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A foliar disease simulation model to assist the design of new control methods against black leaf streak disease of banana

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ABSTRACT

Black leaf streak disease (BLSD), caused by the fungal pathogen *Mycosphaerella fijiensis*, is considered as the most destructive foliar disease of banana. To advance our knowledge of the dynamics of the disease at plant scale as well as of the components of varietal resistance, we designed, calibrated and evaluated a mechanistic model to simulate the disease on a banana plant. The model runs in discrete time at plant scale and describes plant growth and pathogen dynamics under optimal epidemiological conditions. The model is divided into two modules: a deterministic plant sub-model that simulates the simplified architecture and growth of the banana, and a pathogen sub-model that simulates the detailed life cycle of the pathogen including infection, lesion growth, asexual and sexual sporulation, and the dispersal of spores on the plant. The three most influential epidemiological parameters identified by sensitivity analysis of the model (lesion growth rate, infection efficiency, and incubation period) were estimated in a Bayesian framework using Markov chain Monte Carlo methods and acquired data on the dynamics of leaf lesions under natural conditions. The posterior densities provided precise knowledge on pathogen life history traits. The evaluation of the model using an independent data set confirmed the good quality of the predictions. Simulations allowed us to evaluate the impact of host resistance components, auto-infection at plant scale, and of the leaf emergence rate, which is linked with cropping practices, on the severity of BLSD. This foliar disease simulation model will help design new methods of controlling BLSD.

1. Introduction

The aim of host–pathogen modelling is to describe biological knowledge mathematically, or computationally, to advance our understanding of host–pathogen interactions and to provide support for disease management (Jeger, 2004). As emerging infectious diseases caused by fungi are a worldwide threat to food security (Fisher et al., 2012) and occur in a wide range of biological and ecological contexts, many mechanistic models are already available and describe crops of economic importance and their most devastating fungi (De Wolf and Isard, 2007).

Understanding the dynamics of an airborne fungal disease of crop in space and over time using models requires good knowledge of three aspects: (i) the components of the life cycle of the pathogen that affect disease progress (Lannou, 2012), (ii) spore dispersal gradients that affect the spread of the disease (Sackett and Mundt, 2005), and (iii) plant growth architecture, given the high interdependence of host dynamics and the development of the disease (Costes et al., 2013; Ferrandino, 2008).

Generic models have already been developed using a simple structure to describe the main stages of a pathogen's life cycle including infection, incubation, lesion growth, spore production and dispersion (Audsley et al., 2005; Casadebaig et al., 2012; Caubel et al., 2012; Garin et al., 2014). In addition, given the complexity of pathogen life cycles, many authors provide a detailed description of the steps of the cycle using specific assumptions (Rossi et al., 1997, 2008; Xu, 1999; Rossi and Giosuè, 2003; Van Den Berg et al., 2007; Calonnec et al., 2008; Djurle and Yuen, 1991). Spore dispersal gradients describe the primary inoculum, which triggers epidemics, and

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the secondary inoculum including auto-infection processes (infection by spores produced on the same plant), which considerably increases the level of the disease in the plant (Lannou et al., 2008). Spore dispersal gradients can be modeled either by giving a fixed value to the proportion of spores that reach the surface of each leaf (Willocquet and Savary, 2004; Van Den Berg et al., 2013; Rossi et al., 2009) or by using a dispersal function like in the models developed by Calonnec et al. (2008) and Audsley et al. (2005). The latter models focus on whole pathosystems including the effect of plant growth on disease dynamics, either in the same model (Robert et al., 2008) or using an existing specific plant growth model (Milne et al., 2003). Many of these epidemiological models include weather parameters because, in temperate regions, seasons strongly influence the dynamics of both the pathogen's life cycle and host development. In tropical regions, weather conditions, especially temperature, usually favor the development of plant diseases, thereby preventing the drastic extinction of plant pathogen populations, as happens in winter in temperate regions. Moreover in the case of tropical perennial crops like banana, the fact the plant is cultivated for several years greatly favors epidemics (Ploetz, 2007).

One of the main tropical diseases that affects bananas and plantains is black leaf streak disease (BLSD), caused by the fungus *Mycosphaerella fijiensis*. BLSD is considered to be the most damaging and costly foliar disease in commercial banana production (Guzmán et al., 2017), as it causes yield losses ranging from 20% to 100% (Churchill, 2011). Fungicide applications are not environmentally sustainable and in any case, most small producers cannot afford fungicides (Marin et al., 2003; Ploetz et al., 2015). Breeding for resistance is increasingly recognized as the most promising way to sustainably control BLSD (Guzmán et al., 2017; Bakry et al., 2009) but involves spatial and temporal constraints. Indeed, the standardized evaluation protocol for created hybrids requires a lot of space (about 6 m^2 per banana plant) and time (2 years) (Guzmán et al., 2017). The performance of banana quantitative resistance depends on different components of plant resistance that act at several steps in the BLSD life cycle (Abadie et al., 2009; Fouré, 1990; Irish et al., 2013). These components mainly slow the development of BLSD but their epidemiological impact remains unknown. The pathogen's life cycle is complex as it has two modes of reproduction. First, lesions produce asexual spores (conidia) involved in self-infection of the plant that are dispersed mainly over short distances, after which lesions coalesce and produce sexual spores (ascospores) with active projection that are dispersed in the air over greater distances (Rieux et al., 2014).

No BLSD model coupling the pathogen's life cycle of *M. fijiensis* and banana plant growth has been published so far. Hamelin et al. (2016) and Ravigné et al. (2017) recently developed two analytical models exploring the epidemiological dynamics of BLSD. Hamelin et al. (2016) studied how the existence of two types of spores with contrasted dispersal abilities affects invasion speed, but without accounting for plant architecture and growth. Ravigné et al. (2017) studied how the specific density-dependence induced by sexual spore production affects epidemiological dynamics. In this model, banana growth was implicitly accounted for through the transition rates between the different stages in the life cycle of the pathogen, but neither leaf area and position were modelled. Brisson et al. (1998), Tixier et al. (2004) and more recently Poeydebat et al. (2016) and Dépigny et al. (2016) developed four banana crop models based on the leaf area index or leaf area per biomass unit. However, none provided a precise description of the plant leaf in space or a precise description of the infectious cycle (Poeydebat et al., 2016).

The growth of a banana plant depends both on varietal parameters, which are mainly linked with plant architecture (leaf area and shape), and on agronomical parameters, which are linked to leaf emergence. As the level of BLSD at plant scale depends on the dynamics of both banana growth and the lesions on the leaves, it is important to take both into account to understand the effect of host resistance on pathogen dynamics and to provide support for varietal selection in banana breeding programs and cultural control practices. Our objective was thus to design a specific mechanistic disease simulation model that accounts for the complex BLSD biological cycle in a plant growing under optimal epidemiological conditions for disease development, and to calibrate the model using reliable prior knowledge and field experimental data.

First we describe the general structure of the model comprising a plant sub-model and a pathogen sub-model. Second, we present the experimental data acquired for model calibration and the Bayesian method used to estimate the main parameters of the pathogen's life cycle. Third, to illustrate the potential of the model to help design efficient control methods, we evaluate the model using time series of data and contrasted simulations of BLSD dynamics to assess the impact of plant resistance components, spore dispersal and plant growth on disease development.

2. Material and methods

2.1. Biological background

Bananas and plantains are herbaceous flowering plants that produce successive pseudostems whose terminal bud produces the inflorescence and the bunch. One plant cycle has four main stages: planting (in the first cycle) or sucker emergence (the lateral shoot used for the following plants), growth, flowering, and harvest immediately followed by the removal of the plant. The first plant cycle lasts from planting to the removal of the first harvested plant, called the mother plant. The following cycles overlap so that each cycle lasts from the emergence of the sucker, which occurs during the growing period of the plant, until the removal of the harvested plant derived from the sucker (Fig. 1). The lengths of the four main stages depend on both cultural practices (land preparation, pruning, weed control and fertilization) and weather conditions (temperature, radiation and wind) (Stover, 1980). During the growing period, the banana produces functional leaves, which are preformed inside the pseudostem. When flowering starts, leaf emergence stops (Stover, 1980). The leaf emergence rate decreases during the growing period and becomes stable when the flower stalk starts to rise inside the pseudostem (Lassoudière, 2006). In suckers, the leaf emergence rate is slower because their growth is inhibited by the mother plant (Stover and Simmonds, 1987).

Banana leaves are composed of a petiole and two symmetrical blades, which are rolled up inside the pseudostem before leaf emergence. The left blade unfolds first, followed by the right blade until the leaf has completely emerged. After emergence, the surface area of each leaf remains constant, but each successive leaf is larger (Lassoudière, 2006).

The life cycle of the ascomycete heterothallic fungus *M. fijiensis* can be summarized in four main steps: infection, lesion growth, sporulation, and spore dispersal (Churchill, 2011). Infection consists in the deposition of spores on the surface of the leaf and the penetration of germinated spores into host foliar tissues through stomata. After an incubation period, very small lesions (specks) appear (Marin et al., 2003). Under favorable conditions, the lesions grow at a constant logistic rate (Donzelli and Churchill, 2007) and asexual sporulation starts when the lesions have reached a minimum size. During the asexual sporulation step, the quantity of conidia produced by the lesions is proportional to their size and sporulation capacity. Conidia are the main source of auto-inoculum at plant scale (Burt et al., 1999) and are dispersed an average distance of three meters (Rieux et al., 2014). After the asexual sporulation step, growing lesions become sexually mature.