.D). Although it was only slightly significant, UV had a negative impact on lesion densities measured on trap plant. We can hypothesize that UV radiation affected the life time of ascospore. This is in-line with findings of Parnell et al. (1998) that showed that no spores of BLSD an germinate after an exposure of 4 hours to UV.

**D.6. Research perspective**

Overall, our results give an interesting basis of knowledge on how to predict efficient allo-inoculum. In future studies, it should be useful to try to identify the potential sources of ascospores involved in the LDD. For example, it would be important to identify plots of unmanaged banana plants (unmanaged fallows, untreated plantain fields) in the landscape since they can be important contributors to BLSD allo-inoculum. Marked sources of BLSD could be use, similarly to the experimental designs of Rieux *et al* (2014) to understand how allo-inoculum is dispersed from the source. It will also be important to repeat our experiment in other climatic regions (in West Africa or Latin America that produced a lot of banana that are exported) to constitute a dataset in more contrasted ranges of weather variables (higher and lower temperatures as well as bigger amount of rainfall).

A better capacity of prediction of periods of time with higher risks of pathogen dispersal can be useful to adapt cultural practices to the level of risk. By studying weather conditions during the exposure of the trap plant, we could also improve the prediction by

adding the risks of infection of the plant. For instance, tools to predict risk days thanks to weather data could be developed similarly to Skelsey et al. (2009) approach in the case of potato late blight. Our results could also be used to improve forecasting systems that help taking the decision of fungicides applications.

## E. Conclusion

In this experiment, we measured the amount of allo-inoculum of *Pseudocercospora fijiensis* in the air during a year in six locations in Martinique Island, by exposing trap plants during a week and counting lesion densities. We determined time period of influence of rainfall rate, temperature and UV radiation on lesion density measured and established a linear model to predict lesion density with these weather factors. We did not find influence of disease data measured in banana fields on lesion density on trap plants. These results could be used to predict sequential waves of allo-inoculum in banana fields and new infection waves taking into account further post leaf pollution climatic effects.

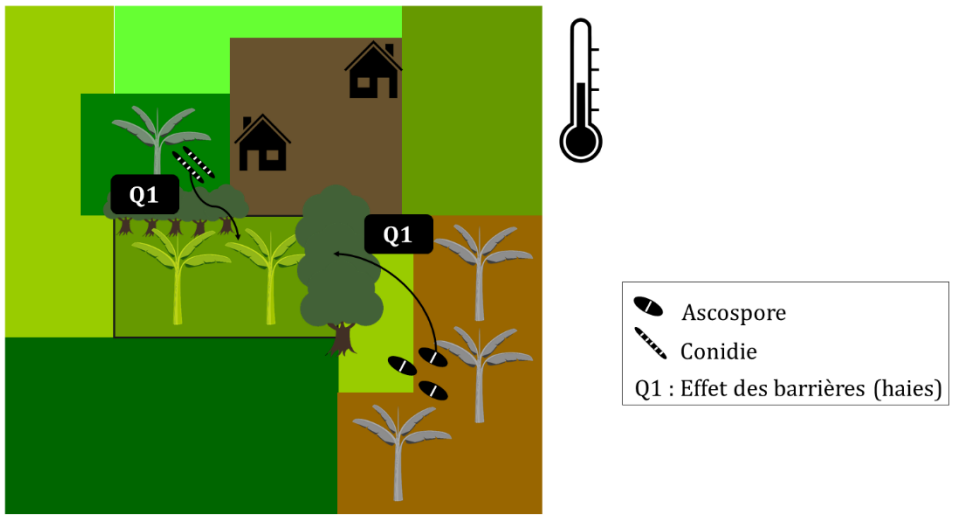
## F. Acknowledgements

We want to thank all field owners who allowed us to place our trap plants for this experiment: VIVIES Eric, POUSTIQUE Didier, GOLDSCHMIDT Pierre and LELEU Romain.

# CHAPITRE 4. Quantification expérimentale de l'effet des haies sur la dispersion des ascospores et des conidies de *Pseudocercospora fijiensis*



Ce chapitre est issu d'un travail expérimental devant répondre à la **question 1** : **comment les haies influencent la dispersion des spores**. 20 essais expérimentaux ont été menés sur 7 haies différentes sur les deux types de spores produits par *Pseudocercospora fijiensis* (4 avec des ascospores et 3 avec des conidies) de novembre 2020 à mars 2022. Le but de ces essais était d'évaluer le potentiel des haies dans la régulation de la cercosporiose noire. Le gradient de haie utilisé dans les expérimentations a permis de déterminer les caractéristiques efficaces contre la dispersion des spores.



# How hedgerow characteristics alter *Pseudocercospora fijiensis* dispersal?

Lucile Delatouche, Philippe Tixier, Jérôme Sainte-Rose, Marie-Odette Daribo, Luc de Lapeyre de Bellaire

## A. Introduction

Black Leaf Streak Disease (BLSD) is the most economically important disease of banana production. This disease is responsible for the main use of pesticide in this crop leading to important fungicide applications and to an active ingredient load approaching 70 kg per hectare per year (De Lapeyre de Bellaire et al. 2010; Risède et al. 2010). In order to make production more ecologically friendly, new agroecological levers need to be developed.

BLSD, caused by the fungus *Pseudocercospora fijiensis* (Guzmán et al. 2018; Rhodes 1964), is a foliar fungal disease of *Musa* spp. provoking leaf spotting and leaf necrosis that inhibits photosynthesis, leading to a decrease of yield and quality by dampening fruit conservation (Guzmán et al. 2018). *Pseudocercospora fijiensis* produced two types of propagules: ascospore by sexual reproduction and conidia by asexual reproduction (Meredith and Lawrence 1969). Conidia are produced in the early stages of the disease and disperse on only few meters away, while ascospores are produced in the necrotic stages (stage 6) and spread over hundred meters (Rieux et al. 2014). Even if dispersal is a key component in disease epidemiology, there is still a lack of knowledge on the effect of different landscape structures on the dispersion of fungal diseases in general (Plantegenest et al. 2007) and in particular for BLSD.

Studies have now confirmed that biodiversity and complex landscape tend to reduce pest damages (Chaplin-Kramer and Kremen 2012; Chaplin-Kramer et al. 2011) both by hosting predators and by limiting the spread of the pest. Very scarce knowledge is available on the effect of landscape composition and landscape structures on the

regulation of disease dynamics, but landscape elements have shown efficient potential mechanisms of regulation of their inoculum as having a direct or indirect barrier effect. As observed, presence of natural or semi-natural areas can reduced pathogens dispersal, however, their disposition and structure can either form corridors or barriers (Delaune et al. 2021; Plantegenest et al. 2007). An indirect barrier effect of hedgerows on the production of inoculum is typically the modification they induce on microclimate. As shown in agroforestry system, hedgerows participate to limit temperature variation and therefore reduce dew on the leaves, which participate to limit the infection of leaves by spores and also the production of spores themselves (Gaulh 1994; Jacome and Schuh 1992; Schroth et al. 2000). Another benefice of agroforestry system is that it reduces of air movement that can limit dissemination of spores (Schroth et al. 2000). Direct barrier effect would function as physical barrier against dissemination of propagules, for example non-host plants capture spores before contaminating susceptible plants. Effectiveness of a barrier is expected to vary with diseases and especially with their characteristics of dispersion. The two main dispersion modes of fungal diseases are by wind or splash (rain). In splash dispersion, architecture of the plant and the spatial arrangement is an important factor that can alter the dispersion of spores. For example, in Vidal (2018), barrier effect against *septoria* in wheat was improved by alternating susceptible with resistant variety thus increase LAI (Leaf Area Index) and density of plants in the rows. This intercropping design reduced susceptible tissue proportion and trapped spore on non-sensitive plants. In wind dispersed disease, alternating rows of resistant or other species and susceptible cultivars is also a lever to reduce disease through spore interception by resistant plants (Boudreau 2013; Bouws and Finckh 2008; Didelot et al. 2007; Gómez-Rodriguez et al. 2003; Vidal 2018). The rate of reduction of the disease can depend on the specie associated, e.g. Fernández-Aparicio et al. (2011) showed the importance of the species associated with faba bean to support a barrier effect to chocolate spot development. The size of the barrier appears to be a key characteristic that participates to its effectiveness, e.g. the wider the non-host or resistant crop the more efficient to stop disease dispersion (Villegas-Fernández et al. 2021). Fernández-Aparicio et al. (2010) demonstrated that at low density, intercropped plants limit horizontal dispersion of *Mycosphaerella pinodes* severity on pea plant, while at high density it alters its vertical dispersion. Planting with a low density of susceptible cultivar can also reduce disease intensity (Fernández-Aparicio et al. 2011). In Schoeny study (Schoeny et al. 2010),

the same disease reduction was observed in low-density (50% ratio) plot and in intercropped plot (dispersion reduction between 39 and 78%). In certain case, intercropping could reduce quantity of spore production by allelopathy effect of the plant in intercrop although this effect often remains poorly studied (Gómez-Rodriguez et al. 2003).

In the same way, the presence of trees is likely to act as barrier to the dispersal of propagules (Aylor 1990; Poeydebat et al. 2018; Schroth et al. 2000). As mentioned above, agroforestry systems have the potential of reducing propagules released (Schroth et al. 2000). Agroforestry showed good results of reduction of lesion density and spore abundance on BLSD (Poeydebat et al. 2018) thus we hypothesis that the presence of hedgerows could also improve its management. Benefits of hedgerow are known in biological control on pest for example, as provider of habitats for crop protection agents (Schroth et al. 2000). In the specific case of the effect of hedgerows on the dispersal of fungi propagule's, the Aylor review (Aylor 1990) showed that windbreaks hedgerows allow reducing propagule's dispersal from infested to healthy fields. To date, no studies addressed the potential barrier effects on the dispersal of spores of *P. fijiensis*.

Here we have carried out an experimental study in order to evaluate potential barrier effects of hedgerows on the dispersion of ascospore and conidia of *P. fijiensis*. We have used hedgerows with different characteristics in order to evaluate how these characteristics could affect this barrier effect. To this end, we carried out 20 experiments on seven existing hedgerows, using a controlled source of spores and trap plants to measure the influence of hedgerows on the dispersal of *P. fijiensis* spores.

## B. Materials & methods

In this work, we carried out two types of experiments (one on each type of propagules) to determine the capacity of regulation of hedgerow on ascospore and on conidia. These experiments included a total of twenty replications, 11 and 9 experiments with sources of ascospore and conidia, respectively. These experiments were performed using seven hedgerows with different characteristics (Table 4.1), 4 being used for the study of barrier effects using ascospore sources and 3 for the study of barrier effect using sources of

conidia. We located trap plants on each side of hedgerows at equal distances to the artificial source of inoculum to measure abundance of spore and collected wind data during the experiments in order to evaluate potential anisotropic effects of hedgerows on BLSD dispersal.

***Table 4.1.*** *Hedgerows characteristics*

| Hedgerow | Experiment | Latitude | Longitude | Spore type | Height (m) | Width (m) | Optical porosity | Hedgerow interception surface (HIS) |
|---|---|---|---|---|---|---|---|---|
| 1 | A4,A6,A8 | 14.691293 | -61.007434 | Ascospore | 4.8 | 1.0 | 0.62 | 3.36 |
| 2 | C7,C8,C9 | 14.657885 | -60.918078 | Conidia | 4.7 | 3.8 | 0.95 | 16.74 |
| 3 | C1,C5,C6 | 14.566732 | -60.974873 | Conidia | 7.3 | 3.1 | 0.89 | 18.40 |
| 4 | A1,A2,A3,A5 | 14.720637 | -60.995838 | Ascospore | 9.2 | 2.8 | 0.88 | 24.90 |
| 5 | C2,C3,C4 | 14.695125 | -60.917391 | Conidia | 9.0 | 3.0 | 0.95 | 25.42 |
| 6 | A10,A11,A12 | 14.694566 | -60.917806 | Ascospore | 6.6 | 8.3 | 0.92 | 50.40 |
| 7 | A7,A9 | 14.780155 | -61.007303 | Ascospore | 8.1 | 11.6 | 0.94 | 93.96 |

### B.1. Hedgerows

Experiments took place in Martinique Island. Two criteria were used for the selection of hedgerows used for our studies: i) they had to be far enough (> 400 m) from any banana trees in order to limit the influence of other sources of spores (Rieux et al. 2014), and ii) hedgerows had to be at least 10 meters long and homogenous. We selected contrasted hedgerows covering a wide gradient of characteristics (Figure 4.1, Table 4.1).



***Figure 4.1.*** *Pictures of hedgerows used during experiments: on the left, hedgerow 1 (HIS=3.36) and on the right: hedgerow 7 (HIS=93.96).*

These characteristics included their shape i.e. height, width (at 1.5 m high and at the canopy) and their optical porosity (Table 4.1) which could influence spore interception. As banana plants are 5 m high, hedgerow's height had to be equal or superior to 5 m. With a laser rangefinder, we measured the height and width at three points on the length of each hedgerow and made an average. For optical porosity, we used the same method that Lazzaro (Lazzaro et al. 2008). The principle is to calculate the percentage of light that can passed throw the hedgerow. We took a picture of each hedgerow from top to bottom, convert the image on 1-bit image and black and white percentages were (Lazzaro et al. 2008). The percentage of hedgerow pixels (black pixels) was assumed to be a predictor of the surface that can intercept spores and was the variable used as optical porosity in our calculations. The optical porosity varied between 0 (transparent) to 1 (opaque). Then for each hedgerow, we have calculated the potential hedgerow interception surface (HIS) using all hedgerow characteristics (height, width, optical porosity) (equation 4.1, Table 4.1), HIS being putatively linked to the capacity of the hedgerow to intercept fungal spores. We sorted the hedgerows per HIS, hedgerow 1 having the lowest HIS and hedgerow 7 the highest HIS (Table 4.1, Figure 4.1).

$$HIS = height * width * optical\ porosity \qquad (4.1)$$

### B.2. Spore source simulation

In our experiment, we simulated two types of sources of spores, one with ascospore (experiments A, Table 4.1) and the other with conidia (experiments C, Table 4.1). For ascospore, we built an artificial banana tree architecture with 6 leaves made of PVC hose, iron wire and mosquito net. We concentrated necrotic banana leaf pieces on these artificial leaves representing approximately 1.5 $m^2$ necrotic surface either 1 million perithecia (Burt et al. 1999) and an important source of ascospore. To provoke ascospore discharge, necrotic leaves were watered every day with about 10 litres of water (Meredith et al. 1973). For sources of conidia, we collected infected banana plants in a field (5 plants renewed 1 time during the experiment) with leaves length between 1 and 1.5 meters and we removed necrotic parts.

### B.3. Trap plants

We used trap plants (young banana plants from in vitro micro-propagation) to determine spore dispersal from the artificial source (Poeydebat et al. 2018; Rieux et al. 2014). Trap plants with new leaf unfurled, were exposed in the field during 9 to 12 days, the unfurled leaf being totally unrolled. Then, they were placed in a greenhouse under a plastic bag in order to maintain humidity at 100%. Temperature ranged between 25 and 29°C for optimal development of lesions during incubation (Jacome and Schuh 1992; Jacome et al. 1991). Lesions were counted after twice incubation time minus two (Rieux et al. 2014) and the daily density (DD) of lesions was calculated (equation 4.2) with the number of lesions divided by leaf area (equation 4.3) and number of day of exposure.

$$DD = \frac{\text{number of lesions}}{Leaf\ area * number\ of\ day\ of\ exposure} \quad (4.2)$$

$$Leaf\ area = Leaf\ length * Leaf\ width * 0.83 \quad (4.3)$$

### B.4. Experiments architecture

We located the source of spores on one side of the hedgerow. Then, all trap plants were placed in line of 5 plants on each side of the hedgerow at equal distances to the artificial source of spores. The distance between the spore source and the trap plants were established in function of their capacity of dispersion. For experiments with a source of

ascospore, trap plants were placed at 10, 20, 30, 40, 50 meters from the source (Figure 4.2A). For experiments with a source of conidia, trap plants were placed at 3, 7, and 11 meters from the source (Figure 4.2B). To guarantee no competition between the trap plants on the line, we spaced them 1.5 meters apart. Finally, the trap plants were installed on poles at 1.7 meters to benefit from the same climatic conditions as a banana tree.

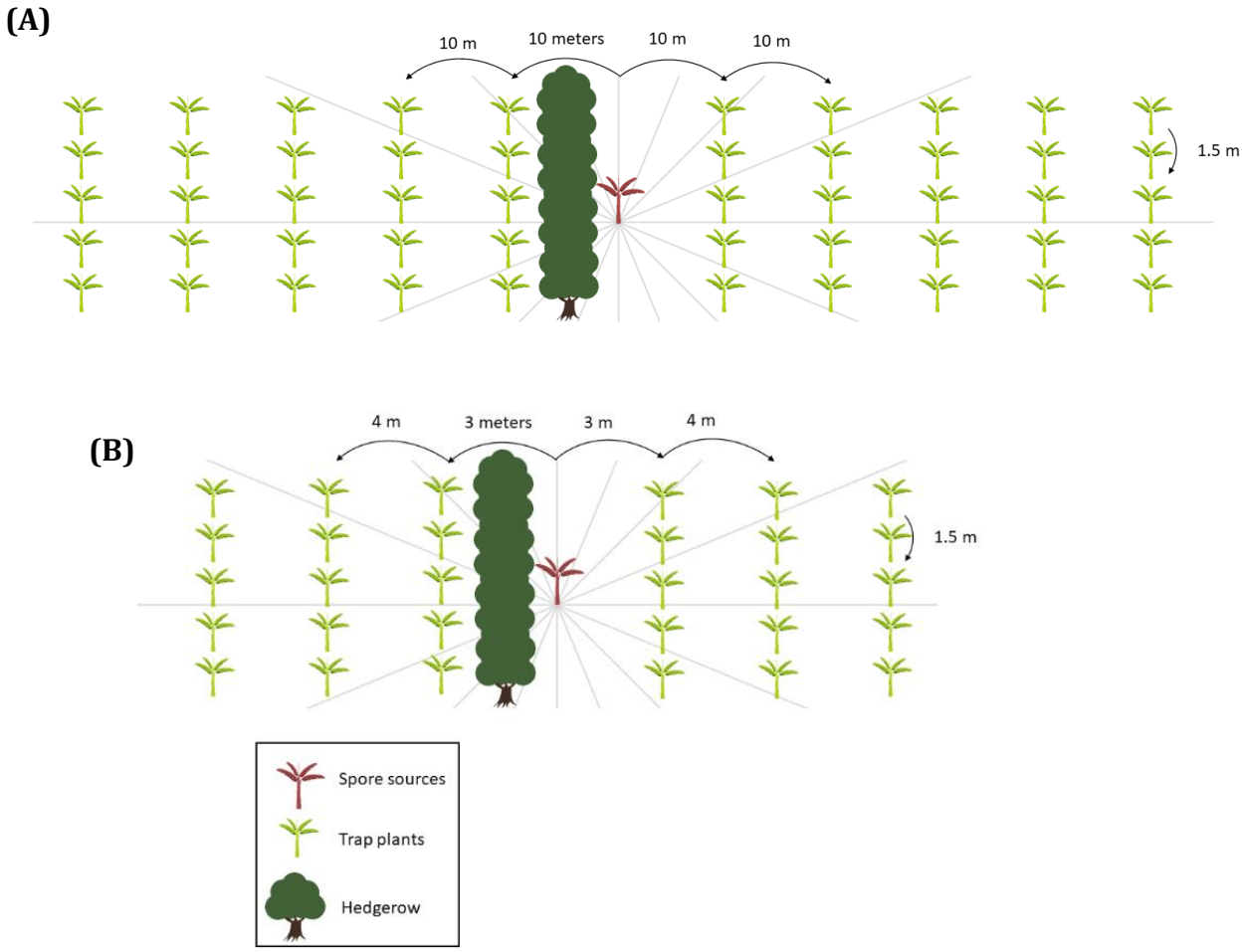



***Figure 4.2.*** *Designs of experiment (A) testing barrier effect of hedgerow on ascospore dispersion (B) testing barrier effect of hedgerow on conidia dispersion. Grey lines defined wind direction sections used on each trap plant to model the impact of the wind on lesion densities.*

### B.5. Wind data

We used a weather station (FROGGIT® WS1800) placed on the plot to have direction (°) to collect speed of the wind ($km.h^{-1}$) every 10 minutes during exposure of the trap plants.

The direction was given in 22.5° sections and we kept that precision in our calculations. We placed the compass rose center on the spore source in order to associate each trap plant to the section corresponding to the wind direction coming from the spore source (Grey lines of Figure 4.2). We considered that winds directed from the source to the trap plant were the most efficient to disperse spores. All recorded wind speeds were summed (by section of 22.5°). For each trap plant, we associated the wind speed sum (WSS) oriented from the source to this trap plant. The WSS associated to each trap plants was then used as a predictor of the lesion density.

### B.6. Statistics

In order to define how characteristics of hedgerow impacted the dispersion of BLSD spores, we modelled the DD of each trap plant with a linear model using GLM (Generalized linear model) including the following variables as predictors: the source side (either the same side as the source or the other one), the distance to the source, the WSS, the hedgerow height, the hedgerow width, the hedgerow optical porosity, and the HIS. After testing these variables following a backward-forward selection procedure, we only kept the significant predictors. All statistical analyses were performed with R 4.1.1 (R Core Team 2021)

## C. Results

*Effect of hedgerows on the dispersal of ascospore*

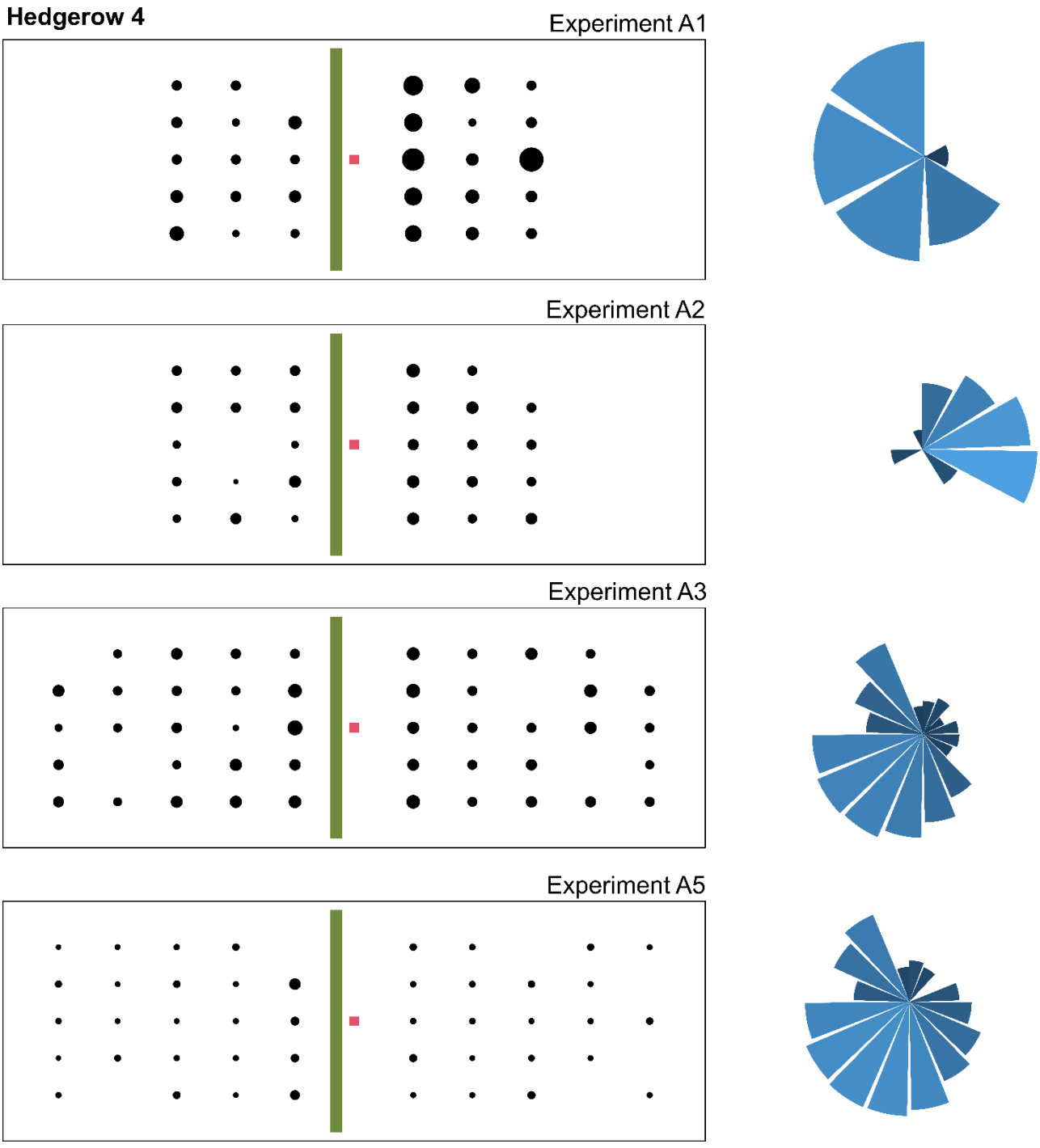
The patterns of DD on each trap plants for the ascospore experiments are presented in Figure 4.3, ranging between 0 and 0.18 lesions.cm$^{-2}$.day$^{-1}$. DD was significantly different between the two sides of the hedgerow, with higher lesion densities on the source side. The DD decreases with the distance to the source and was contrasted for the four tested hedgerows (Figure 4.4). Either hedgerow characteristics (height, width and optical porosity) ($P < 0.05$, $P < 0.0001$, and $P < 0.01$, respectively) or HIS were significant ($P < 0.0001$). We chose to keep HIS as a predictor of DD because it is a variable that integrates all hedgerow characteristics and because it was strongly significant ($P < 0.0001$, estimate

= -0.00072). The two sides of the hedgerow were significantly different, the side of the source exhibited higher DD than the other side. (P < 0.01, estimate = 0.01509). The inverse of the distance to the source had a significant positive effect on DD (P < 0.0001, estimate = 0.52648). The wind (log(WSS)) had a negative significant effect on DD (P < 0.0001, estimate = -0.00371) (Table 4.2). Overall, the model explained 23.9% of the variance of DD ($R^2$ = 0.2392).

***Table 4.2.*** *Equation, description of the variables and Results from the linear model of ascospore lesion density.*

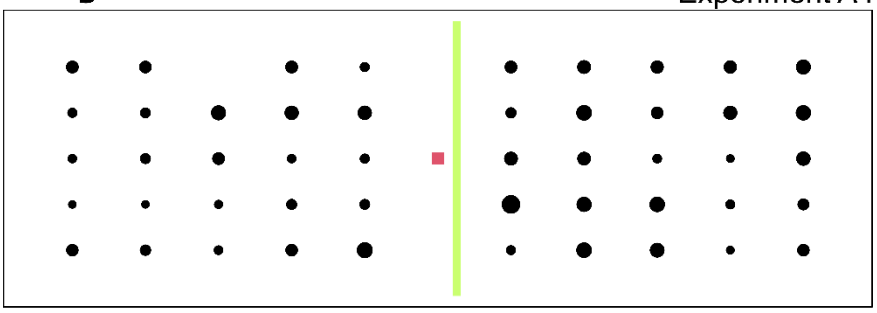
| **Equation** | $DD = \log(WSS) + \frac{1}{distance} + HIS$ | | | | | | |
|---|---|---|---|---|---|---|---|
| **Variables** | **Unit** | **Description** | **Df** | **Estimates** | **AIC** | **δAIC** | **P** |
| **Log(WSS)** | 10 $Km.h^{-1}$ | Logarithm of Wind Speed Sum during exposure in a cardinal direction | 1 | -0.00371 | -2756.1 | 7.9 | 0.00178 |
| **HIS** | - | Hedgerow interception surface = Height * width * optical porosity | 1 | -0.00073 | -2699.1 | 64.816 | <0.0001 |
| **1/distance** | $m^{-1}$ | Inverse of the distance to the source (10,20,30,40,50 meters) | 1 | 0.52648 | -2733.1 | 30.795 | <0.0001 |
| **Side** | - | Side of the trap plant (source side or not-source side) | 1 | 0.01509 | -2758.2 | 5.747 | 0.00565 |

df = degrees of freedom, AIC = Akaike information criterion, δAIC = variation of AIC explained by the predictor, and P = p-value.


Hedgerow 4
Experiment A1
Experiment A2
Experiment A3
Experiment A5

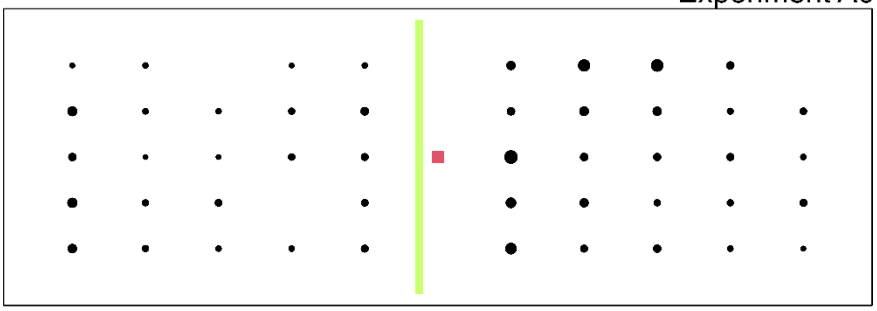
**Hedgerow 1**

Experiment A4



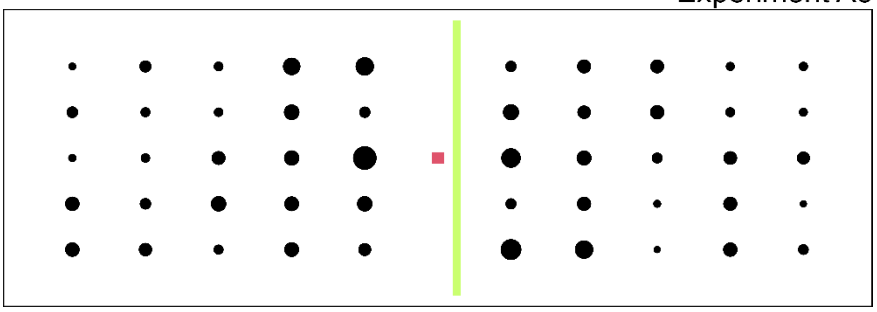


Experiment A6





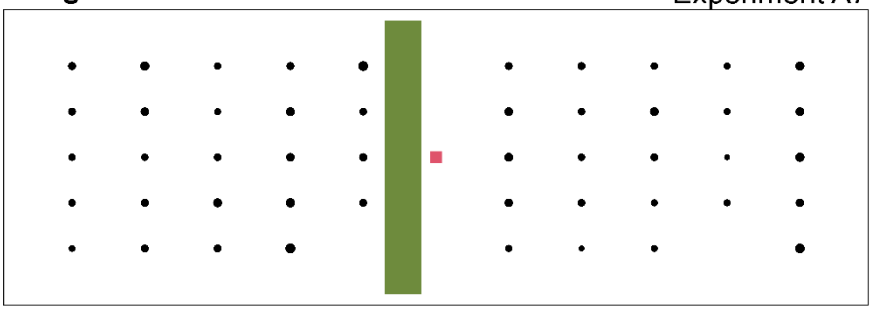
Experiment A8





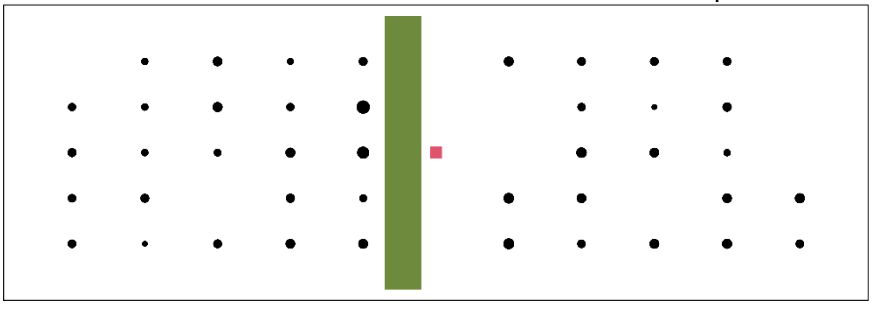
**Hedgerow 7**

Experiment A7





Experiment A9





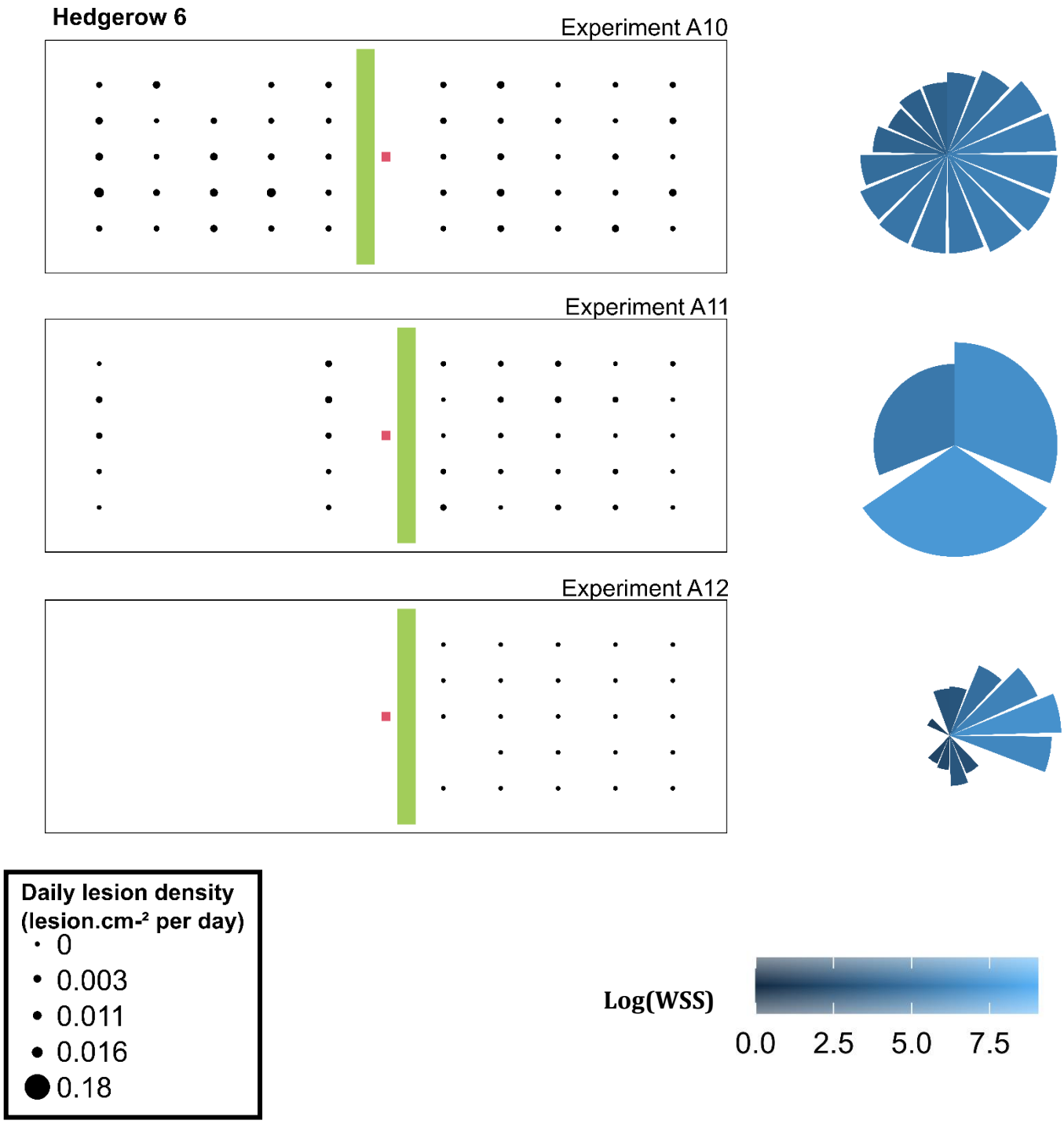



***Figure 4.3.*** *Lesion density by plant by day of exposure (lesion.cm$^{-2}$ per day) at 10, 20, 30, 40, 50 metres of an ascosporous source (red square) and a hedgerow (surface of green rectangle depend on the HIS (Hedgerow Interception Surface) and colour depend of the optical porosity) and wind frequencies (sum of wind forces (km.h$^{-1}$) by direction). Missing points correspond to no information (dead plant).*

With the model presented in Table 4.2, we predicted DD for the four hedgerow characteristics tested in ascospore experiments and in a case without hedgerow, and for two strengths of wind (light and strong). Lesion densities decreased with distance to the source and with the rise of HIS (Figure 4.5). The source side trap plants had higher average DD. Strong winds (corresponding to the maximum average wind in all experiments) led to lower contaminations than light wind (corresponding to the minimum average wind in all experiments). The highest regulation was observed with hedgerow 7 in light wind, which reduces approximately by 65 % lesion densities at 30 m distance to the source compared to the case without hedgerow.

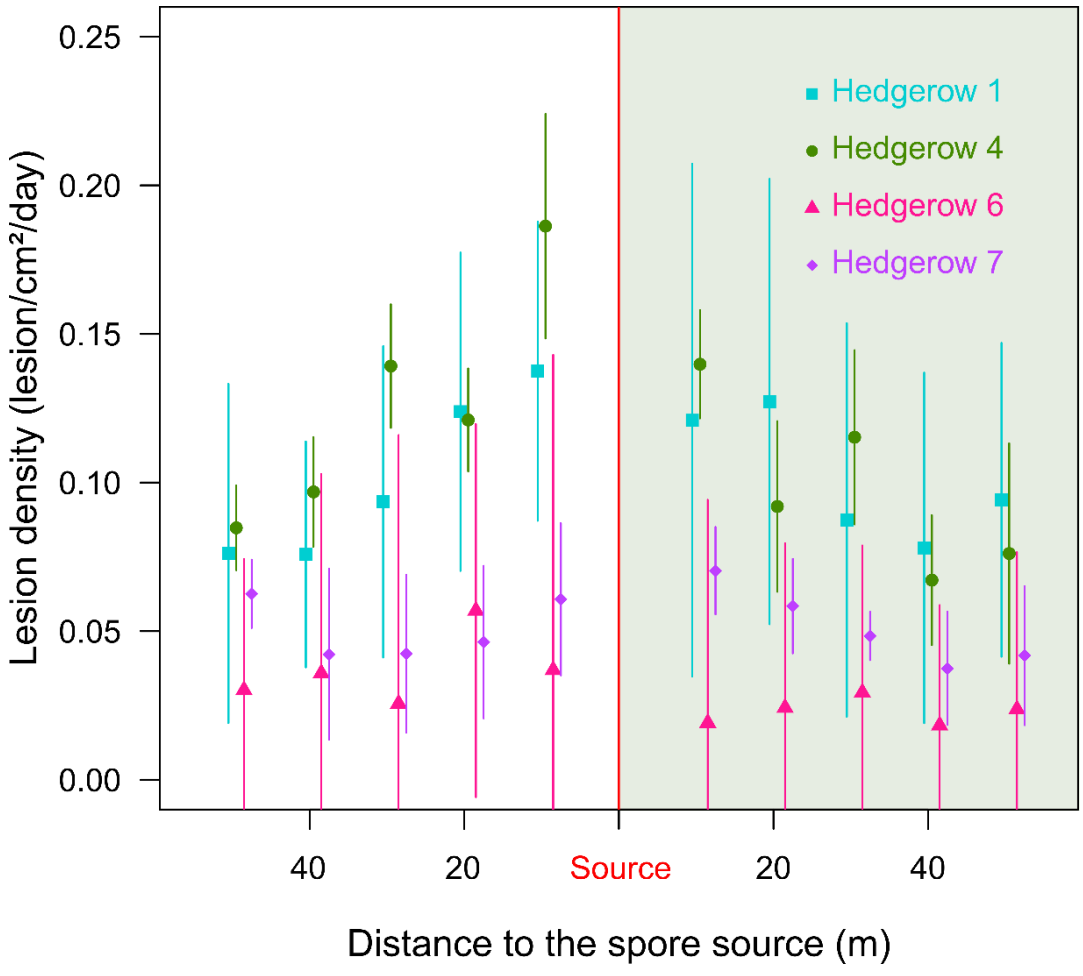



***Figure 4.4.*** *Mean and standard deviation of lesion densities (lesion.cm$^{-2}$ per day) observed in experiments with ascospore, in function of the distance (m) to the spore source and the side of the hedgerow (on the right, trap plants are separated from the source by the hedgerow).*

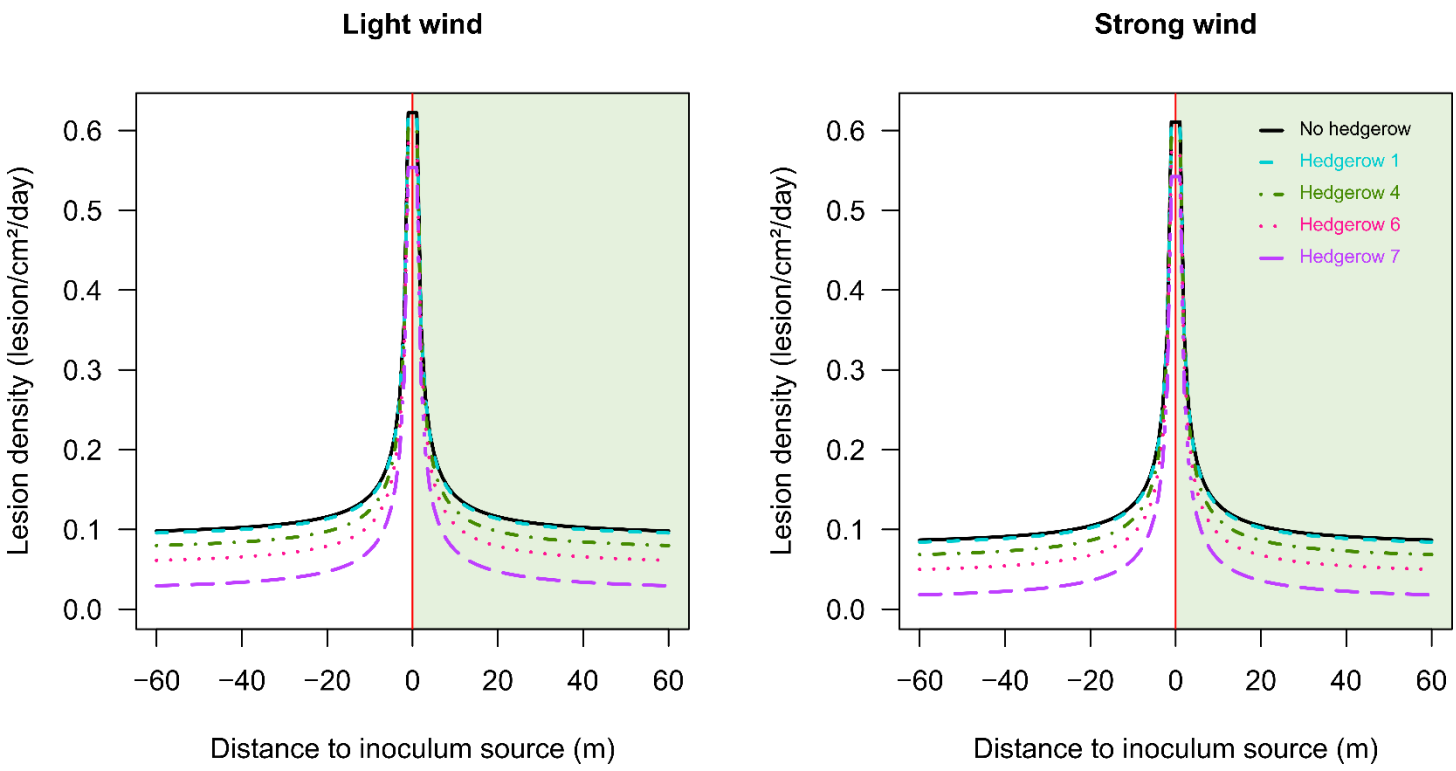



***Figure 4.5.*** *Modelling of daily lesion density on trap plant by distance from the ascosporous source and the side of the hedgerow (on the right, trap plants are separated from the source by the hedgerow), with five hedgerow types defined by their HIS (HIS (Hedgerow Interception Surface) = height * width * optic al porosity) for two wind forces (minimum average amount of wind from the source for a banana plant in an experiment (22.8 km.h$^{-1}$) and average amount of wind from the source for a banana plant in an experiment (53.2 km.h$^{-1}$)).*

*Effect of hedgerows on the dispersal of conidia*

In conidia experiments (Figure 4.6), we observed lesion densities ranging between 0 and 0.037 lesions.cm$^{-2}$.day$^{-1}$, according to the tested hedgerows. The effect of the hedgerow was the same on both side (P = 0.9041). DD did not decrease significantly with the distance between row at 3 m and row at 11 m of the source of spores (P = 0.9599) (Figure 4.7). DD was not significantly altered by the height of the hedgerow so we did not use HIS as a descriptor of the hedgerow but only the optical porosity which add a strong significance. After model selection, DD was significantly predicted by the optical porosity (linear regression P < 0.0001, estimate = -0.39747), the wind (log(WSS)) (P < 0.05,

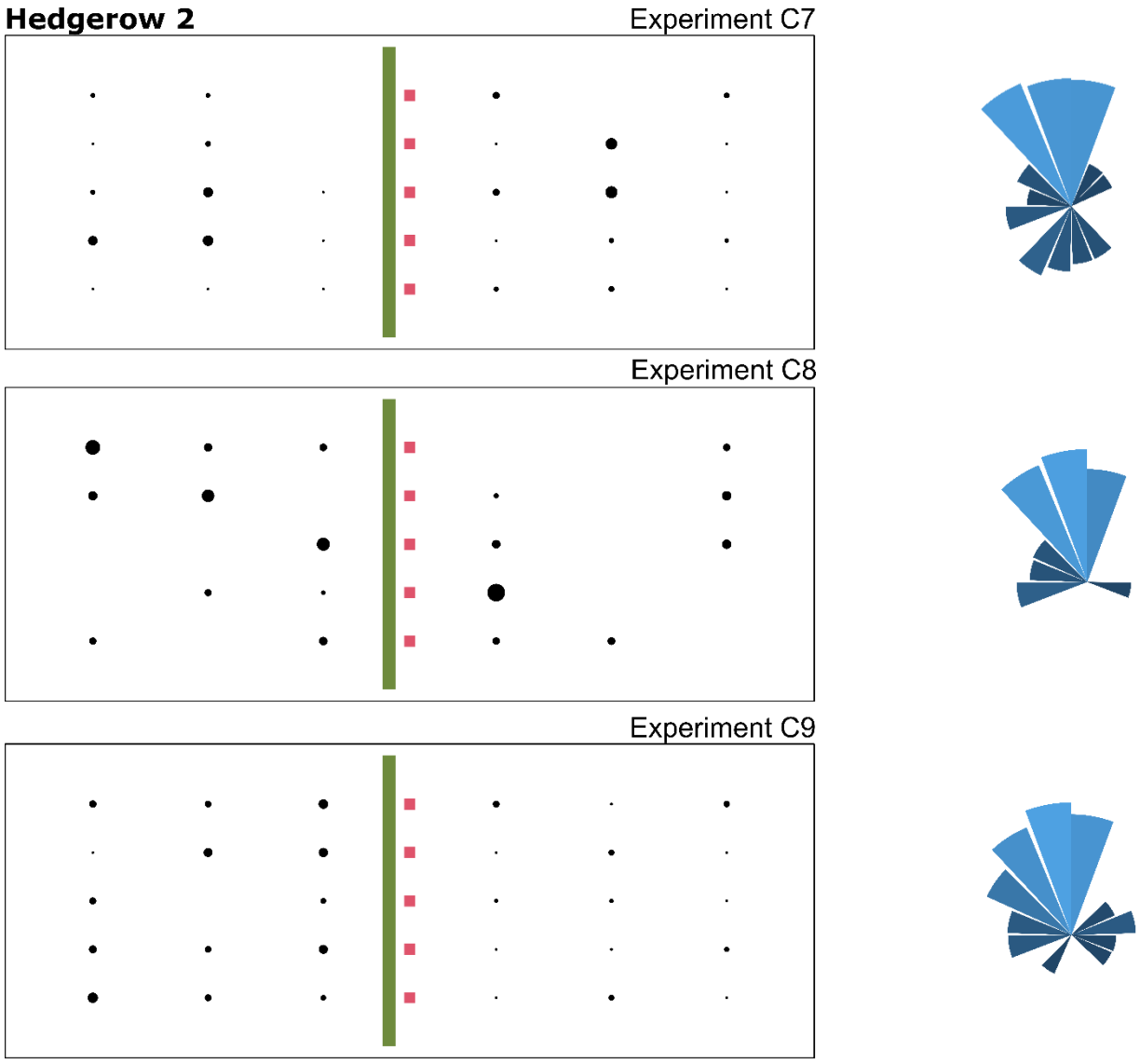
estimate = 0.03573), and their interaction (linear regression P < 0.05, estimate = -0.03844) (Table 4.3).

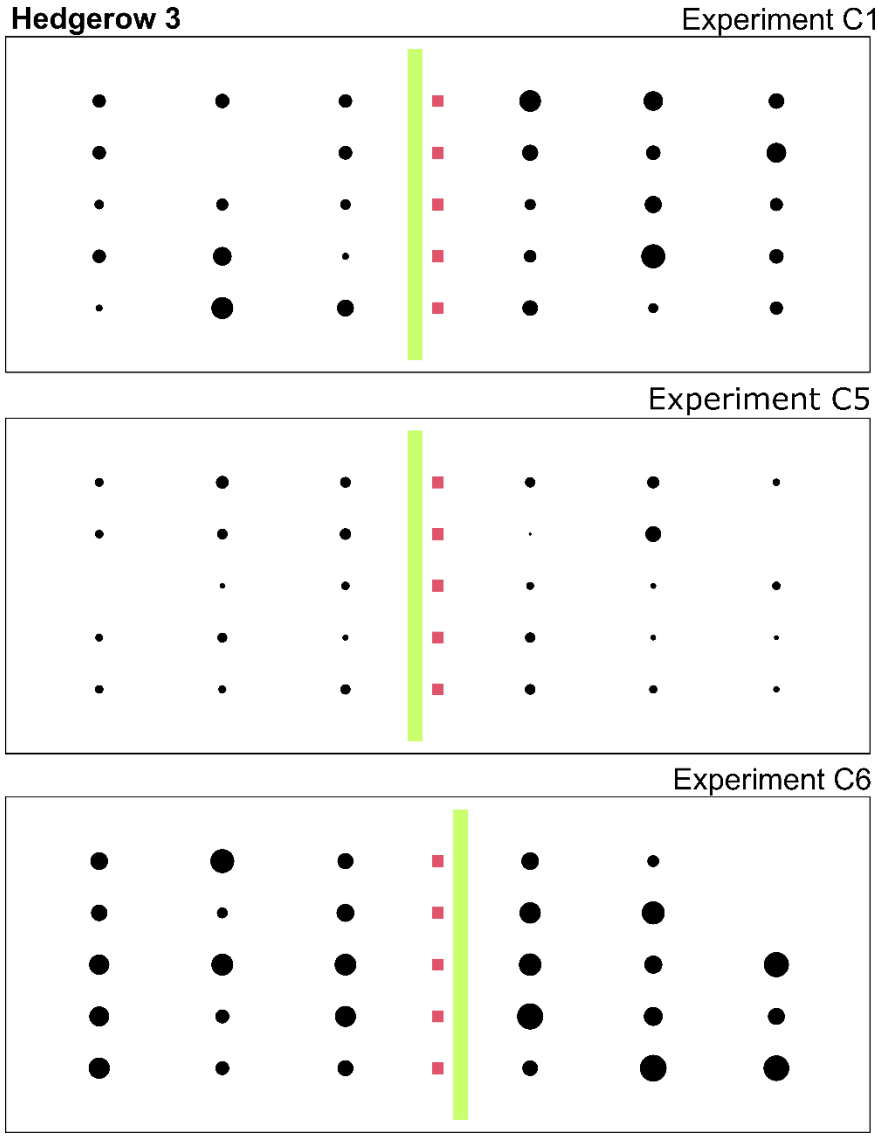
***Table 4.3.*** *Equation, description of the variables and results from the linear models of conidia lesion density.*

| **Equation** | $DD = \log(WSS) * porosity$ | | | | | | |
|---|---|---|---|---|---|---|---|
| **Variables** | **Unit** | **Description** | **Df** | **Estimates** | **AIC** | **δAIC** | **P** |
| **Log(WSS)** | 10 Km.h$^{-1}$ | Logarithm of Wind Speed Sum during exposure in a cardinal direction | 1 | 0.03573 | -1578.3 | 2.2 | 0.02749 |
| **Optical porosity** | - | Hedgerow optical porosity included between 0 (no hedgerow) and 1 (opaque hedgerow) | 1 | -0.39747 | -1516.0 | 137.2 | <0.0001 |
| **Log(WSS):Optical porosity** | - | Interaction between logarithm of Wind Speed Sum and Optical porosity | 1 | -0.03844 | -1578.7 | 2.5 | 0.03467 |

df the degrees of freedom, AIC the Akaike information criterion, δAIC the variation of AIC explained by the predictor, and P the p-value.

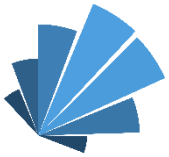
Our model predicted that hedgerows with high optical porosity (closed to 1, opaque) led to lower DD compared to hedgerows with low optical porosity (Figure 4.8). Interestingly, the interaction between the optical porosity of hedgerows and wind suggests that the hedgerow does not have the same effect with light wind or strong wind. A hedgerow with high porosity tends to increase DD while the wind increases, and inversely low porosity hedgerows tends to be more effective at reducing DD when the wind increases (Figure 4.8).


Hedgerow 2
Experiment C7
Experiment C8
Experiment C9


Hedgerow 3
Experiment C1
Experiment C5
Experiment C6







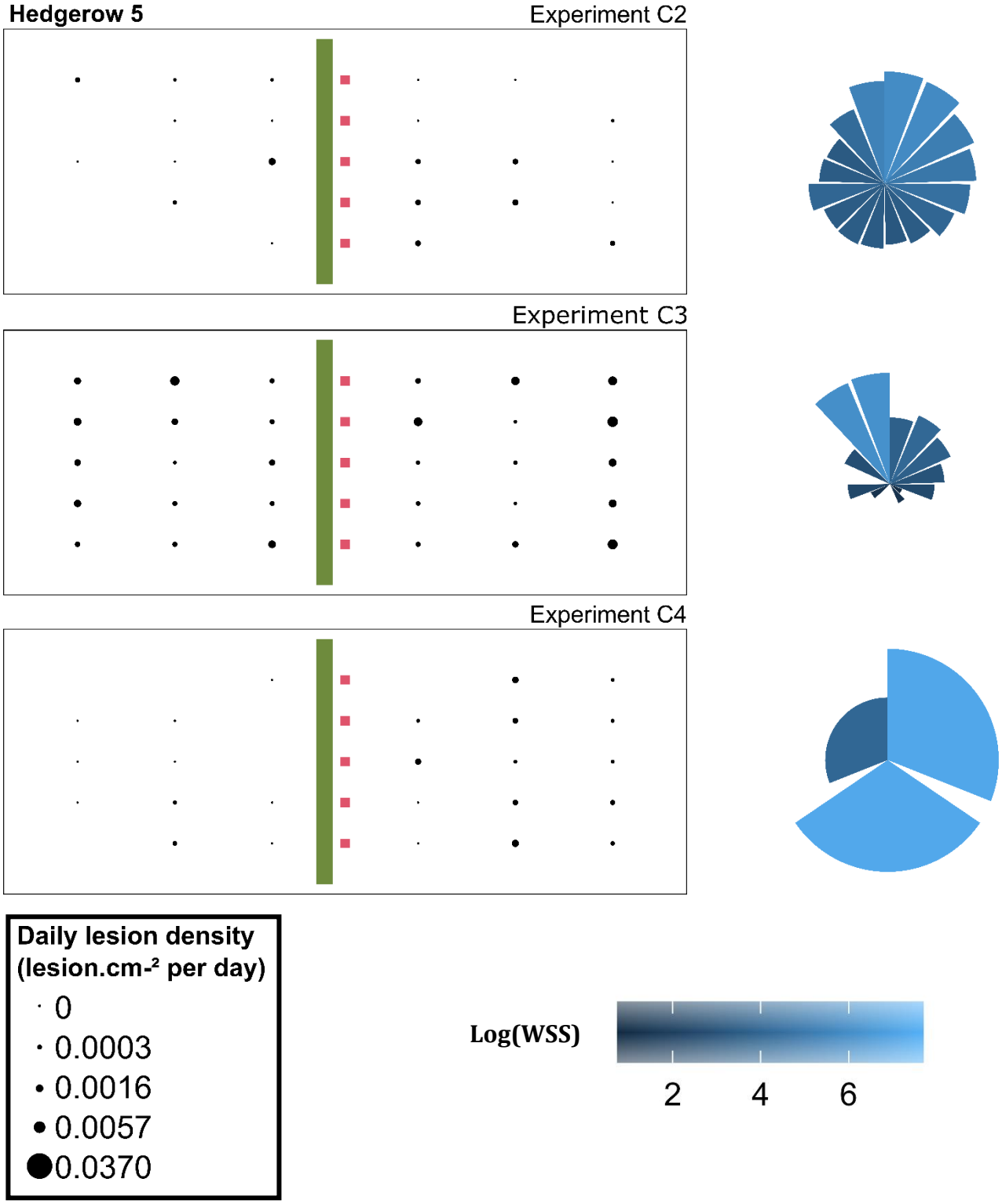



***Figure 4.6.*** *Lesion density by plant by day of exposure (lesion.cm$^{-2}$per day) at 3,7,11 metres of a line of conidia sources (red squares) and an hedgerow (surface of green rectangle depend on the HIS and colour depend of the optical porosity) and WSS (wind speed sum (km.h$^{-1}$) by direction).*

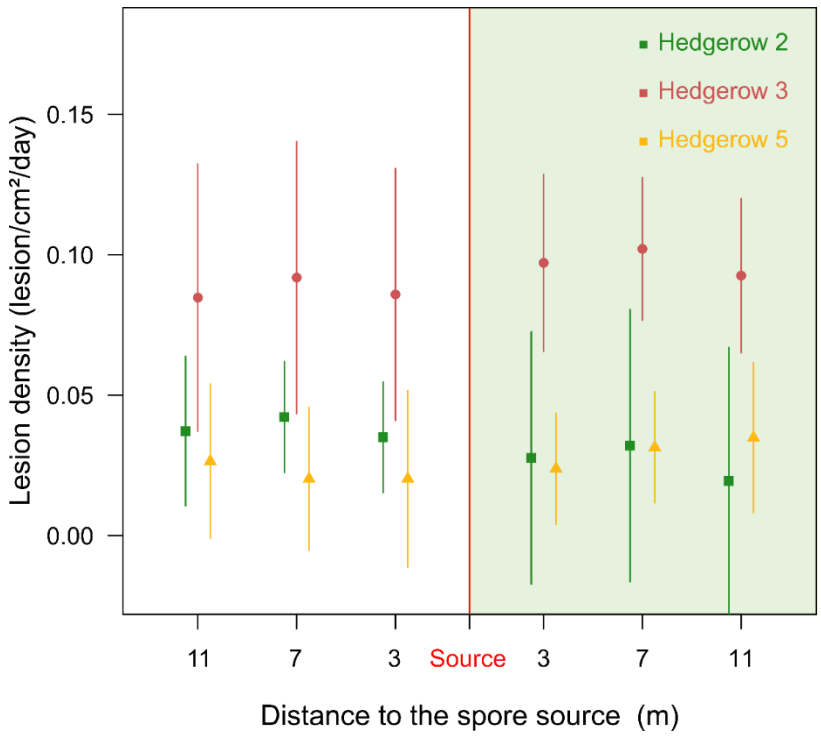



***Figure 4.7.*** *Mean and standard deviation of lesion densities (lesion/cm²/day) observed in experiments with conidia in function of the distance (m) to the spore source and the side of the source (on the right, trap plants are separated from the source by the hedgerow).*

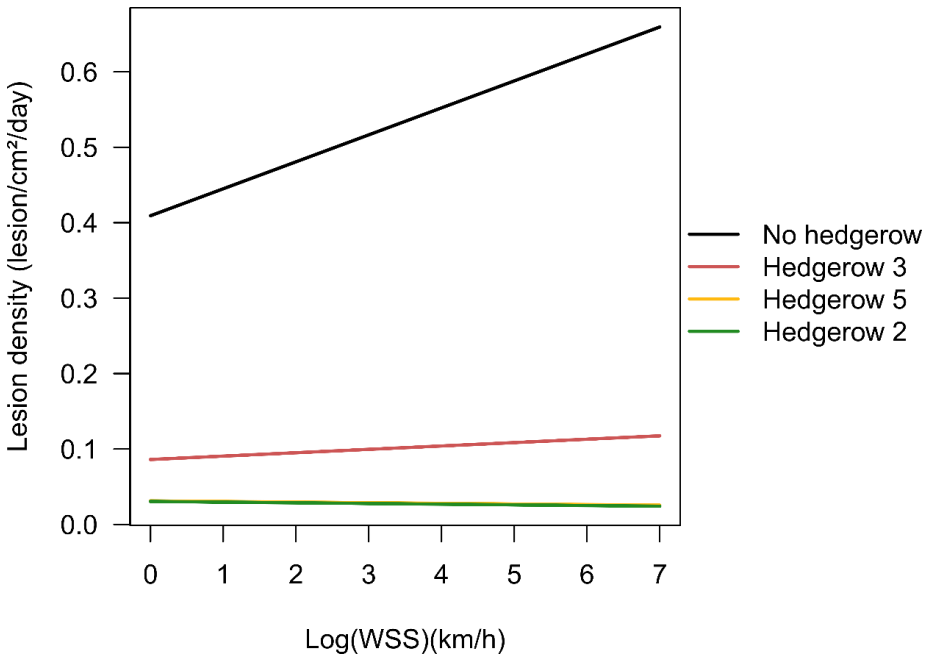



***Figure 4.8.*** *Modelling of Daily lesion density (lesion/cm²/day) on trap plant by logarithm WSS (Wind speed sum (km.h$^{-1}$)) on the three hedgerows of the experiments (Hedgerows 2, 3, 5 with optical porosities respectively 0.813, 0.951, 0.953) and a simulation of experiment with no hedgerow.*

## D. Discussion

Our experiments aimed at determining characteristics of the hedgerows that impact dispersion of ascospore and conidia of *P. fijiensis*. Our approach allowed us to study the impact of a gradient of hedgerows on the dispersion of both types of spore.

The analyse of the results allowed to determined that depending on the type of propagules (conidia or ascospore) the significant characteristics of the hedgerow were not the same. In both cases, hedgerow can be efficient to reduce lesion density of BLSD. With ascospore, we observed a significant difference between sides of the trap plant (source or not-source) that traduced a barrier effect of the hedgerow by intercepting a quantity of the spores. In conidia, we did not observe any unilateral effect but rather a global effect of the hedgerow on the density of lesion. To limit ascospore dispersion, height, width and optical porosity of the hedgerow were significant. Conidia dispersion were limited significantly only with optical porosity. The wind was significant for both of the propagules but impacted the barrier effect of the hedgerow differently because of their capacity and technic of dispersion. There are few studies in the literature on the impact of hedgerows on fungal disease dispersal. The height of the hedgerow can affect dispersion of pest that are wind dispersed (Tabilio et al. 1998), depending of the dispersion height of the pest. Our results in conidia dispersion showed that height of the hedgerow does not appear to be significant in the gradient of hedgerow tested (between 4.7 to 9.0 m). As conidia have a tendency of falling more than flying (on the contrary of ascospore) (Burt et al. 1997), hedgerow height could be efficient as soon as its higher than the source. For ascospore dispersion, the height, the width and the optical porosity were negatively correlated to density of lesion individually as well as combined in an indicator of hedgerow interception surface (HIS). The higher the HIS, the higher the surface of non-susceptible surface that participates intercepting spores (Schroth et al. 2000). Hedgerows are also impacting the aerology by acting like a windbreak and disrupting the airflow (Cleugh 1998). By acting like a wind-breaker and limiting wind strength, probably reducing the release of spores in the air. Hedgerows also change wind dynamics and thus spore pathway potentially protecting susceptible culture from contamination. As the wind release conidia, modifying its strength or its direction could impact the quantity of propagules in the air (Burt et al. 1997). The significance of the side of the hedgerow in the case of ascospore and not in the case of conidia could be explain by the importance of the

wind in the release of conidia (Burt et al. 1997). The wind influence, with conidia source, is affected by the porosity of the hedgerow: lesion densities increase with the wind in when the hedgerow has a low porosity and decrease when hedgerow is sparse. Strong winds allow to release more conidia than light wind with a thick hedgerow. Lowest lesion densities with strong wind in sparse hedgerow could be explain with the difficulty of landing of the spore. Ascospores are lighter and because of that the wind strength necessary for their release and flight will be lower. This difference of importance of the wind was already observed by aerology experiments of Burt (Burt et al. 1997). The main influence of hedgerow for reducing DD will be by intercepting the spores in the hedgerow, higher is the HIS, more ascospores can be caught. Therefore, hedgerow roles could be multiple for BLSD management: limiting external contamination by intercepting spores but also reducing auto-contamination by wind-breaking and changing aerology in the field. Dispersion dynamics observed in Rieux study were decreasing exponentially with the distance to the ascospore source, it was very low after 100 m. In our study, we observed this pattern with the hedgerows the less efficient (low HIS) (Figure 4.4, Hedgerow 1) but the lesion densities were lower and decreased more slowly with the distance on experiment with hedgerows with high HIS (Figure 4.4, hedgerow 7). For conidia, we did not see any impact of the distance to the source on the lesion density in the 11 m measured, as in Rieux *et al.* study.

Our spore sources have proved its efficiency in other studies (Rieux et al. 2014) as well in our experiment. The level of inoculum collected from trap plants varied between experiments at the same site. This was likely due to the amount of inoculum in the source, depending on where and when necrotic leaves were collected, and the weather during the experiment, as rain events caused spore release and UV radiation reduced spore capacity of infection (Parnell et al. 1998). Our maximum of lesion densities per day was in an ascospore experiment as in Rieux study (2014) and was around 0.18 lesion.cm$^{-2}$.day$^{-1}$ . Our method intended to be as closed as possible to a field situation. By using trap plants, we only measured infectious spores on the contrary with Burkard trap (Gaulh 1994) or Rotorod sampler (Uchôa et al. 2021) that cannot distinguish alive and dead spores affected by UV radiation (Parnell et al. 1998). Because there is no highly fungicide resistant strains of *P. fijiensis* in Martinique island, it was not possible to use this technique to trace its dispersal, unlike other studies such as Rieux (2014) which used sources with highly resistant to Quinone outside inhibitors fungicides. That is why to distinguish our

sources of spore from other sources implied locating our experiment more than 400 m away from any banana plant). Based on knowledge (Rieux et al. 2014) it was sufficient to limit contamination of other sources.

In future studies, it would be interesting to model how hedgerows disposition could improve BLSD regulation in a field in order to establish which hedgerow patterns are likely to best control BSLD. Such a modelling approach would certainly be useful to explore in different climate and field shape, how hedgerows surrounding banana field can protect from long distance dispersal from ascospore inoculum sources (Tabilio et al. 1998) and how tree lines between banana trees rows, as agroforestry systems (Norgrove and Hauser 2013; Poeydebat et al. 2018), can protect from field auto-contamination. We did not precise an hedgerow type in our study but as Poeydebat *et al* showed that plant richness in the strata 1-5m reduced fungal spore abundance of *P. fijiensis* (Poeydebat et al. 2018), we can suppose that multi-species hedgerows and thus multi-stratums hedgerows should also be more effective.

Our results suggest that hedgerows alter the dispersal of spores through different mechanisms, including air flows disturbance and spore trapping. It could be relevant to better understand how air flows are altered by hedgerow, for instance in the fields using a smoke to visualized these flows or even in controlled conditions as in wind tunnels. As a perspective in order to better understand the spore trapping effect of hedgerows, it might be possible to directly quantify captured spore by leaves of the tree of hedgerows thanks to highly sensitive techniques as digital PCR (Wen et al. 2020).

## E. Conclusion

In this work, we conducted two experiments in order to study how hedgerow alter dispersal of conidia and ascospore of *P. fijiensis*. With our experiments, we were able to determine which characteristics of hedgerow enhance their barrier effect depending of the propagules: height, width and optical porosity of the hedgerow reduce the propagation of ascospore and, optical porosity of the hedgerow decreases conidia propagation. We observed also that hedgerow barrier effect was a global effect and not unilateral effect. We measured wind impact on the two propagules dispersion as well.

These results can be used to develop new control strategies of BLSD and reduce fungicide treatments. However, experiments in field need to be done to measure effectiveness of hedgerow to determine the best arrangement of hedgerow in the field.

## F. Acknowledgements

We thank all the people who allowed us to do our experiments on their land: Mrs Mazaloubeaud from DENEL SA, Mr Lanes, Mr Camon, Mr Cartesse, Mr Vivies from RHUMS MARTINIQUAIS SAINT-JAMES SAS, Mr Bally, Mrs Depaz, Mr Napol, Mr Milome, and Mr Hayot. We also thank Emmanuel Husson from SICA-CERCOBAN for his help to find field experiment.

# CHAPITRE 5. Discussion générale et Conclusion



*Photo de Jérôme SAINTE-ROSE*

L'objectif de ce travail de thèse était d'acquérir des connaissances pour mieux raisonner la gestion d'une maladie fongique à dispersion aérienne à l'échelle du territoire, notamment dans le contexte de la gestion de la cercosporiose noire en Martinique. Les questions de recherche abordées ici impliquent de traiter de processus se déroulant à plusieurs échelles : de la parcelle, voire de la plante, jusqu'au territoire dans sa globalité. Dans la première partie, nous avons modélisé des données de vitesse d'évolution de la maladie pour pouvoir analyser leur variation avec la composition paysagère entre 200 et 1000 mètres autour de la parcelle. Pour comprendre les variations d'allo-inoculum en fonction des facteurs climatiques, nous avons mené des expérimentations à l'aide de plantes pièges disposées dans des sites loin de bananiers à plusieurs périodes de l'année. Enfin, nous avons étudié l'effet des haies en tant qu'élément paysager, pour *in fine* déterminer si elles peuvent être utilisées comme levier de gestion de la cercosporiose noire. Ces trois parties se complémentent pour répondre à la question globale de savoir comment organiser le paysage autour d'une exploitation ou d'une parcelle afin de réguler la maladie.

## A. L'étude de l'effet du paysage

L'étude de l'effet du paysage dans la partie 1 a permis d'acquérir des connaissances sur l'impact de la composition du paysage sur la dynamique de la maladie. La forêt, les zones de sources potentielles (présence de bananiers non traités) sont statistiquement présentes en plus grande quantité dans les zones où les niveaux de la maladie sont plus importants. Au contraire, la présence de bananiers traités, de cultures non hôtes et de haies, augmente là où la maladie se développe moins vite. Le mode d'action de chacun de ces éléments paysagers sur la dynamique de la maladie reste encore à préciser. Dans le cas des haies, ces mécanismes sont mieux connus grâce aux approches expérimentales menées dans ce travail (voir section B de ce chapitre). Dans le cas de l'effet de la composition paysagère à plus grande échelle, nous sommes contraints de formuler des hypothèses sur leurs effets. Ainsi, la composition du paysage peut i) influer sur le microclimat, par exemple la présence d'un nombre important d'arbres peut être à l'origine de modifications du microclimat, avec des conditions plus humides pouvant offrir de meilleures conditions au développement du champignon, ii) diminuer

l'abondance d'inoculum et créer des discontinuités entre les hôtes sensibles ce qui peut entraver les processus de dispersion du champignon, iii) modifier la pression de la maladie en augmentant la quantité d'actions prophylactiques sur la zone (en particulier fongicide). Les zones de bananiers traités contraignent la progression épidémique selon nos résultats, surtout quand leur surface dépasse 30% sur un buffer de 1 kilomètre. Cette observation dénote de ce qui est observé dans d'autres études traitant de la présence de spores à différents endroits au sein du paysage, qui sont en général en plus grande abondance dans les zones hôtes (Delaune et al. 2021; Grinn-Gofroń et al. 2020). Ce résultat s'explique probablement par l'effet de la régularité des pratiques de gestion dans les parcelles cultivées, diminuant ainsi l'abondance d'inoculum et tout particulièrement d'ascospores.

A part pour les haies, les variables de composition du paysage avaient un effet maximal pour des rayons de 1000 mètres autour des parcelles analysées. Ce rayon d'action correspond à ceux observés dans les études de la composition paysagère sur les pathogènes notamment pour la forêt et les zones hôtes (Delaune et al. 2021).

A la différence de nombreuses études d'écologie du paysage qui montrent un effet bénéfique de la proportion d'habitats semi-naturels sur la régulation des ravageurs par des ennemis naturels (Bianchi et al. 2006; Tscharntke et al. 2007), notre étude sur la régulation de la MRN montre que ce sont plutôt les processus influençant directement l'inoculum de la MRN qui sont en jeu et probablement beaucoup moins des mécanismes médiés par d'autres communautés. L'effet du paysage sur des communautés régulatrices, comme par exemple sur le phyllobiome, n'est pas à exclure mais cela reste extrêmement peu étudié. Ainsi, la notion de 'microbial landscape' reste en émergence (Khatri et al. 2023).

Ces connaissances sont nouvelles pour la communauté scientifique et technique, et pourraient à l'avenir servir dans le développement d'outils pour la gestion de la cercosporiose noire. La prise en compte de ces données permet de réfléchir à l'aménagement du territoire et d'avoir une stratégie de gestion de la maladie longue durée grâce aux éléments paysagers. A l'exception des haies qui peuvent facilement être implantées, la composition paysagère est beaucoup plus difficilement modifiable par un seul acteur. En revanche, ces informations peuvent être utilisées pour réfléchir à des gestions territoriales multi-acteurs et être implémentées dans des outils d'aide à la

décision pour la mise en place de la gestion à l'échelle du territoire. La composition paysagère résulte largement des politiques de gestion et d'aménagement du territoire. En Martinique, compte-tenu de l'intrication de l'activité agricole au milieu des espaces naturels, d'habitation, et des autres activités économiques, intégrer la question de la régulation de la MRN dans la gestion du territoire reste un objectif complexe qui nécessite de considérer de nombreuses autres contraintes, e.g. place des habitats dans le paysage, jardins de particulier contenant des bananiers, culture du plantain. Nos résultats soulignent l'importance des surfaces de bananiers traités pour la régulation de la MRN et, à l'opposé, l'influence des bananiers non traités sur l'épidémie de la maladie : cela suggère que i) une meilleure gestion des plantes hôtes et ii) une coordination dans la mise en œuvre des pratiques de gestion, devraient être des leviers à mieux mobiliser dans le futur. Par exemple, il pourrait être possible de former des responsables de zones pour la mise en œuvre des pratiques prophylactiques sur les bananiers (en tout premier lieu l'effeuillage), cela pourrait concerner les producteurs de bananiers plantains, voire les particuliers pouvant avoir des bananiers dans leurs jardins. Enfin, nos résultats sur l'effet de la composition paysagère devraient inciter les producteurs de bananes à mieux se concerter dans la mise en œuvre des pratiques de gestion. Nous pouvons supposer que si des producteurs ont des pratiques insuffisantes de gestion de la maladie, ils pourraient être responsables de la production d'une partie importante de l'inoculum.

Cette réflexion sur la mise en œuvre des pratiques à l'échelle du territoire était au cœur du projet Banamosaic (projet dont cette thèse fait partie) qui avait pour objectif la détermination de nouveaux leviers territoriaux de gestion des bioagresseurs du bananier en Martinique. Dans le cadre de ce projet, deux bassins pilotes ont été sélectionnés, composés de bananeraies de petites surfaces et de paysages contrastés d'une zone à l'autre. Après des entretiens individuels avec les agriculteurs pour comprendre leurs pratiques et leurs problématiques, nous avons mené des ateliers de co-conception pour réfléchir à la mise en place de leviers de gestion collective et territoriale de la cercosporiose noire. La gestion territoriale aurait pour objectif de créer de larges zones produisant le minimum d'inoculum, mais la fragilité et la demande régulière d'entretien du matériel de traitement handicapent le partage et le traitement collectif sur plusieurs exploitations. L'utilisation d'autres leviers de gestion telle que la mise en place de haies pourraient permettre d'améliorer la gestion de la maladie.

Les connaissances développées lors de ce travail pourront être prises en compte dans de futures études sur la gestion agroécologique de la cercosporiose et dans le développement d'outils pour la mise en place de leviers de gestion de la maladie à l'échelle du territoire.

## B. Les haies et la gestion agroécologique de la cercosporiose

La première partie de cette thèse sur la modélisation de l'effet de la composition paysagère a permis de mettre en lumière que la présence de haies autour d'une parcelle (dans un rayon de 200 mètres) diminuait les niveaux de maladie. Son effet courte distance suggère différents impacts sur la maladie et le pathogène : i) le ralentissement des épidémies par un effet microclimatique ou ii) une diminution de la dispersion du pathogène (effet barrière / d'interception). Lors de nos essais (Chapitre 4), nous avons étudié comment les haies influencent la dispersion de *P. fijiensis*. Pour cela 7 haies ayant des caractéristiques contrastées ont été sélectionnées. Un dispositif expérimental a été mis en place avec une source de spores d'un côté de chaque haie et de plantes pièges des deux côtés. Nous avons choisi des haies dans des lieux à minimum 400 mètres de distance de tous bananiers pour éviter les contaminations par une autre source. Cependant, lors de nos travaux pour mesurer l'allo-inoculum, nous avons vu que nous pouvions détecter des spores même à plus de 300 mètres des bananiers. Bien que nos mesures de densité de lésions aient pu être influencées par de l'allo-inoculum, les niveaux mesurés lors de nos essais sur les haies sont en moyenne deux fois plus élevés que ceux mesurés en moyenne sur les essais sur l'allo-inoculum. Pour chaque essai, les densités de lésions ont été mesurées sur les plantes pièges placées de chaque côté de la haie (sur une distance de 50 m et 11 m, respectivement pour les ascospores et les conidies). Nous avons utilisé des sources constituées de feuilles de bananiers recueillies dans des bananeraies abandonnées. Au cours de l'année et des saisons, la quantité de spores sur les feuilles récoltées a pu évoluer et le potentiel de sporulation des sources a pu changer entre les essais. Les densités de lésions mesurées entre les essais ont pu être impactées par la variabilité des quantités de spores produites et libérées entre les sources. Le nombre d'évènements pluvieux durant l'exposition des plantes a pu faire varier la quantité d'ascospores libérées (Meredith et al. 1973). Les rayonnements UV ont également pu impacter la capacité d'infection des spores en inhibant la germination des spores (Parnell

et al. 1998). Toutefois, il est important de noter que la densité de lésions mesurées sur les plantes pièges variaient en fonction des caractéristiques de la haie. Pour les conidies (spores à dispersion courte distance), la diminution des quantités d'inoculum piégé a été identique des deux côtés de la haie (côté exposé directement à la source et côté protégé par la haie) et dépendante des caractéristiques de la haie. En ce qui concerne les ascospores (spores à dispersion longue distance), les haies ont eu un effet barrière en diminuant plus fortement l'inoculum mesuré sur les plantes pièges protégées par la haie que celles exposées directement à la source. La haie a donc pu agir de deux manières : i) en interceptant les spores ou ii) en déviant leur trajectoire en modifiant l'aérologie autour de la haie (Dupont et al. 2022). L'effet de la haie dépend des caractéristiques de cette dernière pour les deux types de spores. Les plantes pièges ont l'avantage de ne détecter que les spores vivantes pour obtenir un résultat cohérent par rapport aux processus épidémiques, sans compter les spores mortes.

Bien que n'ayant pas travaillé sur des espèces d'arbres spécifiques, nos expérimentations ont été menées sur des haies indigènes de la Martinique, permettant ainsi de mettre en avant des leviers de gestion grâce à des arbres locaux et adaptés au contexte de production en Martinique. Dans les essais avec des sources d'ascospores, les densités de lésions mesurées ont été négativement corrélées avec la hauteur, la largeur et la porosité de la haie, tandis que les densités de lésions mesurées dans les essais avec une source de conidies ont seulement été négativement corrélées avec la porosité de la haie. Dans cette analyse, nous avons pris en compte certaines caractéristiques de la haie pour évaluer son efficacité mais à l'avenir, les traits et les fonctions de la haie sur l'abondance d'inoculum et la durée d'incubation et de latence pourront être étudiés spécifiquement de la même manière que sont abordés les services écosystémiques rendus par les couverts végétaux par exemple (Damour et al. 2014;  Violle et al. 2007). Les traits peuvent concerner des caractéristiques générales de la haie ainsi que des caractéristiques très spécifiques des espèces d'arbres présents (e.g. la pilosité des feuilles) (DELMOTTE 2020) (Figure 5.1, carré orange). Ces traits peuvent influencer l'efficacité de la haie mais aussi conditionner leur mode d'action (Figure 5.1, carré bleu) sur la réduction de la pression de la maladie.

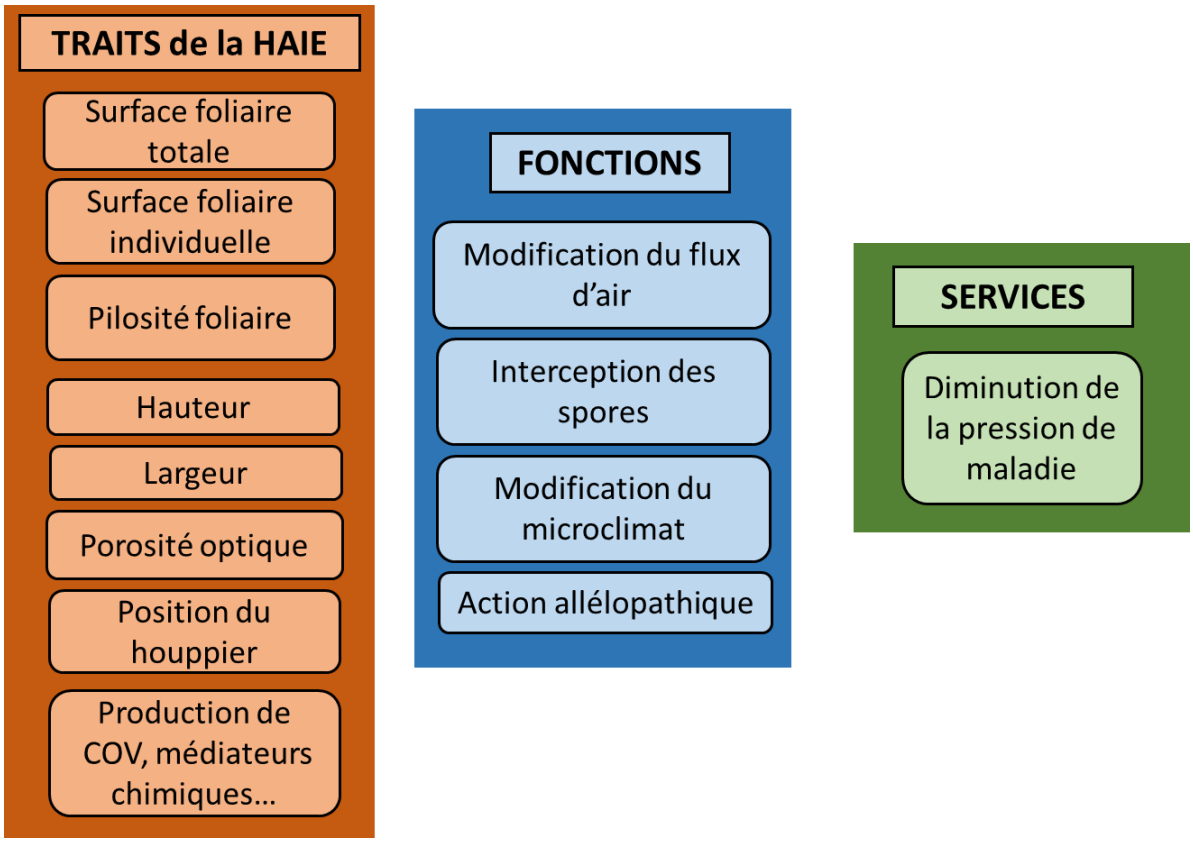



***Figure 5.1.*** *Schéma des traits fonctionnels de la haie sur la diminution de la pression de maladie fongique.*

L'emplacement et le type de haies dans un agrosystème bananier pour optimiser la régulation de la cercosporiose noire, dépendra du type de contamination que l'on veut éviter. Pour éviter les contaminations externes, les types de haies qui seront le plus efficace sont les haies hautes et opaques qu'il faudrait disposer à l'extérieur de l'exploitation, perpendiculairement au vent principal et/ou en séparation des autres exploitations alentour (Figure 5.2, parcelle rouge = contamination externe). Dans le cas d'un effeuillage bien fait, les sources d'ascospores seront éradiquées de l'exploitation, les conidies composeront majoritairement l'auto-inoculum. Nos résultats suggèrent que pour limiter cette contamination, il serait possible d'installer des haies en remplacement de rangs de bananiers. La question de la densité de ces haies au sein des parcelles reste à définir par de futures expérimentations pour avoir une régulation optimale de l'abondance des spores (Figure 5.2). Ce type de haie n'a pas les mêmes exigences que les haies contre la dispersion des spores, la hauteur des haies n'a pas été significative sur les densités de lésions mesurées mais leur opacité s'est montrée essentielle pour avoir une bonne efficacité.

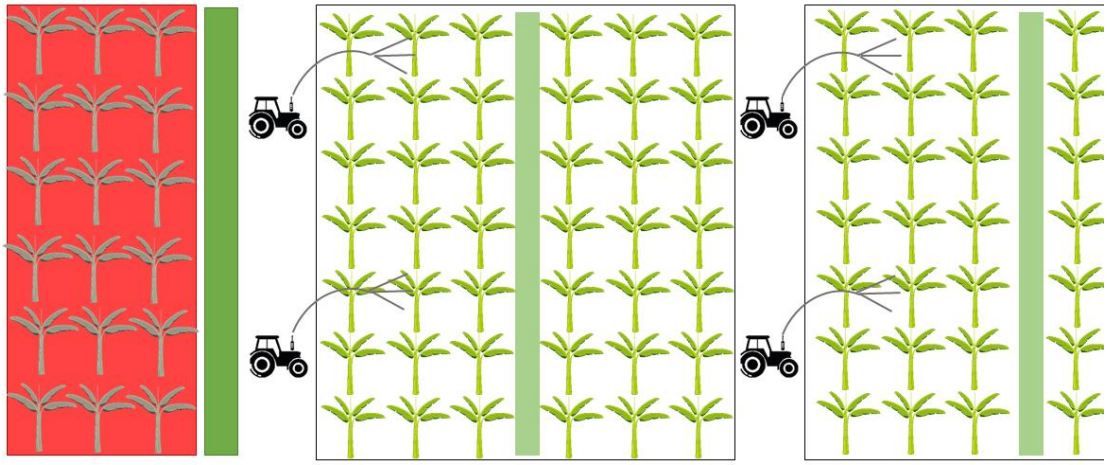


***Figure 5.2.*** *Exemple d'un design d'intégration de haies au sein d'une exploitation bananière de Martinique.*

Bien que les haies diminuent la quantité de spores, elles ne peuvent pas remplacer un traitement antifongique. Elles s'inscrivent comme un levier intéressant dans une stratégie agroécologique de gestion de la MRN. Les haies doivent donc être placées à des endroits compatible au niveau technique (e.g. permettant aux engins agricoles de passer sans diminuer leur efficacité de traitement) (Figure 5.2). La distance entre les haies dans la parcelle reste à vérifier dans de futures études et expérimentations au champ. Au vu de nos résultats sur les conidies, les quantités de spores ne variaient pas en fonction de la distance à la source sur les 11 mètres de mesure, la haie avait une efficacité constante sur cette distance. Avec les ascospores, les quantités de spores mesurées décroissaient avec la distance mais son pic d'efficacité semblait apparaitre autour de 30 mètres. Dans les futurs essais, les distances étudiées entre les haies pourraient donc se situer entre 11 et 30 mètres. Les haies demandent également de l'entretien : en fonction du type de haie mis en place et de ses caractéristiques, les services et les coûts économiques et humains associés ne seront pas les mêmes. Les bénéfices en plus de la régulation de la cercosporiose peuvent être une production fruitière, une production de biomasse, une protection face au vent et à l'érosion.

L'emplacement des haies doit aussi être en corrélation avec l'environnement et le climat de la parcelle. Les variables climatiques sont une composante importante des différentes phases du cycle épidémique ; par exemple, le design des haies ne doit pas engendrer une augmentation de l'humidité de la parcelle. Ainsi, nous pouvons faire l'hypothèse que les

endroits avec peu de vent et/ou très humides seront moins favorables pour l'installation de haies. En revanche, les endroits fortement exposés au vent semblent favorables à l'installation de haies à la fois pour l'interception des spores et pour leur effet brise-vent (sachant que les bananiers sont sensibles aux fortes bourrasques qui déchirent leurs feuilles).

Ces travaux sont pionniers dans l'étude de l'effet des haies pour réguler la cercosporiose noire. D'autres expérimentations pourront succéder pour l'évaluation de cet effet. Par exemple, l'évaluation d'agrosystèmes bananiers avec des haies à différents espacements entre les rangs pourraient être conduite grâce à des plantes pièges réparties au sein de la parcelle pour comprendre comment la dynamique spatiale des spores est affectée. Les perturbations aérologiques provoquées et la capacité d'interception des spores par les haies seraient également des pistes intéressantes à investiguer. Afin de pouvoir fournir des recommandations en termes d'espèces à associer, il pourrait être possible de mieux établir la relation entre les traits des arbres composant les haies et les mécanismes de modification des flux d'air et d'interception des spores. Dans les études de dérive de pesticides et de pollution, il a été observé une réduction des particules en présence de haies notamment des haies larges (Blanuša et al. 2020; Heshani and Winijkul 2022; Langenbach et al. 2022).

En ce qui concerne les processus aérologiques, comme étudié dans l'expérimentation de Dupont (2022), il pourrait être possible de mesurer la perturbation du vent (force, orientation…) en fonction de la densité d'arbres dans la haie. Plusieurs expériences montrent que les haies peuvent modifier le flux d'air, ce qui réduit la quantité de particules (Heshani and Winijkul 2022) et pourrait impacter la répartition des spores dans la canopée de la même manière (Ma et al. 2019). Pour mieux comprendre la capacité d'interception des spores, il pourrait être intéressant de mobiliser des approches de modélisation comme cela a pu être fait dans la simulation de Ma (2019) ou en utilisant des approches avec des marqueurs ainsi que des approches de biologie moléculaire afin de quantifier directement l'ADN des spores (probablement possible avec des approches très sensibles telles que les méthodes de PCR digital (Hindson et al. 2011)).

Enfin, un travail d'intégration des données d'effet du paysage, de dispersion longue distance et d'effet des haies pourrait être développé. L'objectif appliqué d'une telle intégration serait d'établir les bases d'une gestion agroécologique de la MRN en fonction

du contexte paysager, climatique et des niveaux d'allo-inoculum. Cela pourrait se faire avec des approches de modélisation mécanistes, comme par exemple avec un modèle qui intègre les variable biotiques, abiotiques et d'habitats pour constituer une carte de risques des ravageurs à l'échelle des régions (Lacasella et al. 2017). Même si cela semble possible et scientifiquement très intéressant, la dimension assez stochastique des processus de dispersion rend la prédiction des flux de spores à l'échelle d'un territoire hasardeuse, surtout pour obtenir une résolution fine à la parcelle (Zamberletti et al. 2022). Une approche de modélisation de type statistique ou semi-qualitative pourrait permettre de représenter les effets de l'ensemble des variables d'intérêt de manière parcimonieuse. De la même manière que dans les calculs de risques d'exposition aux pesticides (Tixier et al. 2008), la création d'un indicateur de risques d'exposition à la cercosporiose permettrait de prendre en compte les différents facteurs influençant le développement de la maladie sans une prédiction trop fine qui s'avèrerait fausse.

## C. L'effet des facteurs météorologiques sur l'allo-inoculum

La méthode utilisée pour mesurer l'allo-inoculum sur différents lieux de la Martinique nous a permis de prendre en compte uniquement les spores vivantes. Comparée à d'autres méthodes de quantification de spores (pièges à spores comme Burkard), cette approche permet uniquement de quantifier les spores pouvant infecter une plante hôte et donc d'avoir une meilleure évaluation du risque de la maladie. Entre 2020 et 2021, nous avons mesuré cet inoculum durant une année complète.

La même dynamique de densités de lésions est observée entre les sites de mesure, avec les deux mêmes pics en novembre 2020 et juin 2021. La production d'allo-inoculum semble dépendre majoritairement d'effets globaux, climatiques, par rapport à des effets locaux, de paysage. L'analyse de ses données nous a permis de mieux comprendre les facteurs climatiques qui déclenchent et influencent la présence d'allo-inoculum de *P. fijiensis*. Les facteurs météorologiques sont pour de nombreux pathogènes, les facteurs qui influencent le plus significativement leur abondance (Courson et al. 2022). Les effets météorologiques ont montré un effet plus fort que la composition du paysage sur les spores fongiques en suspension dans l'air dans d'autres études (Crandall and Gilbert

2017) et la co-évolution des 6 sites tend à montrer que c'est également le cas sur MRN. La dispersion longue distance est un aspect essentiel dans l'épidémiologie du champignon (Rieux et al. 2014). Comprendre ses dynamiques et les facteurs qui l'impactent permet à la fois de développer les connaissances sur la biologie du champignon et de déterminer des zones et des jours à risque. Ces données peuvent être utilisées dans des modélisations épidémiologiques pour prendre en compte les quantités d'allo-inoculum et pour améliorer les prédictions des outils d'aide à la décision pour les traitements.

Dans le cadre d'autres travaux de recherche en collaboration avec Anne Legrève (professeure à UC Louvain), nous avons effectué des captures de spores en altitude (10, 100, 500 mètres) grâce à un drone et un hydro-ULM, pour évaluer la présence de spores à haute altitude et des processus de dispersion à très longue distance dans des courants aériens rapides. Une détection de spores a été faite à 500 mètres avec l'hydro-ULM, ce qui signifie que leur capacité de dispersion en hauteur leur permettrait de parcourir de très longues distances et peut être de se disperser d'île en île. Capturer des spores avec ces méthodes ne permettrait pas de confirmer que les spores sont vivantes mais permettrait de mesurer d'éventuels gradients verticaux et d'explorer le rôle de cette dispersion verticale dans les processus épidémiques.

## D. Conclusion

Ce travail de thèse a permis d'approfondir les connaissances à la fois sur l'influence du paysage et des variables climatiques sur la dynamique de la cercosporiose noire du bananier en Martinique, ainsi que sur l'impact des variables météorologiques sur la production d'allo-inoculum et l'impact des haies sur la dispersion des spores de *Pseudocercospora fijiensis*. La présence d'allo-inoculum est principalement dépendante de la pluie, la température et le rayonnement UV (Figure 5.3). En ce qui concerne le paysage, la forêt et les bananiers non traités favorisent le développement de la maladie, à l'inverse des bananiers traités, des cultures non hôtes et des haies qui le contraignent. Nous avons mesuré l'effet des haies sur la capacité de dispersion des conidies et des ascospores de *P. fijiensis*. La réduction de dispersion des ascospores dépend de la hauteur, largeur et porosité optique des haies. Pour les conidies, c'est essentiellement la porosité optique des

haies qui réduit leur dispersion. Ces travaux ouvrent un champ très divers de recherche et de développement de techniques de lutte à l'échelle territoriale.

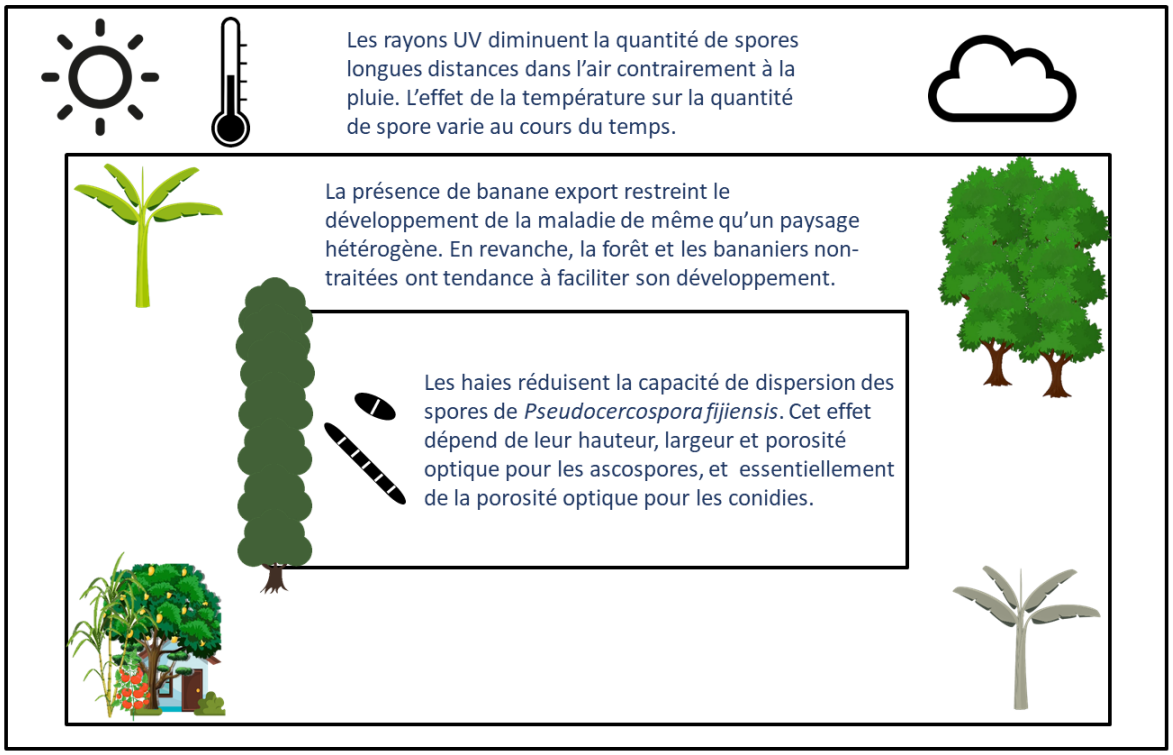



***Figure 5.3.*** *Schéma des conclusions de la thèse*

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**Résumé :** Cette thèse vise à comprendre l'impact du paysage sur les dynamiques épidémiques de la *Pseudocercospora fijiensis*, provoquant la cercosporiose noire du bananier ou maladie des raies noires (MRN), pour *in fine* optimiser sa gestion. Ce travail repose sur une approche intégrative de l'épidémiologie de cette maladie qui prend en compte les facteurs météorologiques, les pratiques culturales, et les effets de la structure paysagère. Afin de comprendre les déterminants de la dynamique de la maladie à l'échelle de la parcelle, une analyse par modèle dynamique a été menée sur les données d'état d'évolution (EE) de la MRN en Martinique. Le modèle développé a permis une quantification fine de la dynamique temporelle, l'effet des applications de fongicides et du climat (évaporation Piche) sur l'EE, et les résidus du modèle ont été utilisés comme évaluateur de l'effet du paysage sur la dynamique de la maladie (forêts, haies, zones hôtes traitées, zones de potentielles sources, zones non-hôtes). Ensuite, afin de mieux comprendre comment les haies influencent la dispersion de *P. fijiensis*, nous avons réalisé des essais expérimentaux sur 7 haies avec les deux types de spores du champignon, conidie et ascospore. Les résultats montrent que pour les sources d'ascospores, la nature de la haie définie par sa surface d'interception (combinaison de la hauteur, la largeur et la porosité optique de la haie) influence négativement la dispersion de *P. fijiensis*. Dans le cas des sources de conidies, seule sa porosité optique a influencé la densité de lésions. Un autre facteur-clé dans l'épidémiologie est la capacité de dispersion longue distance. Afin de l'évaluer, nous avons mesuré la quantité de spores dans l'air 10 fois sur l'année 2021 à l'aide de plantes pièges et avons comparé nos résultats aux variables climatiques (pluie, température, UV, évaporation Piche). Les variables climatiques influencent significativement la quantité de spores mesurée dans les jours précédents l'exposition. Ces résultats ont permis d'acquérir de nouvelles connaissances sur *Pseudocercospora fijiensis* et sa dispersion, notamment sur l'impact des différentes composantes du paysage, ce qui permettra de mobiliser de nouveaux leviers pour la gestion agroécologique de la MRN à l'échelle territoriale.

**Summary:** This PhD aims to understand the impact of the landscape on the epidemic dynamics of *Pseudocercospora fijiensis*, which causes banana black leaf streak disease (BLSD), in order to optimise its management. This work is based on an integrative approach to the epidemiology of BLSD that takes into account meteorological factors, cultural practices and the effects of landscape. In order to understand the causes of the disease dynamics at the plot scale, a dynamic model analysis was conducted on a database of the stage evolution of the disease (SED) in Martinique. The model allowed a precise quantification of the temporal dynamics, the effect of fungicide applications, and the effect of weather (Piche evaporation) on the SED and the model residuals were used as an estimator of the effect of the landscape on the disease dynamics (forests, hedgerows, treated host areas, potential source areas, non-host areas). Then, in order to better understand how hedgerows influence the dispersal of *P. fijiensis*, we performed experimentations on 7 hedgerows with both types of spores, conidia and ascospora. The results showed that for ascospora sources, the nature of the hedgerow defined by its interception surface (combination of height, width and optical porosity of the hedge) negatively influences the dispersal of *P. fijiensis*. In the case of conidia sources, only its optical porosity influenced lesion density. Another key factor in the epidemiology is the long distance dispersal capacity. In order to evaluate this, we measured the amount of spores in the air during the year 2021 using trap plants and compared our results to weather variables (rain, temperature, UV, Piche evaporation). The weather variables significantly influence the amount of spores measured in the days before exposure. These results have enabled us to acquire new knowledge on *Pseudocercospora fijiensis* and its dispersal, particularly on the impact of various landscape components, in order to mobilise new levers for the agroecological management of BLSD at the territorial scale.