Research on Endophytic Bacteria: Recent Advances with Forest Trees
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6.1 Introduction

Plants can be considered as complex microecosystems that provide different habitats to a variety of microorganisms. These habitats are represented by the plant external surfaces as well as internal tissues (McInroy and Kloepper 1994). Whereas the importance of microbial colonisation of plant surfaces in plant growth promotion has been well understood for a long time, interior tissue colonisation was, until recently, largely perceived as being related only to the perpetuation of systemic diseases. It is now well known that tissues of healthy plants are also colonised internally by various microorganisms that establish neutral or, more interestingly, beneficial interactions with their host plants. The term “endophyte” is commonly used to describe such microorganisms.

Although a variety of definitions have been applied to the term “endophyte”, it refers mainly to bacteria and fungi that live inside plant tissues without causing disease (Wilson 1995; see Chap. 1 by Schulz and Boyle). Whether or not latent pathogens can be considered endophytes has been a major topic of debate in the general acceptance of this definition (Misaghi and Donndelinger 1990; James and Olivares 1997; see Chap. 1 by Schulz and Boyle).

The best-characterised microbial endophytes are fungi of the Balansiaceae, for which the most compelling evidence of plant–microbe mutualism has been provided (Clay 1988; Schardl et al. 2004). Some of the non-balansiacaceous endophytic fungi are also mutualistic with their hosts (Carroll 1988; see Chap. 15 by Schulz), and produce compounds that render plant tissues less attractive to herbivores, while other strains may increase...
host plant drought resistance. In return, fungal endophytes are thought to benefit from the comparatively nutrient rich, buffered environment inside plants.

Apart from fungi, bacteria belonging to various genera have also been shown to exist inside plants without causing apparent disease symptoms. Some of these bacteria are known to impart benefits to their host plants by the same mechanisms as their soil- or rhizosphere-colonising counterparts. The primary mechanisms thought to lead to beneficial effects for the plant are nitrogen fixation (Boddey and Döbereiner 1995) and bio-control of pathogenic and detrimental microorganisms, either through direct antagonism of pathogens or by inducing systemic resistance to such organisms (Hallman et al. 1997). Other known mechanisms by which beneficial bacteria can have a positive influence on plant performance are the production or stimulation of plant growth hormones and facilitation of nutrient uptake [see Chaps. 3 (Kloepper and Ryu) and 4 (Berg and Hallmann)].

Since their first reported isolation from potato plants (Tervet and Hollis 1948; Hollis 1951), all the information available on endophytic bacteria has been derived from studies on plant species of agricultural and horticultural importance. The endophytic bacteria of rice (Reinhold-Hurek and Hurek 1998), corn (Triplett 1996) and sugarcane (Döbereiner et al. 1995) are by far the best studied so far. In contrast to these crop species, very much less is known about bacterial endophytes of trees. Some trees survive and grow well in very difficult terrain under extreme conditions, for example lodgepole pine (*Pinus contorta* Dougl. var. *latifolia*) in interior regions of British Columbia and western Alberta, Canada, as well as *Tecomella undulata* (Bignoniaceae) in the extremely arid deserts of northwestern India. It is possible that endophytic bacteria that enhance host survival and growth in exchange for protection in the relatively buffered environment of internal plant tissues may be involved under such extreme environmental conditions (Law and Lewis 1983).

Although the realisation of this possibility has led to occasional reports of endophytic bacteria in asymptomatic angiosperm and gymnosperm tree species, little is known about their diversity and influence on plant growth. The earliest report of bacterial endophytes from trees was from Gardner et al. (1982), who isolated representatives of 13 genera from xylem fluid of rough lemon rootstock, and found population sizes ranging from $10^2–10^4$ colony forming units (cfu) g$^{-1}$ xylem fluid. Only 48 of the 850 isolates turned out to be phytopathogenic, but the role of the other 802 isolates was not determined. Similarly, several strains of *Pseudomonas syringae* were isolated and characterized from inside pear seedlings by Whitesides and Spotts (1991), but their exact role could not be determined.