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Review

Bacterial endophytes as potential biocontrol agents of vascular wilt diseases – Review and future prospects

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HIGHLIGHTS

- Bacterial endophytes have various possible disease suppression mechanisms.
- We present a number of case studies of bacterial endophytes antagonistic to wilts.
- The challenges encountered are discussed.
- Several strategies that can optimize the endophytic research are presented.

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ABSTRACT

Vascular wilts are devastating plant diseases that can affect both annual crops as well as woody perennials, hence inducing major food losses and damaging valuable natural ecosystems. Because of ecological and economical reasons, the management of vascular wilt diseases by conventional chemical methods is raising concerns. More environmentally friendly alternatives such as the use of microbial antagonists to control phytopathogens are now of growing interest. The fact that bacterial endophytes are able to colonize an ecological niche similar to that of vascular wilt pathogens favors them as potential biocontrol agents against wilt diseases. Several possible disease suppression mechanisms of beneficial bacteria were proposed, among them induction of systemic resistance, growth promotion, competition, etc. However, there are still numerous challenges for the development and exploitation of bacterial endophytes such as the inherent characteristics of the endophyte itself or the environmental conditions. The optimization and improvement of the strategies employed in the endophytic research from early stages can help finding effective and competent biocontrol bacterial endophytes. Additionally, the use of genomic technologies and interdisciplinary research approaches in investigating the biocontrol potential of specific bacterial endophytes can deepen our knowledge of their mode of action and its regulatory backgrounds which may lead to more predictable and consistent beneficial effects from these microorganisms.

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1. Introduction

The ecological and environmental risks of the use of synthetic chemicals for controlling vascular wilt diseases are the cause of public concerns. Through this report we will present the potential of bacterial endophytes in wilt diseases biocontrol. We will start this review with a brief introduction on the major vascular wilt diseases and their causing pathogens. Then, we will discuss the characteristics of bacterial endophytes including source, structure and population dynamics as well as their possible mechanisms of disease suppression. Few case studies of isolated endophytic bacteria that showed biocontrol potential against vascular wilt diseases will be presented as examples. In the rest of this review we will focus on the rationale and strategies that can be applied to obtain competent endophytic biocontrol agents and also the challenges encountered during the development and the use of bacterial endophytes as antagonistic microorganisms. We will finish this paper with an overall overview of the innovative approaches and technical procedures that can be used to optimize the endophytic research.

2. Vascular wilt diseases

Vascular wilts are devastating plant diseases that can affect both annual crops as well as woody perennials, hence inducing major food losses and damaging valuable natural ecosystems (Yadeta and Thomma, 2013). Wilts occur as a result of the presence and activities of pathogens (generally fungi or bacteria) in the xylem vascular tissues of the plant. Once the plant is infected, these pathogens enter the water-conducting xylem vessels where they proliferate and hinder the transportation of water and minerals. Pathogens usually continue to spread internally through the xylem vessels until eventually the death of the entire plant (Agrios, 2005).

Two major genera of fungi are known to cause vascular wilts and they are characterized by a wide host range: *Fusarium* and *Verticillium*. *Fusarium* affects numerous field crops such as cotton and tobacco, plantation crops such as banana, coffee, sugarcane and few shade trees (Agrios, 2005). *Verticillium* attacks diverse plant species causing wilts and losses of varying severity. Mainly two species are involved: *Verticillium dahliae* and *Verticillium alboatrum*. *Verticillium* is widespread in economically important crops such as cotton (Bölek et al., 2005) and vegetables such as tomatoes (Sharma and Nowak, 1998). The symptoms of *Verticillium* wilts are similar to those of *Fusarium* wilts, starting with yellowing followed by chlorosis and necrosis of leaves occurring on one or both sides of the leaf or the whole plant. Consequently, vascular discoloration and stunting may be apparent (Ting, 2014).

Other genera of wilt causing fungi are *Ceratocystis,* that causes vascular wilts in oak, cocoa, and eucalyptus trees, and *Ophiostoma,* that causes vascular wilts of elm trees (Yadeta and Thomma, 2013). Fungal vascular wilt pathogens usually enter their host plants through the roots with the exception of *Ophiostoma* spp. and the oak wilt pathogen *Ceratocystis fagacearum*, that are transmitted by beetles (Hayslett et al., 2008; Juzwik et al., 2008; Harwood et al., 2011).

Vascular wilts caused by bacteria affect mostly herbaceous plants such as several vegetables, field crops, ornamentals, and tropical plants (Agrios, 2005). Different bacterial genera contain vascular wilt pathogens, such as *Ralstonia*, *Clavibacter*, *Pseudomonas*, and *Erwinia*. After the wilt causing bacteria infect the plant, they start to multiply, and move through the xylem vessels. They interfere with the translocation of water and nutrients which will cause drooping, wilting, and the death of the aboveground parts of the plants (Agrios, 2005). These bacterial pathogens overwinter in plant debris in soil, seeds, vegetative propagative material, or in their insect vectors as dormant cells (Agrios, 2005). They can enter plant tissues through wounds, cracks, or natural openings or can be delivered into the xylem by insect vectors. Nematodes seem to facilitate the infection by wilt bacteria in at least some of the vascular wilts.

Controlling vascular wilt pathogens can be challenging because there is no efficient treatments to cure the infected plants, so generally they should be removed from the infected areas. Additionally, many of the vascular wilt causing pathogens are soil-borne that produce persistent resting structures that can survive for long periods, which make controlling these diseases more difficult (Yadeta and Thomma, 2013). Traditional methods of chemically controlling vascular wilt diseases can be expensive and ineffective, and have a negative impact on environment and human health (Griffin, 2014), therefore finding other environmentally friendly means of controlling these diseases became a necessity. One of the promising approaches is the use of biological agents antagonistic to the microorganisms/pests that cause the disease such as bacterial or fungal endophytes (Agrios, 2005).

Several reasons explain the appeal of using endophytes as biocontrol agents: i) the fact that it offers a natural means of control and can lessen dependency on hazardous chemicals (Griffin, 2014), ii) being potentially self-sustaining and able to spread on their own after initial establishment, iii) reducing the input of non-renewable resources as well as allowing a long-term disease suppression in an environmentally friendly manner (Whipps, 2001; Quimby et al., 2002; Yuliar et al., 2015). Bacterial endophytes are able to colonize an ecological niche similar to that of plant pathogens, especially vascular wilt pathogens, which can favor them as potential biocontrol agents against wilt diseases (Ramamoorthy et al., 2001). In this review we will be focusing on the biocontrol potential of bacterial endophytes against vascular wilts.

3. Bacterial endophytes

The term endophyte is applied to microorganisms that spend the whole or part of their life cycle within plant tissues and cause no apparent infections or symptoms of disease (Wilson, 1995; Azevedo et al., 2000; Bacon and White, 2000; Saikkonen et al., 2004). Almost all vascular plant species examined to date were found to harbor bacterial and/or fungal endophytes (Arnold et al., 2000; Sturz et al., 2000; Tan and Zou, 2001). It is thought that bacterial endophytes originate from the bacterial communities of the rhizosphere and phylloplane, as well as from endophyte-infested seeds or planting materials. They gain entrance to the plant through natural openings or wounds (Hallmann et al., 1997). Overall, the endophytic community is of dynamic structure and is influenced by diverse factors, such as the physicochemical structure of the soil, plant growth phase, plant physiological state, and environmental conditions (Hallmann et al., 1997; Reiter et al., 2002; Ardanov et al., 2012; Mercado-Blanco and Lugtenberg, 2014) (Fig. 1). Also, they have been isolated from diverse plant tissues such as seeds, tubers, roots, stems, leaves, and fruits (Hallmann et al., 1997). In most plants, roots have the higher numbers of endophytes compared with above-ground tissues (Rosenblueth and Martinez Romero, 2004; Rosenblueth and Martínez-Romero, 2006). Bacterial endophytes in a single plant host are not restricted to a single species but comprise several genera and species (Rosenblueth and Martínez-Romero, 2006). The most commonly isolated bacterial genera are *Pseudomonas, Bacillus*, *Enterobacter*, and *Agrobacterium* (Hallmann et al., 1997).

When compared to the rhizosphere and rhizoplane bacterial communities, bacterial endophytes are likely to interact more closely with their host plant because they are provided with a