



## Review

## Dealing with the variability in biofumigation efficacy through an epidemiological framework

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## ABSTRACT

Biofumigation, as originally defined, is the use, in agriculture, of the toxicity of *Brassica* crop residues to control soilborne plant pathogens. This toxicity is specifically attributed to the release of toxic isothiocyanates, through the hydrolysis of glucosinolates present in the crop residues. This technique is considered a possible alternative to the use of pesticides, but field studies have generated conflicting data concerning the efficacy of biofumigation at field scale, limiting the use of this technique. Analytical studies based on a systematic approach involving evaluation of the potential effects of isothiocyanates can be used to address this problem in a rigorous manner. However, many recent studies have indicated that the mechanisms underlying biofumigation are much more complex than a simple toxic effect of residues. In this review, we dissect and discuss the problems encountered when trying to understand the variability in biofumigation efficacy and propose an integrative epidemiological approach to overcome these problems. This approach involves separating the effects of the different parameters of the system, such as the effects of different management phases of the biofumigant crop (i.e. the period of biofumigant crop growth and the phase during which crop residues are pulverised and incorporated into the soil) on the epidemiological mechanisms driving the development of an epidemic (density of primary inoculum and dynamics of disease progression). Finally, we propose new avenues of research into biofumigation in which the use of epidemiological tools and methods may improve our understanding of the factors underlying variation in the efficacy of biofumigant crops.

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## 1. Introduction

The term “biofumigation” was coined by Kirkegaard et al. (1993) as “a crystallising term” to describe the suppressive effects of *Brassica* species on noxious soilborne organisms due specifically to the release of isothiocyanates (ITC) through the hydrolysis of glucosinolates (GSLs), catalysed by myrosinase isoenzymes (Matthiessen and Kirkegaard, 2006). ITCs have been shown to have toxic effects on many organisms, including mammals, birds, insects, molluscs, aquatic invertebrates, nematodes, bacteria and fungi (Brown and Morra, 1997; Ulmer et al., 2001; Buskov et al., 2002; Lazzeri et al., 2004; Noret et al., 2005). Indeed, ITCs are general biocides with a biological activity resulting from interaction with proteins (Brown and Morra, 1997). Allelopathy, defined by Rice (1984) as “the direct or indirect, positive or negative effect of one

plant on another, through the release of biochemical compounds into the environment”, has long been observed in *Brassica*, giving these plants their reputation as “poor companion plants” (Matthiessen and Kirkegaard, 2006). In 1996, the International Allelopathy Society broadened the definition of allelopathy to refer to “any process involving secondary metabolites produced by plants, micro-organisms, viruses and fungi that influence the growth and development of agricultural and biological systems”. The term “biofumigation” was then used to distinguish between the general phenomenon of allelopathy and the use in agriculture of isothiocyanates from biological sources for the suppression of soilborne pests and diseases (Brown and Morra, 1997). The technique of biofumigation based on the use of isothiocyanate-generating *Brassica* species as biologically active green manures (Matthiessen and Kirkegaard, 2006) involves growing a biofumigant crop during the intercrop phase. The toxic compounds are released principally after the crushing of the crop residues. The toxic potential of biofumigant crops is greatest during flowering (when GSL levels in tissues are highest i.e. when the rate of GSL production in the tissues is highest, Clossais-Besnard and Larher, 1991; Bellostas et al., 2007). The aim is therefore generally to

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crush the crop and incorporate its residues into the soil (usually into the top 10–20 cm depth) at this time.

The contribution of many ITCs to the biocidal activity of *Brassica* residues has been clearly demonstrated *in vitro* (Brown and Morra, 1997), but the many studies carried out in agricultural conditions have not systematically shown a pathogen-suppressing effect of the ITCs released by residues. Many studies have been conducted in the field, on various pathogens and Brassicaceae biofumigant species. However, the observed levels of efficacy differ widely between studies, both for a given species from the Brassicaceae and for a given pathogen (Tables 1 and 2). The lack of robustness of biofumigation is a major problem for its application in various cropping systems and its widespread adoption. According to Matthiessen and Kirkegaard (2006), the empirical approach used in many studies of biofumigation is the main problem. Indeed, according to these authors, the studies carried out to date provide insufficient information about the approaches used, including, in particular, the GSL content of the plants used, making it difficult to determine the role of ITC in the responses observed. They also lack data to establish a causal relationship between the quality of biofumigant crop management and the level of suppression observed. Furthermore, study conditions (e.g. site of the study, soil characteristics), biofumigation techniques (e.g. whether the residues are incorporated, growing season, time between residue incorporation and sowing of the commercial crop), type of control used (bare soil versus a non-biofumigant crop) and the disease variables assessed (e.g. disease incidence or severity) vary considerably between studies (Tables 1 and 2), making it very difficult to perform a global analysis of the factors underlying the variation. Most of these studies focused on demonstrating the efficacy, or otherwise, of the technique. The experiment was not repeated in many of these studies, some of which tested a large number of factors simultaneously (e.g. different varieties of biofumigant crops in interaction with different species of pathogens), making it difficult to identify the sources of variability of biofumigation efficacy.

Kirkegaard and Matthiessen (2004) outlined general mechanisms by which the incorporation of *Brassica* crop residues might influence the growth and yield of the following crop, highlighting the diversity of these mechanisms. Some of the mechanisms presented are not related to control of the disease and are common to most cover crops (e.g. impact on soil organic matter content, with effects on nutrition and soil structure). The pathways involved in disease reduction include direct effects associated with the release of GSL and ITC by the residues, “non-host” and “trap plant” effects of the biofumigant crop and indirect effects on the pathogen associated with changes in the structure of soil microbial populations and antagonists of the pathogen. Indeed, it is clear from the results obtained in agricultural conditions to date (see Table 1) that the toxicity of the residues (which is thought to reflect the GSL content of the tissues) after their incorporation into the soil is not well correlated with the efficacy of biofumigation for decreasing disease expression. Several authors have discussed the lack of a direct relationship between the GSL concentration of the residues and their ability to decrease pathogen activity (Mazzola et al., 2001, 2007; Cohen et al., 2005; Larkin and Griffin, 2007; Yulianti et al., 2007). In reality, as biofumigation involves many biological parameters (e.g. the biofumigation crop, the pathogen and other micro-organisms likely to interact with the pathogen and to be affected by the release of ITC) and physical parameters (e.g. soil and climate characteristics), many factors are likely to be involved in the variability of biofumigation efficacy, probably with complex interactions between the multiple variables. As indicated by Kirkegaard and Matthiessen (2004), the “biofumigation” linked to the release of ITC by the residues of *Brassica* crops is just one of many ways in which these residues may influence the growth of the commercial

crop. For these reasons, these authors proposed a systematic approach to research in the field of biofumigation through analytical studies. This approach makes it possible to focus on the key factors underlying variation thought to have a significant effect on biofumigation efficacy.

Several review articles have already focused on the mechanisms by which ITC and other degradation products of GSL are generated (Bones and Rossiter, 1996; Brown and Morra, 1997; Rosa et al., 1997; Fahey et al., 2001). Others (Brown and Morra, 1997; Rask et al., 2000; Gimsing and Kirkegaard, 2009) have considered the fate of GSL-derived compounds in the soil, their mechanisms of action and their toxicity to organisms. Several reviews (Kirkegaard and Matthiessen, 2004; Morra, 2004; Matthiessen and Kirkegaard, 2006; Kirkegaard, 2009) have also discussed various biophysical factors underlying the variation in biofumigation efficacy and proposed measures for decreasing this variability. However, no study has investigated the benefits of epidemiological approaches for capturing and linking the ecological mechanisms of biofumigation and the epidemiological attributes of the pathogens targeted. This review deals specifically with this aspect, because we believe that the efficacy of biofumigation in various cropping systems depends primarily on an understanding of all the biological mechanisms involved. We have limited our consideration of target pathogens to soilborne micro-organisms in this review, but the epidemiological mechanisms discussed here could easily be applied to other crop pests.

## 2. Epidemiological attributes of soilborne diseases and entry points for management

Disease propagation is favoured by short distances between susceptible plants. In the case of strictly soilborne diseases, dispersal within a crop has been shown to be limited to a given field and crop, and the mounting of disease levels to epidemic proportions requires the presence of several successive susceptible crops and, therefore, several years, in many cases. Such epidemics are described as polyetic (Zadoks, 1999). Primary inoculum (i.e. initial soilborne inoculum) is the cause of the first root infections (primary infections) producing infectious tissues from which transmission may occur, through secondary infections from an infected site on a root to a healthy site on the same root (auto-infections), or from an infected root to neighbouring plant roots (allo-infections) (Gilligan, 1985; Jeger et al., 1987) (Fig. 1). This process follows polycyclic dynamics, resulting in patches of diseased plants in the field, due to the limited spatial dispersion of the pathogen (Gilligan, 1985). Some diseases display monocyclic development, in which the primary inoculum is the only source of contamination. This is the case for the cyst nematode *Globodera rostochiensis*. Van der Plank (1963) distinguished between these two types of epidemic on the basis of the rate of development of the base cycle,  $r$ . For monocyclic dynamics, disease progression was typified by the monomolecular model, as follows:

$$dy/dt = r \cdot (1 - y) \quad (1)$$

and for polycyclic dynamics, Van der Plank (1963) adapted the differential equation of the logistic model as follows:

$$dy/dt = r \cdot y \cdot (1 - y) \quad (2)$$

where  $r$  is the apparent infection rate, as coined by Van der Plank (1963),  $y$  the proportion of diseased plants or tissues and  $t$  the time (see Madden et al., 2007, for more detailed information on the terms  $\times 0$  and  $r$ ).

Within this framework, pathogen populations may thus be controlled by two main crop protection methods: those intended to

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