

Modelling the dynamics of a plant pathogen and a biological control agent in relation to flowering pattern and populations present on leaves



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ABSTRACT

A flexible model for biological control of a plant pathogen affecting host flowers is developed which takes into account the transfer of both the plant pathogen and the biological control agent (BCA) from the leaves to flowers. Because flowers, other than in ornamental plants, are largely ephemeral, the emphasis in analysis is on the rates of transfer and establishment on flowers. The form of the model analysed depends upon: the pattern of flowering for a particular host plant, a single instantaneous flush or continuous seasonal production; the effect of flowering phenology and morphology on transfer of both the pathogen and BCA; and the transient dynamics of such transfer. In the case of a single instantaneous flush, the relative importance of mycoparasitism and competition in protecting flowers during their short period of blooming is assessed. Where flowering is continuous but transfer lags behind because of floral phenology or morphology, a comparison is made between the initial levels of the pathogen and the BCA as they transfer to the flowers, depending again on the relative contribution of mycoparasitism and competition over the extended period of blooming. Differential rates of transfer of the pathogen and the BCA, depending on their time-dependent population densities on leaves, have a major impact on eventual biocontrol outcomes. The model results are used to analyse biocontrol strategies for contrasting host-pathogen systems which show different flowering patterns and biological control mechanisms. For *Erwinia amylovora* causing fireblight in pome fruit trees, an inundative biocontrol strategy targeting flowers is supported. In *Botrytis cinerea*, there is considerable potential for a strategy based on the establishment of BCAs on leaves for some of the plant hosts affected.

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1. Introduction

Biological control of plant diseases is potentially an important component of sustainable management of plant diseases. In this, it mirrors the use of natural enemies (parasitoids and predators) and microbial agents in the management of arthropod pests. However, for plant diseases the potential has yet to be realised, for both foliar and soil-borne diseases. There are several possible reasons for this, partly due to regulatory issues (Laengle and Strasser, 2010), but also due to basic differences from arthropod biocontrol. The mechanisms of biological control are more varied than those of arthropod pests; they include competition, antibiosis, mycoparasitism and induced

resistance. Also, the ecological underpinnings of biological control have been much less developed for plant diseases than for arthropod pests. Theoretical models have long been developed in the latter case (e.g. Ives, 1992; Mills and Getz, 1996), whereas other than some early simulation models (Knudson and Hudler, 1987), there have been few attempts to develop similar models for plant disease biocontrol until recently (Gubbins and Gilligan, 1996; White and Gilligan, 1998; Xiao and van den Bosch, 2003; Jeger et al., 2009; Cunniffe and Gilligan, 2011).

The model of Jeger et al. (2009) provided a general modelling framework for biological control of foliar plant disease as a tool to assess the efficacy of the different biocontrol mechanisms noted above. Recently Latif et al. (2013, 2014) used this framework to evaluate induced resistance as a mechanism of biological control. The model of Jeger et al. (2009) was further elaborated using numerical approaches to compare the relative effects of using a single biological control agent (BCA) with two biocontrol mechanisms

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compared with two BCA each with a single mechanism (Xu et al., 2010b, 2011b). A finding from the numerical studies was that two BCAs would rarely combine synergistically when used under homogeneous conditions; and that some combinations of mechanisms within a single BCA were more effective than others. The definition of “synergy” in combined use of BCAs was based on Bliss Independence (Xu et al., 2011a) but in other studies reviewed was almost never defined rigorously; indeed most published results indeed showed antagonistic interactions. The question of the effects of variability, whether arising from demographic stochasticity, spatial heterogeneity, sub-population structure, or environmental conditions, has recently been addressed in part (Xu and Jeger, 2013a, 2013b). Two BCAs would rarely combine synergistically under temporally fluctuating conditions; however, synergy among two BCAs under spatial heterogeneity is possible especially when two BCAs differ greatly in their development among two niches (Xu and Jeger, 2013b). Another claimed advantage of combined use is the reduced variability that can result (Guetsky et al., 2001, 2002), although this has not been adequately documented.

The general model (Jeger et al., 2009) did not distinguish the foliar, or above-ground, plant parts that were affected by the disease, nor any variation in biocontrol efficacy depending on the plant part infected. This is an important niche issue, as pathogens such as *Botrytis cinerea* can infect and cause symptoms on leaves, flowers and fruits. In other cases some diseases are quite specific to the plant part affected, for example flowers; however, infection of flower structures during the flowering period can cause subsequent effects on the whole plant (Table 1). Some BCAs are effective only on leaves of some host plants; others move from leaves to flowers, where their effectiveness may be different (either greater or lesser).

Improved efficacy, as a result of combined use of BCAs that occupy a different niche (rhizosphere) than the pathogen (foliar) has been reported (Le Floch et al., 2007, 2009). As a consequence of such reports, it is relevant to include appropriate partitioning of plant parts in a model to take into account niche properties of biological control. Few studies have taken into account niche considerations in biological control of plant pathogens.

In the theoretical model of Jeger et al. (2009) there was no niche separation according to the plant part involved: the host population (foliar surface area) was considered to be non-differentiated and of a constant size. It was partitioned into non-overlapping categories of tissue area: healthy and susceptible (H_s), healthy and resistant (H_r), occupied by a BCA (H_b), diseased and infectious (i.e. producing inoculum) (I), and diseased but non-infectious (R); with parameters representing flows between them (Fig. 1a). An important distinction is made between the rates of colonisation of healthy and diseased plant tissue by the BCA, reflecting their competitive and mycoparasitic abilities respectively. In this study, we consider the foliar surface area to be the leaves and the steady-state populations on leaves to be the source of the pathogen for infection of flowers; and similarly for colonisation by the BCA. We then need to consider the pattern of flower production.

Much work has been done on the phenology of flower production in terms of temperature and photoperiod across a range of horticultural (Berninger, 1992; Fisher et al., 1996; Monaghan et al., 2004), agronomic (Cober et al., 2001) and “wild” or non-crop plants (Chew et al., 2012; Chidumayo, 2003; Yamamura et al., 2007), but much less on the pattern of flower production. There is a switch between vegetative and reproductive growth: in some hosts, e.g. apple, cereals, flowering occurs effectively as a single flush within a relatively short period of time; and in others, e.g. oil seed rape, day-neutral strawberry, continues over an extended period of time. The extent of flowering may be determined by host factors such as leaf production and stem elongation. The timing of flowering is also

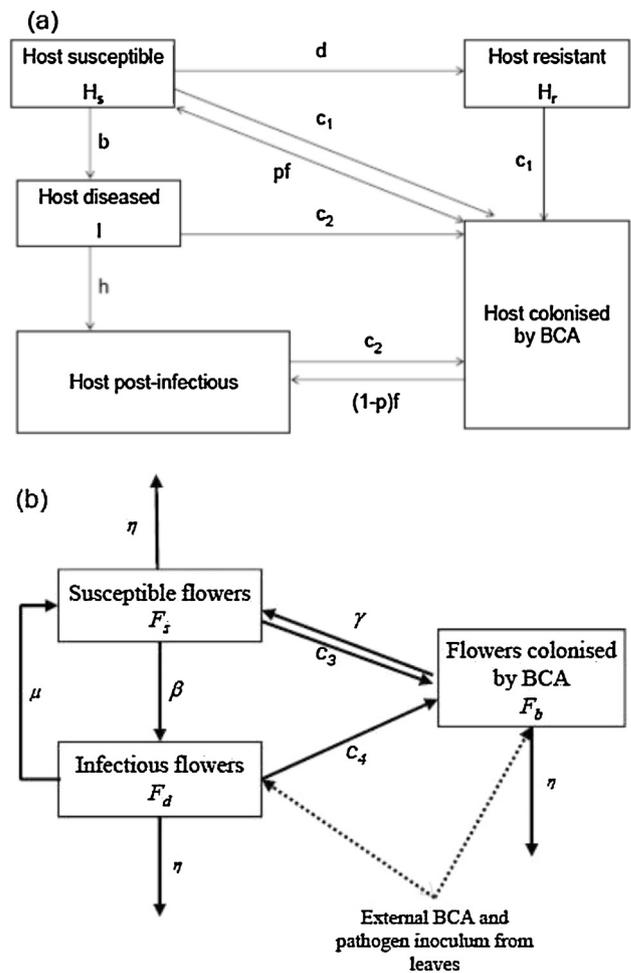


Fig. 1. A flow diagram (a) for the original model (Jeger et al., 2009) on biocontrol of foliar pathogens, indicating relationships among the host categories along with the rate parameters, describing inter-relationships among host, pathogen and a biocontrol agent (BCA). A simplified version (b) of this model was developed for modelling biocontrol of diseases on flowers, assuming steady-state leaf populations during the flowering period. Parameters are described in Table 2. The dotted lines represent the transfer of the pathogen and BCA from the steady state leaf populations.

important: in some cases, flowers are produced early in the period of vegetative growth but associated with flower buds, as in apple; in others, flowers are produced late in the vegetative period, as in late-season strawberry. It is also the case that “transfer” of the pathogen/BCA from leaves to flowers may occur rapidly as flowers emerge from buds, or may be delayed because of morphological features. The flowering period is often ephemeral but important, as it provides a stepping stone for the infection of harvested produce, e.g. grain or fruits (Guijarro et al., 2008).

In this paper we derive model variants to cover different possible scenarios corresponding to these patterns of flower emergence in relation to the patterns of infection/colonisation by the pathogen/BCA. We develop a simple deterministic model for the case in which the leaf BCA/pathogen population has approached steady-state values as in the original model (Fig. 1a), flowers emerge either as a single instantaneous flush, or continuously, and the pathogen colonises the newly emerged flowers, as does the BCA. We analyse the extent to which the pathogen can colonise the flowers in the presence of the BCA and, as in the original model, examine the sensitivity of the model outputs to selected parameter combinations. Finally, we comment on some specific pathogen/BCA interactions on flowers in relation to the model variants developed.

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