



Review

Fungistasis and general soil biostasis – A new synthesis

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ABSTRACT

In most soils, fungal propagules are restricted to a certain extent in their ability to grow or germinate. This phenomenon, known as soil fungistasis, has received considerable attention for more than five decades, mostly due to its association with the general suppression of soil-borne fungal diseases. Here, we review major breakthroughs in understanding the mechanisms of fungistasis. Integration of older fungistasis research and more recent findings from different biological and chemical disciplines has led to the consensus opinion that fungistasis is most likely caused by a combination of microbial activities, namely withdrawal of nutrients from fungal propagules and production of fungistatic compounds. In addition, recent findings indicate that there are mechanistic links between these activities leading towards an integrated theory of fungistasis. Among the potentially fungistatic compounds volatiles have received particular attention. Whereas it has long been assumed that fungistasis is the result of the metabolic activity of the total soil microbial biomass, more recent research points at the importance of activities of specific components of the microbial community. These insights into fungistasis have also formed the basis for strategies to increase general soil suppression. Besides these basic and practical aspects of fungistasis, its impact on fungal ecology, in particular on fungal exploration strategies, is discussed. Finally, we take a closer look at plant–soil feedback experiments to demonstrate the occurrence of fungistasis-like phenomena and to suggest that fungistasis may be part of a much wider phenomenon: general soil biostasis.

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1. History

The term fungistasis, sometimes also referred to as mycostasis, was first coined by Dobbs and Hinson (1953) to describe the widespread occurrence of inhibition of germination of fungal spores or growth of fungal hyphae in soils. Several definitions of fungistasis have circulated through the literature, with the differences mostly related to the types of fungal structures they include. Here, we will use the definition given by Watson and Ford (1972), who refer to fungistasis when (a) viable fungal propagules, which are not subject to endogenous or constitutive dormancy, do not germinate in soil at their favorable temperature and moisture conditions, or (b) growth of fungal hyphae is retarded or terminated by conditions of the soil environment other than temperature and moisture. According to this definition, germination or growth should proceed to a certain extent in a suitable, nutrient-free environment, utilizing nutrient resources present in spores or

translocated via hyphae (Fig. 1). In the original paper of Dobbs and Hinson (1953), these nutrient-free environments included water, sand and silica gel.

Fungistasis became a 'hot topic' in the 1960s and 1970s, as extensively reviewed by John Lockwood, who himself spearheaded these developments (Lockwood, 1977). Research in the 'Lockwood-era' was mainly focused on understanding (1) the mechanism of fungistasis and (2) the relationship with suppression of soil-borne plant diseases. In addition, many papers addressed different methods used to assess soil fungistasis. Major observations, ideas and concepts originating from this period are given in sub-sections that follow.

The topic of fungistasis received less attention in the 1980s and early 1990s, as research interests shifted to unraveling mechanisms of specific disease suppression and the application of biocontrol agents to suppress soil-borne plant pathogens (Mazzola, 2002; Weller et al., 2002; Borneman and Becker, 2007). However, since biocontrol strategies have generally yielded inconsistent results in their practical application, there has been a general revival of interest in fungistasis and general soil suppression since the late 1990s. This revival coincided with the increasing interest in topics related to sustainable agriculture (Doran and Zeiss, 2000).

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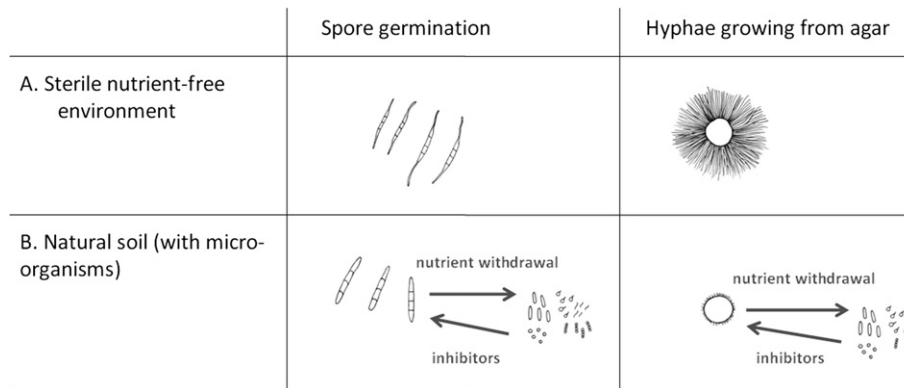


Fig. 1. Illustration of soil fungistasis. Germination of fungal spores and extension of fungal hyphae from a nutrient source do proceed (much) better in artificial nutrient-free environments than in natural soils. Soil microbes can be largely responsible for fungistasis namely by 1) withdrawing nutrients from fungal propagules or by 2) producing fungitoxic compounds. There is increasing evidence that mechanistic links between these microbial activities will lead to the actual explanation of fungistasis.

1.1. Methods

In most studies, fungistasis has been quantified on the basis of germination of spores by microscopic observation (Lockwood, 1977). Spores are typically incubated directly in soils or in/on materials that have been in constant or temporary contact with the soil. After an incubation period, the percentage of germinated spores can be determined microscopically. This simple methodology is still in use. Next to spore germination, hyphal growth has also been used for fungistasis assays (De Boer et al., 2003). Protocols for both spore germination and hyphal growth assays are given by Alabouvette et al. (2006). The control consists of growth/germination in a nutrient-free environment, such as purified sand, whereby endogenous nutrients need to be used by the fungus to support germination or hyphal growth (the latter for instance via translocation from a nutrient-rich agar disc) (Fig. 1). The strength of a soil's fungistatic potential is given by the reduction of spore germination or hyphal growth induced by a soil in comparison to the control.

1.2. Inhibition versus nutrient deficiency

The microbial basis of fungistasis has generally been inferred from experiments demonstrating a relief of fungal inhibition after soil treatments (e.g. autoclaving) that result in partial or complete killing of soil microbes. Complete sterilization does, however, not always result in a complete relief of fungistasis, and the remaining inhibition, typically attributed to abiotic factors like pH or minerals, has been referred to as 'residual' fungistasis (Dobbs and Gash, 1965). Although it has long been accepted that soil-borne micro-organisms play the key role in fungistasis, the microbial mechanism that gives rise to fungistasis has been a topic of considerable debate.

Dobbs and Hinson (1953) originally attributed fungistasis to the presence of inhibitory compounds, mainly of microbiological origin, and this concept was subsequently supported by several others (e.g. Hora and Baker, 1970; Watson and Ford, 1972). The contribution of inhibitors to fungistasis has, however, been disputed by Lockwood and co-workers (Lockwood and Lingappa, 1963; Lockwood, 1977), who argued that withdrawal of nutrients from fungal propagules by the soil microbial community was the most likely cause of fungistasis.

The inhibition and nutrient-deficiency theories clearly differ with respect to the major type of microbial involvement in fungistasis. The inhibition theory maintains that microbial production of inhibitory compounds impedes fungal development, whereas the

nutrient-deficiency theory states that microbial withdrawal of nutrients limits fungal germination or growth (Fig. 1). Major reasons for Lockwood to question the involvement of inhibitors were: (1) the temporary relief of fungistasis after addition of nutrients to non-sterile soils, (2) the inverse relationship between propagule size (assumed to reflect the amount of nutrients present inside the propagules) and the sensitivity to fungistasis, and (3) the increase of fungistasis sensitivity by creating artificial nutrient-withdrawal conditions.

However, a number of arguments were given to support the inhibition theory. Firstly, the relief of fungistasis by addition of nutrients can often be inconsistent. Furthermore, fungistatic compounds have been extracted from soil in a number of cases (Watson and Ford, 1972). In particular, the detection of volatile inhibitors provided strong evidence argument in favor of the inhibition theory, since this type of inhibition could be demonstrated without any direct or indirect (e.g. via materials put on the soil surface) physical contact of the fungal propagules with the soil, thus excluding the possibility of nutrient withdrawal (Hora and Baker, 1970; Balis, 1976).

Interestingly, after evaluating all the fungistasis-related literature, Lockwood (1977) argued that the most likely explanation for fungistasis is probably a combination of the nutrient-deficiency and inhibition theories. Hora and Baker, followers of the inhibition theory, reached the same conclusion in the same year (Hora et al., 1977). We will show here that recent findings indicate that there is mechanistic link between these theories leading towards an integrated theory of fungistasis.

1.3. Relationship between fungistasis and disease suppression

As pointed out by Lockwood (1977), fungistasis should be considered as a bulk soil phenomenon. The bulk soil environment is unfavorable for plant-pathogenic fungi, since most of them have weak saprotrophic abilities, making them unable to compete with heterotrophic bacteria and saprotrophic fungi for the limited supply of available carbon sources present (Garrett, 1970). To survive longer periods in the bulk soil, many plant-pathogenic fungi have propagules that can remain in a quiescent state, therefore reducing the amount of endogenous energy necessary for maintenance (Mondal and Hyakumachi, 2000). Thus, fungistasis may be beneficial for some plant-pathogenic fungi, as it can prevent germination/growth under conditions when no host is present. However, prolonged fungistasis may lead to an irreversible loss of viability of fungal propagules (Lockwood, 1977), and the intensity of

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