Endophytes vs tree pathogens and pests: can they be used as biological control agents to improve tree health?

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REVIEWS

Endophytes vs tree pathogens and pests: can they be used as biological control agents to improve tree health?

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Abstract Like all other plants, trees are vulnerable to attack by a multitude of pests and pathogens. Current control measures for many of these diseases are limited and relatively ineffective. Several methods, including the use of conventional synthetic agro-chemicals, are employed to reduce the impact of pests and diseases. However, because of mounting concerns about adverse effects on the environment and a variety of economic reasons, this limited management of tree diseases by chemical methods is losing ground. The use of biological control, as a more environmentally friendly alternative, is becoming increasingly popular in plant protection. This can include the deployment of soil inoculants and foliar sprays, but the increased knowledge of microbial ecology in the phytosphere, in particular phylloplane microbes and endophytes, has stimulated new thinking for biocontrol approaches. Endophytes are microbes that live within plant tissues. As such, they hold potential as biocontrol agents against plant diseases because they are able to colonize the same ecological niche favoured by many invading pathogens. However, the development and exploitation of endophytes as biocontrol agents will have to overcome numerous challenges. The optimization and improvement of strategies employed in endophyte research can contribute towards discovering effective and competent biocontrol agents. The impact of environment and plant genotype on selecting potentially beneficial and exploitable endophytes for biocontrol is poorly understood. How endophytes synergise or antagonise one another is also an important factor. This review focusses on recent research addressing the biocontrol of plant diseases and pests using endophytic fungi and bacteria, alongside the challenges and limitations encountered and how these can be overcome. We frame this review in the context of tree pests and diseases, since trees are arguably the most difficult plant species to study, work on and manage, yet they represent one of the most important organisms on Earth.

Keywords Endophytes · Biological control · Trees · Pathogen · Pest · Disease

Introduction

Importance of trees and their diseases

Being some of the largest organisms on Earth, trees in forest and woodland settings cover 40% of the Earth's terrestrial surface (Fao 2010). This forms a major part of the global biomass and provides habitat for large numbers of animal and plant species with varying levels of association. To humans, the importance of trees for food, timber and non-timber resources has been historically and widely identified (Cazorla and Mercado-Blanco 2016). Carbon sequestration is one of the most significant ecosystem services provided by trees, with

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total carbon stocks in UK forests (including soil) alone calculated at 800 megatons (Quine et al. 2011).

The economic value of trees and shrubs in urban landscapes has been increasingly recognised since the turn of the millennium, with the popularisation of electronic tools for estimating this value, e.g. i-Tree software, and research revealing a suite of functional benefits; providing habitat to urban wildlife, reducing air pollution, intercepting rainfall, shading and reducing heat absorption by man-made surfaces (Binner et al. 2017; Nowak 2004; Tyrväinen et al. 2005; Xiao and Mcpherson 2002). The cultural services provided by trees are also significant, offering both physical and mental health benefits. The capitalised value of the social and environmental benefits provided by woodlands and forests in the UK alone was estimated to be over £29 billion (Lawrence et al. 2009; Willis et al. 2003).

However, trees in particular can be susceptible to attack from pests and diseases (Table 1), especially if invading from other geographical locations (Hansbrough 1965; Tubby and Webber 2010). Most diseases are caused by microbial pathogens (fungi, bacteria and viruses), the effects of which are amplified during periods of unfavourable environmental conditions including unseasonal temperature shifts and extremes in rainfall patterns (Cazorla and Mercado-Blanco 2016) and anthropogenic climate change (Dukes et al. 2009; La Porta et al. 2008; Sturrock 2012; Sturrock et al. 2011; Tubby and Webber 2010).

Tree pest invasions are also increasing alongside climate change and expanded global trade and may act in tandem with native or invasive diseases, as vectors or co-occurring on hosts, to greatly reduce the populations of particular tree species (Brasier 2008; Tubby and Webber 2010), with the potential to ultimately cause their local extinction.

Plant susceptibility to pests and diseases is often related to the stress level of the individual. Unfortunately, trees in urban areas, which have a particularly high value to humans, often face high stress levels. In urban areas, stress can arise from mismatching of the planting stock's ecological traits to the planting site, root deformities, damage and desiccation, planting at improper depths in unsuitable soils, poor nutrient and water availability, and increased exposure to pollutants, xenobiotics and contaminants (Aldhous and Mason 1994; Ferrini and Nicese 2002; Gilman et al. 2015; Grossnickle 2005; Pauleit 2003; Percival et al. 2006; Pfeiffer et al. 2014; Sjöman and Busse Nielsen 2010). Monocultures also pose a specific problem, as plants grown in monoculture are more susceptible to pest and disease outbreaks and are sensitive to changes in climate, which are less likely with polycultures (Sjöman et al. 2012). Lax biosecurity, including the importation of planting stock and tree products, can also drive biological invasions by tree pests and diseases, as has been demonstrated in Europe (Brasier 2008; Epanchin-Niell 2017; Potter et al. 2011). Some non-native pests are highly destructive and can cause substantial damage to forests and urban/suburban trees (Aukema et al. 2011). Such invasions often lead to significant changes in forest structure and species composition, which in turn lead to changes in ecosystem functions (Lovett et al. 2016). Given the range of pests and diseases that trees are facing, the long generation time of trees, the practical difficulty of working with many of them, and also the speed with which the environment is changing, we are faced with a very difficult challenge – how do we improve our disease and pest management to help trees survive?

Classical control approaches for tree pests and diseases

The application of plant protection products (PPPs) for the control of tree pests and diseases is already often limited by ecological concerns and modulated by the particular local context, as exemplified by the varied management of oak processionary moth, *Thaumetopoea processionea*., in Europe (Tomlinson et al. 2015). However, PPPs are well accepted within commercial tree fruit production and the tree care industry of North America.

Presently, PPPs are generally synthetic chemicals that disrupt the cellular function, or life cycle of the target organism. Other PPPs work on a physical basis e.g. killing insect or acarid targets on contact via suffocation, or abrasion of the exoskeleton and subsequent desiccation. These products are typically those formulated for use in agriculture. Aboveground and external tree pests and diseases are often controlled with aqueous sprays of PPPs to the foliage and bark. Specialised high-pressure spray systems can be used for such applications to large trees (Hirons and Thomas 2018).

Internalised pests and diseases, such as nematodes, are more difficult to reach due to their physical concealment within the host; adjuvants (additives) may improve the penetration of externally applied PPPs for such targets e.g. through bark (Garbelotto et al. 2007),

Table 1 Examples of some current major pathogens and pests of trees

Pathogen	Host	Symptoms	Reference
Oomycete *Phytophthora ramorum*	*Larix* spp. and *Quercus* spp. (sudden death)	Shoots and foliage can be affected. Visible as wilted, withered shoot tips with blackened needles. Trees with branch dieback can have numerous resinous cankers on the branches and upper trunk. It has killed millions of native oak and tan-oak trees in the USA	Davidson et al. (2003)
Fungus *Ceratocystis fagacearum*	*Quercus* spp. (wilt)	Symptoms vary between oak species. White oaks may suffer from scattered dieback in the crown to the death of a single limb of major fork. Red oak succomb to the disease usually within a month. Early foliar symptoms start as vein banding whch later develop to foliar necrosis. Thus far only recorded cases in the USA.	Juzwik et al. (2008) Yang and Juzwik (2017)
Fungus *Ceratocystis platani*	*Platanus* spp.	Wound coloniser causing cankers, xylem staining and restriction of water flow throughout the tree resulting in eventual death of the tree. In oriental plane, *Platanus orientalis*, parts of the crown can suddenly die. Can be identified by cankers on the trunk, defined by bluish-black to reddish-brown discolouration of sapwood and necrosis of the inner bark. Found in the United states and across Europe, such as in Greece, France and Turkey.	Ocasio-Morales et al. (2007) Lehtijarvi et al. (2018)
Fungus *Hymenoscyphus fraxineus*	*Fraxinus* spp. (Chalara ash dieback)	*Dark brown/orange lesions on leaves, diamond-shaped lesions may occur on stems which, if girdled, can cause wilting. The wood beneath lesions usually is strongly stained. Dieback can be seen throughout the crown, with dieback shoots and twigs at the edges of crowns. Originating in Asia but a serious pathogen across Europe.*	*Landolt* et al. (2016) *McMullan* et al. (2018)
Fungus *Cryphonectria parasitica*	*Castanea* spp. (blight)	Attacks the bark by entering cracks or wounds which may lead to crown dieback. Discolouration of the bark and dead bark forms sunken cankers. Pin-head sized, yellow-orange pustules develop on the infected bark and exude long, orange-yellow tendrils of spores in moist conditions. Pale brown mycelial fans may be found in the inner bark. Discolouration of the bark may be more visible in younger trees. Widespread thoughout the eastern US, China, Japan and many European countries with an abundance of sweet chestnut.	Rigling and Prospero (2017)
Fungus *Ophiostoma ulmi* and *O. novo-ulmi*	*Ulmus* spp. (Dutch Elm Disease)	Symptoms emerge in early summer as clusters of wilting/yellowing leaves that turn brown and fall. A mixture of healthy and suffering foliage may be seen as the disease progresses throughout the tree. Affected shoots die back from the tip and twigs may turn downwards. Exposing the outer wood on symptomatic twigs should reveal dark brown or purple streaks. When cut across, a dark brown stain may be present in the outer wood. Common across Europe, North America and Western Asia.	Brasier and Buck (2001)
Fungus *Rigidoporus microporus*	*Hevea* spp. (white root rot)	Fungal mycelium can be found on the tree collar. Multi-layered fruiting bodies form at the base of the tree and white/white-brown rhizomorphs can be seen on the root surface. Off season flowering may occur as well as yellow-brown discolouration of the foliage. Significant funal pathogen to timber and rubber industry in Indonesia, Malaysia, Sri Lanka and the Ivory coast.	Siri-udom et al. (2017) Khairuzzaman et al. (2017) Hamidson and Naito (2004)
Fungus *Colletotrichum acutatum*	*Olea* spp. (anthracnose)	Fruit rot. Soft to dark brown rot that produces an orange, gelatinous matrix in moist conditions and	Talhinhas et al. (2011)

Table 1 (continued)

Pathogen	Host	Symptoms	Reference
		mummification in dry as the fruit loses moisture. In spring there may be extensive yellowing of the leaf blade which in summer leads to premature fall of infected leaves. Found in the majority of olive growing countries.	Cacciola et al. (2012)
Fungus *Cytospora chrysosperma, Phomopsis macrospora,* and *Fusicoccum aesculi*	*Populus* spp. (canker)	Young twigs form brown, sunken, rough circle areas in the bark which may spread to the larger branches. Large cankers may form on the branches an trunk. Orange/orange-brown discolouration of bark is often seen exuding orange-brown viscouse liquid. Fruiting bodies in the bark make the canker appear pimpled. In later stages of infection, perithecial stroma form in the dead cankered areas. Widespread across North America, Europe and China.	Ren et al. (2013)
Fungus *Heterobasidion spp.*	Conifers and some deciduous trees	Symptoms may vary depending on the pathogen involved and host plant. White root rot fungus that in early stages of growth causes staining and discolouration of the host wood. Initial decay is usually pale yellow, developing to light brown and resulting in a white pocket rot with black flecks. Eventually results in tree death. Widespread across the Northern Hemisphere and cases in Australia.	Asiegbu et al. (2005) Garbelotto and Gonthier (2013)
Fungus *Dothistroma septosporum* and *Dothistroma pini*	Conifers (Dothistroma (red band) needle blight)	Yellow bands on needles develop into red bands, where small, black fruiting bodies can occur. Can cause needle dieback, defoliation and eventual tree death. Occurs worldwide. Severe cases in Southern hemisphere plantations of New Zealand, Australia, Chile and Kenya. Also found in North America, Canada and Europe.	Schneider et al. (2019) Barnes et al. (2004) Bradshaw (2004)
Bacterium *Xylella fastidiosa*	*Vitis* spp., *Citrus* spp., *Olea* spp. and several species of broadleaf trees	Leaf scorch/browning, wilting foliage and withering of branches. In extreme cases can result in dieback and stunted growth. Cases found in the Americas, Taiwan, Italy, France and Spain.	Simpson et al. (2000) Araújo et al. (2002) Almeida et al. (2019)
Most likely a decline syndrome with possible Bacterial pathogen components: *Brenneria goodwinii*, *Gibbsiella quercinecans, Rahnella victoriana*	*Quercus* spp. (Acute oak decline)	Stem bleeds occur on the trunk, weeping dark, translucent liquid. Bark cracks, which may reveal underlying dark, necrotic tissue. Lesions and 'D' shaped exit holes of *Agrilus biguttatus* may be present in the bark.	Denman et al. (2014)
Chronic oak dieback – Complex disorder or syndrome (also referred to as oak decline, dieback-decline)	*Quercus* spp. (particularly *Q. robur*)	Results from a combination of abiotic and biotic factors. Early foliage deterioration, gradual branch death and dieback in the crown. Abiotic stressors and weakening of trees allows for opportunistic attack from insects and disease which can result in tree death. Seen in the UK and across Europe.	Thomas et al. (2002) Gagen et al. (2019) Mitchell et al. (2019)
Bacterium *Xanthomonas citri* subsp. *citri*	Citrus cultivars (canker)	Distinct raised, necrotic lesions on fruits, stems and leaves. As the disease progresses, lesions on the stem can appear as corky, rough, dead tissue with a yellow halo. Present in South America, Africa, Middle East, India, Asia and South Pacific.	Graham and Leite (2004) Ference et al. (2018)
Bacterium *Erwinia amylovora*	Pome trees and rosaceous plants (fireblight)	Affects all above ground parts of the plant. The floral recepticle, ovary and peduncles turn a greyish green, eventually whithering to black. Creamy white bacterial droplets may emerge from affected tissues in humid conditions. Shoots wilt rapidly, forming 'Shepard's crooks', that turn necrotic. In later stages, bark becomes	Mohan and Thomson (1996) Johnson (2015) Schropfer et al. (2018)

Table 1 (continued)

Pathogen	Host	Symptoms	Reference
		cracked, sunken and may leak amber bacterial ooze. Found across North America, Central Europe, Israel, Turkey Lebanon and Iran.	
Bacterium *Candidatus Liberibacter* spp.	Citrus trees (Huanglongbing disease)	Blotchy, asymmetric mottling of newly mature leaf blades. Fruit may exhibit stunted growth, premature drop and low soluble acid content. Found across Asia, America and Africa.	Kalyebi et al. (2015)
Bacterium *Pseudomonas syringae* pv *aesculi* (*Phytophthora cactorum* and *Ph. plurivora*)	*Aesculus hippocastanum* (Bleeding canker of Horse Chestnut)	Rusty-red/brown/black gummy ooze found on the bark. Dead phloem under the bleeds which may appear mottled orange-brown. In extensive cases where affected areas encircle the trunk or branch, leaf yellowing and defoliation may occur and eventual crown death. Fungal bodies may also be seen in areas of dead bark. Found across the UK and Europe, including France, Netherlands, Belgium and Germany.	Webber et al. (2008) Green et al. (2009) Green et al. (2010)
Asian longhorn beetle *Anoplophora glabripennis*	Wide range of broadleaved trees	Adults are about 20-40mm long, black with white makings and long, black and white antennae. Oval shaped pits on scraoed into the bark where eggs are laid, occasional sap may be visible bleeding from the damaged areas. Galleries in bark may be up to 10mm in diamteter and several cm long. Wood shavings may be found in distinctive chambers where pupation occurs. Large, circular exit holes from emerging adult beetles in the upper trunk and branches, usually 10mm in diameter. Piles of sawdust may be found at the base of infested trees. Originally from China and the Korean peninsula, now found in the USA, Italy and across the EU.	McKenna et al. (2016) Haack et al. (2010)
Beetle *Dendroctonus micans*	*Picea* spp.	Resin bleeding on stems with resin tubes coloured purple-brown with bark particles where the female enters the trunk. Attacks may occur anywhere on tree. Found across Europe.	Yaman et al. (2010) Wainhouse et al. (1990)
Leaf miner *Cameraria ohridella*	*Aesculus* spp.	In early summer, elongated blotches appear white at first but turn brown throughout the foliage. Caterpillars or pupal cocoons may be seen within mined areas. Heavily infested trees may drop their leaves prematurely. Spread throughout central and eastern Europe.	Pocock and Evans (2014) Gilbert and Tekauz (2011)
Lappet moth *Dendrolimus pini*	*Pinus* spp.	Needle defoliation and subsequent tree death. Prescence of cocoons on trunk. Native to Europe, Russia and Asia.	Ray et al. (2016)
Oak processionary moth *Thaumetopoea processionea*	*Quercus* spp.	Voraciously feed on the foliage of oak trees. Large populations lead to significant defoliation, making the tree susceptible to other threats. Found in Central and Southern Europe. In the UK, outbreaks are localised to London and a few neighbouring counties.	Freer-Smith et al. (2017) Quero et al. (2003)
Ambrosia beetle (Black timber bark beetle), *Xylosandrus germanus*	Wide range of hardwood host species	Infestations can be indentified by entry holes into the bark and distinctive, compact cylindrical frass about 3-4cm in length. Other indications of their presence include wilting and yellowing of the leaves, defensive sap production and dieback. Native to East Asia but has spread across North America, Europe and the Caucasus region.	Agnello et al. (2015)
Citrus longhorn beetle *Anoplophora chinensis*	Deciduous and shrub species	Adult males are about 21mm long, females 37mm. They are black with white markings, with distinctive, long antennae. Symptoms include feeding damage from adult beetles on bark and twigs, circular exit holes in bark and 'T' shaped oviposition slits where eggs are laid within the bark tissue. Tunnelling in bark and larval galleries may cause structural weaknesses, disrupt the	Eschen et al. (2015) Eyre et al. (2010) Haack et al. (2010)

Table 1 (continued)

Pathogen	Host	Symptoms	Reference
		vascular system and result in eventual plant death. Native ranges of China, Japan and Sout East Asia although incidences have occurred in Europe, such as in the Netherlands, Germany, France, Italy, Croatia, Switzerland and the UK.	
Oak Pinhole Borer *Platypus cylindrus*	*Quercus* and other hardwood species	Adult beetles are blackish in colour, 5-7mm long. Usually establishing in stressed trees, galleries about 1.6mm wide are made in the bark with bore dust appearing pale and fibrous. The beetles introduce ambrosia fungi for their nourishment, principly *Raffaelea* spp., which stains the surrounding wood blacky-brown. Found across Europe and North Africa with some incidences occuring in healthy Portuguese trees.	Belhoucine et al. (2011) Bellahirech et al. (2016) Inácio et al. (2011)
Pine wood nematode *Bursaphelenchus xylophilus*	*Pinus* spp. (wilt disease)	Discolouration of some/many branches from green to yellow. Rapid loss of resin flow occurs in 48 hours. Found in Japan, China, Korea, Taiwan, Portugal and Spain.	Futai (2013) Odani et al. (1985)

although many products will still not be transported significantly within the tree. Some PPPs can be injected into the vascular system at the base of the tree and transported upwards e.g. emamectin benzoate used in the control of Emerald Ash Borer larvae in North America (Smitley et al. 2010). The neonicotinoid compound imidacloprid is a soil applied insecticide that is taken up through roots and into the whole plant. However, neonicotinoids face severe restrictions on their use in many countries due to associations with negative impacts on bees (Goulson 2013). Control of fully internalised diseases of trees are also a particular issue, for instance, one of the difficulties in controlling *Verticillium dahliae* and *Xylella fastidiosa* in olive (*Olea europaea*) and grapevine (Baccari and Lindow 2011) is due to the inaccessible location of the pathogen within the vascular system (Cazorla and Mercado-Blanco 2016). Similar difficulties are faced in the control of Huanglongbing disease, *Candidatus liberibacter* spp., which causes citrus greening and is a phloem-limited phytoplasma spread by insect vectors (Abdullah et al. 2009).

Root and soil-borne pathogens have been treated by injections into the soil of PPPs or sterilizing agents such as phenolic compounds or methyl bromide gas (Martin 2003; West and Fox 2002). While many synthetic PPPs break down quickly when exposed on stems or foliage, soil applied compounds may persist for extended periods once bound to soil particles (Edwards 1975).

Stump treatments, e.g. urea, sodium borate, or the saprobic fungus *Phlebiopsis gigantea*, have also been applied to exclude and reduce the build-up of fungal pathogens that can also utilize buried dead wood saprobically, often *Heterobasidion* spp., but may also exclude *Armillaria* spp. and other basidiomycetes, while allowing non-pathogenic species to proliferate (Nicolotti and Gonthier 2005; Nicolotti et al. 1994; Vasiliauskas et al. 2004).

In Europe, and elsewhere, environmental concerns have fuelled a movement away from synthetic “chemical” PPPs or those based on toxic heavy metals e.g. copper (Lamichhane et al. 2018). In the absence of other effective controls this reduction in authorised pesticides may conflict with protecting vital resources such as food and timber.

Biocontrol agents (BCAs)

An area that is gaining much more attention in recent years is biological control (or biocontrol) – the use of biological agents to counter a pest or disease. The desired outcome of a biological control application is to reduce the pathogen or pest population below a threshold of ecological and economic impact, ideally enabling the host to regain health and eventually restoring the invaded community to the pre-invaded state (Bale et al. 2008). This approach is highly favourable because most BCA source species are already present in the host’s environment, and in some cases provide a narrow range of target specificity, so are less likely to be harmful to non-target organisms. BCAs can come in many forms, from viruses or bacteriophage, to bacteria or fungi, and even higher organisms like nematodes, mites or insects (Lenteren et al. 2018).

As PPPs, BCAs are generally applied in similar ways to synthetic compounds and the selected application method typically aims to maximise contact with the target organism. *Bacillus subtilis* QST 713 is a commercialized bacterial strain used in biocontrol programmes around the world (Abbasi and Weselowski 2014). For foliar pathogens like *Botrytis* of fruit or nut trees, *B. subtilis* QST 713 is applied as an aqueous spray, whereas for protection against *Phytophthora* root rots it is applied as an aqueous drench, e.g. via pressurized soil injection systems or irrigation. BCAs may also be physically incorporated into soils (Abbasi and Weselowski 2015). For example, *Trichoderma* strains, often grown on a solid food source such as grain, but also as spore powders, are variously mixed into the soil around roots or placed in cores in close proximity to roots for the treatment of root diseases (Srivastava et al. 2016). One study demonstrated that trunk injections of various *Bacillus* strains into the vascular system of Avocado trees, *Persea americana*, reduced the disease severity of *Phytophthora cinnamomi* infections (Darvas and Bezuidenhout 1987). However, as with the majority of studies discussed in this review, this control method does not appear to have been commercialized or widely utilized to date.

Nematodes, which are used against slugs and snails or insect larvae feeding on roots within the soil, may be dispersed in water and applied to the target area as a drench. Although relatively understudied, nematodes and other soil microfauna e.g. springtails, also have potential in the integrated control of soil borne fungal plant pathogens (McGonigle and Hyakumachi 2001, Riffle 1973, Tomalak 2017). Control of stem boring *Zeuzera pyrina* larvae has been demonstrated by injecting nematode suspensions into the stem cavities created by the larvae (Ashtari et al. 2011). The spores of *Verticillium* strain WCS850 have been applied to Elm trees (*Ulmus* spp.) via punctures in the bark of the tree to induce host resistance to Dutch Elm Disease, caused by the pathogens *Ophiostoma ulmi* and *O. novo ulmi.* The BCA itself does not move far from these sites and the disease is controlled via plant-mediated effects (Scheffer et al. 2008).

Natural enemies are also a popular option for biological control of insect pests in agroforestry settings (Dix et al. 1995). Insects as BCAs have shown great applicability for controlling pests of woody plants, forming around 55% of such introductions up until 2010. The establishment rates of natural enemies and success rates were higher when targeting pests of woody plants than other pests (Kenis et al. 2017). Aphids cause extensive economic losses around the world, as one of the major pest groups of crops plants but are also problematic for trees. To control and counter this, aphid predators, including ladybird larvae, lacewings and gall midges as well as adult spiders, carabids (Carabidae) and rove beetles (Staphylinidae) are used in integrated pest management strategies (Evans 2009; Gardiner & Landis 2007; Messelink et al. 2013; Schmidt et al. 2004; Snyder & Ives 2003). However, the efficiency of control is limited due to insufficient post-application persistence, slow kill rate and high host specificity, in combination with generally high production and maintenance costs, and thus contribute to restricted use in pest control.

The greatest challenges of using BCAs with trees, however, relate to the scales associated with trees – many are very large, thus restricting access to the whole tree and canopy, and woodlands can occupy great areas. Arguably, there is also a dearth of information on many tree diseases and pests, especially for newly emergent outbreaks where monitoring endeavours are struggling to keep up with the incidence and speed of outbreaks (Boyd et al. 2013).

Other major challenges in developing BCAs are the identification, characterisation, formulation and application of the agents. Laboratory analyses may not be reliable predictors of the protective capability of biocontrol agents. For example, the modes of action for most BCAs are still not fully understood, and there is no efficient and effective screening method for identifying field-competent BCAs by laboratory tests (Parnell et al. 2016). The development of appropriate screening methods for BCAs may therefore rely on studies of their interaction with plants, which would slow the screening process. Factors affecting production and delivery of a BCA from laboratory to field include loss of viability, storage stability, environmental conditions, compatibility with other microorganisms, and consistent efficacy over multiple time periods including seasonal variations (Bashan et al. 2013; Slininger et al. 2003). In comparison to synthetic PPPs, storage requirements for preserving BCA product efficacy can be far more varied and particular, which has been a major issue historically (Bashan et al. 2013; Corkidi et al. 2005).

In this review, we will examine the options for using BCAs for tree diseases and consider how they might be used. In particular, we will focus on endophytes, which are a relatively understudied group. Presented here are examples of endophytes reported as biological control agents in the literature, and most have not been commercialized, but have proven effects under laboratory conditions.

Endophytes as BCAs

Endophytes are defined as microorganisms that accomplish part of their life cycle within living host tissues without causing apparent damage to the plant (Schulz and Boyle 2005; Sun et al. 2014). In all ecosystems, many plant parts are colonized by endophytes (Brundrett 2002; Mandyam and Jumpponen 2005). Depending on the species and the interaction, endophytes may be located in roots, leaves or needles, shoots, or adapted to growth within the bark (Grünig et al. 2008; Rodriguez-Cabal et al. 2013; Sokolski et al. 2007; Verma et al. 2007). Endophytes may grow inter– and intra– cellularly as well as endo– and epi– phytically (Schulz and Boyle 2005; Zhang et al. 2006). However, endophytes can switch their behaviour depending on a set of abiotic and biotic factors, including the genotypes of plants and microbes, environmental conditions, and the dynamic network of interactions within the plant biome (Hardoim et al. 2015; Schulz and Boyle 2005).

Plant ecosystems rely heavily on their microbial communities to optimise health (Pfeiffer et al. 2014), though this intimate association can be a fine balance between mutualism and disease (Knief 2014). Microbes (as epiphytes) can colonise the surfaces of roots (rhizoplane) and leaf/shoot (phylloplane) as well as the internal spaces of plants (as endophytes), with overall abundance being higher for epiphytes compared to endophytes, and rhizosphere compared to phyllosphere (Lindow and Brandl 2003). These differences may reflect the short life span of leaves, nutrient richness in the rhizosphere, and the ability of microorganisms to survive in soil in a dormant state for long periods of time (Vorholt 2012) or due to the physiochemical variations between these two respective environments (Lindow and Brandl 2003).

Endophytes can act in defence against pathogens and disease (Ownley et al. 2004), as well as provide protection or act as deterrents to insect herbivores and nematodes (Breen 1994; Slippers and Wingfield 2007; Vega et al. 2008). However, these defensive properties may not be unanimous to every endophyte-host-pathogen interaction, as shown by Gonthier et al. (2019) where investigations into the protective benefits of ectomycorrhizal fungus *Suillus luteus* in Scots pine (*Pinus sylvestris*) against the fungal pathogens *Heterobasidion irregular* and *Heterobasidion annosum* found that it only reduced host tree susceptibility to *H. annosum*, not both pathogens.

The roles of endophytes in disease and pest resistance are comparatively understudied, but recent work has started to highlight the importance of endophytes, in particular, as an increasingly popular biological control option (Dutta et al. 2014; Gao et al. 2010). Endophytes are also being increasingly recognised as potential controls of significant economic threats such as the invasive spotted lanternfly in North America (Eric et al. 2019).

Isolation and identification of endophytes

Traditionally, the research of endophytes has focussed on identification of culturable fungi and bacteria from plants has involved culturing them from plant tissue on different media. Although successful, it is apparent from the use of culture independent approaches (e.g. metagenomics), that the true diversity and abundance of the endophytic community has not been fully represented or utilized (Bisseling et al. 2009). As a result, it is highly likely that a range of potential candidate organisms with beneficial and exploitable biocontrol capabilities are being overlooked (Moricca et al. 2012; Ragazzi et al. 2001). Slower growing endophytic species are likely to be outcompeted or inhibited in the medium by more rapidly growing species. Other species may be as yet unculturable due to lack of a key growth component, because of an obligate relationship with their host plant for survival or due to a range of environmental parameters. Culture-dependent methods tend to favour the dominant endophytic species, so rarer species that have an irregular existence, are likely to be missed in any sampling effort (Moricca and Ragazzi 2008). However, methods used to isolate, and study endophytes have continued to be improved in light of developments in genetics and genomics. The advancements in next generation sequencing (NGS) has greatly improved the study of endophytes by allowing enormous amounts of genetic sequence data to be processed in parallel at a fraction of the cost of traditional methods (Knief 2014; Rastogi et al. 2013). Metagenomic analysis employing NGS of whole microbial communities allows much deeper and more accurate DNA sequencing, thus providing insight into the composition and physiological potential of plant-associated microorganisms. NGS reveals both culturable and unculturable endophytes that may be beneficial microbes and appropriate isolation media can then be developed to further study these species of interest (Akinsanya et al. 2015). For example, the presence of endophytic fungi in roots of different plant species in a temperate forest in Japan were identified using NGS (Toju et al. 2013), while whole genome analysis of endophytic microbes has revealed the genetic features that directly or indirectly influence the various bioactivities and colonisation preferences (Kaul et al. 2016). Identification, isolation and characterisation of genes involved in beneficial endophyte-host interactions is critically important for the effective manipulation of the mutualistic association between the two. Endophyte genomic analysis has provided a new tool to pick apart the mechanisms of endophytic associations and to reveal the requisite features needed to inhabit plants. Studies have revealed a wide range of specific genes commonly found across genomes that are important for endophytic lifestyles and symbioses. These include genes coding for nitrogen fixation, phytohormone production, mineral acquisition, stress tolerance, adhesion and other colonization related genes (Firrincieli et al. 2015, Fouts et al. 2008, Kaul et al. 2016, Martínez-García et al. 2015).

Examples of tree endophytes as BCAs

As BCAs, endophytes have diverse mechanisms of action, categorised into direct, indirect or ecological effects (Gao et al. 2010). Endophytes may possess the ability to directly inhibit pathogens by producing antifungal or antibacterial compounds. For example, the endophytic bacterium *Bacillus pumilus* (JK-SX001) is particularly efficient at reducing the infection rate and severity of canker caused by three pathogens (*Cytospora chrysosperma*, *Phomopsis macrospora* and *Fusicoccum aesculi*) in Poplar cuttings. This *Bacillus* strain produces a combination of extracellular enzymes (including cellulases and proteases) and other secondary metabolites that are thought to inhibit the mycelial growth of the pathogen (Ren et al. 2013). When *B. pumilus* (JK-SX001) was applied as a root drench, the bacterial cells migrated from the roots up to the leaves and were reported to also increase host photosynthetic activity and ultimately increase biomass production in the saplings, while suppressing pathogenic activities. These results were promising, but the experiments were performed under greenhouse conditions using fast growing, young cuttings that were sensitive to the canker pathogens. These young trees were easier to inoculate and probably more likely to respond to pathogens and colonisation by endophytes than mature trees.

In another study, the pathogen *Phytophthora meadii*, which causes abnormal leaf fall of rubber trees (*Hevea brasiliensis*), was suppressed using the endophytic bacterium *Alcaligenes* sp. (EIL-2) isolated from healthy rubber tree leaves. In dual cultures, *Alcaligenes* sp. (EIL-2) produced a substance that inhibited hyphal growth of the pathogen. When the endophyte was applied as a foliar and soil drench to one-year old greenhouse plants prior to infection by the pathogen, infection rates were reduced by more than 50% (Abraham et al. 2013). Whilst promising in scope, trials need to be conducted in natural systems to ascertain effectiveness *in situ*.

Species of *Pseudomonas* were the most commonly isolated endophytes antagonistic to the oak wilt fungus, *Ceratocystis fagacearum* (Brooks et al. 1994). When grown in dual culture, these endophytes produced siderophores and/or antibiotic compounds in response to the pathogen. Injecting trees with *Pseudomonas denitrificans* reduced crown loss to *C. fagacearum*, but the response varied depending on what time of year the inoculum was introduced. Seasonal changes affect the physiological state of trees and therefore the availability of nutrients in their vascular system to the introduced endophytes (Brooks et al. 1994), which is likely to influence efficacy of the endophytic BCA.

Berger et al. (2015) compared foliar applications of phosphite, and the endophytes *Trichoderma aureoviride* UASWS and *T. harzianum* B100 on reducing the necrotic area of *Phytophthora plurivora* lesions on oak leaves (*Quercus robur*). Results showed that given the diffusable nature of phosphite it was able to reduce necrosis on both treated and untreated leaves. However, with UASWS and B100, only untreated leaves showed reduced necrosis suggesting that the interaction was affected by a number of fungal secondary metabolites. However, when applied via trunk injections (endotherapy) a similar endophyte, *T. atroviride* ITEC was able to significantly reduce the necrosis size, compared to the control and the phosphite treatment, on 30-year-old beech trees (*Fagus sylvatica*) artificially inoculated with *P. plurivora.* It is clear from this example that the effectiveness of an endophytic BCA is likely to be influenced by the mode of application.

Endophytes may induce such delocalized plant defence reactions, called induced systemic resistance, leading to a higher level of host tolerance toward pathogens (Robert-Seilaniantz et al. 2011; Zamioudis and Pieterse 2012). There is increasing evidence that in the initial stages of endophyte colonisation, interactions between beneficial microorganisms and plants trigger an immune response in plants similar to that against pathogens, but that, later on in the plant growth stage and/or interaction stage, mutualists escape host defence responses and are able to successfully colonize plants (Zamioudis and Pieterse 2012). The shoot endophyte *Methylobacterium* sp. strain IMBG290 was observed to induce resistance against the pathogen *Pectobacterium atrosepticum* in potato, in an inoculum density-dependent manner (Pavlo et al. 2011). The observed resistance was accompanied by changes in the structure of the innate endophytic community. Endophytic community changes were shown to correlate with disease resistance, indicating that the endophytic community as a whole can play a role in disease suppression (Pavlo et al. 2011). Inoculation of white pine (*Pinus monticola*) seedlings with native fungal endophytes reduced disease severity caused by *Cronartium ribicola,* the causal agent of white pine blister rust. The results were temporally persistent suggesting a form of induced resistance. However, the authors did not measure any gene expression or defence pathways to confirm this hypothesis (Ganley et al. 2008).

Inoculation of part of a plant with an endophyte may benefit plants via the production or suppression of phytohormones; for example, genes encoding proteins for biosynthesis of indole acetic acid (IAA) (Zúñiga et al. 2013), cytokinins (CKs) (Bhore et al. 2010) and gibberellins (GAs) (Shahzad et al. 2016) are often present in the metagenome of plant endophytic bacterial communities (Liu et al. 2017). Induction of jasmonic acid biosynthesis enhances localized resistance to biotic agents such as *Hylobius abietis* (large pine weevil) (Heijari et al. 2005), *Ceratocystis polonica* (bluestain fungus) (Krokene et al. 2008; Zeneli et al. 2006) and *Pythium ultimum* (white root rot) (Kozlowski et al. 1999). Mycorrhizae can influence tree susceptibility and tolerance to economically important root pathogens such as *Heterobasidion* spp. and *Armillaria mellea*, even in the absence of direct antagonism of the pathogen by the endophyte (Gonthier et al. 2019; Nogales et al. 2010). Mycorrhizae are well recognized for their positive influence on tree growth and health so may antagonise pathogens via plant-mediated responses or ecologically through inhabiting the same niche, as is seen in other endophytes. The economically important tropical tree, *Theobroma cacao,* is a natural host to endophytes that can significantly reduce the foliar damage caused by a *Phytophthora* species (Arnold et al. 2003). Leaves inoculated with endophytes showed reduced leaf necrosis and mortality when exposed to the foliar pathogen compared to endophyte-free leaf controls. The method of defence appears to be either direct or ecological and not one of induced plant resistance. Only leaves inoculated with the endophytes were resistant to *Phytophthora* infection. This may pose a problem for feasible endophyte application as a BCA if effective disease control is dependent on each individual leaf being sprayed with the endophyte inoculum.

Host-associated microbes can colonize the host horizontally via the environment, vertically from within the parent to the offspring, or by mixed transmission modes (Bright and Bulgheresi 2010). Ecological and evolutionary relationships affect transmission mode and vice versa (Frank et al. 2017). Theory predicts that vertical transmission evolves when symbiotic partners are mutualistic, as a way to ensure faithful transmission of the beneficial symbiont from one generation to the next (Herre et al. 1999). Vertical transmission of bacterial symbionts from parent to offspring is, indeed, common in systems where the symbiont provides an indispensable function, as in the extensively studied nutritional symbioses between bacteria and insects (Moran 2006). Vertical transmission via seeds is also well documented for certain groups of fungal endophytes, e.g., the well-studied *Epichloë* fungal endophytes of grasses (Schardl 2001).

Entomopathogens including fungi, nematodes and bacteria, naturally play important roles in regulating insect populations and are being exploited in biocontrol strategies (Lacey et al. 2015). Miller et al. (2002) investigated the effects of endophytic organisms in white spruce trees (*Picea glauca*) on the pest spruce budworm. They observed that larval growth was significantly affected by the presence of the endophytes, with some strains proving toxic to the insects. Production of endophytic metabolites is thought to have been the antagonistic factor and in a follow-up study conducted by Miller (2008), the presence of rugulosin toxin produced by the needle endophyte in nursery grown *P. glauca* significantly reduced budworm (*Choristoneura fumiferana*) growth. Decreased palatability for insects and antagonism towards pathogens of needles might be possible benefits for the host trees. Sieber (2007) also found that the colonization of elm bark by *Phomopsis velata* had significant effects on two beetle pests of bark, *Scoltus scolytus* and *Scolytus multistriatus*. These beetles are known vectors of the Dutch Elm disease pathogen *Ophiostoma ulmi* and on introduction of *P. oblonga*, there was a noticeable reduction both in beetle galleries as well as larval success rate thus providing evidence in support of an effective biocontrol agent. In addition to the discovery of more effective isolates and toxins, an increase in the use of entomopathogens will rely on innovations in formulation and better delivery systems.

Challenges in biocontrol of tree pathogens and pests with endophytes

Climate change has and will continue to alter the ranges of pests and diseases and aid their establishment by subjecting plants to stress (Shaw and Osborne 2011). Occurrence of extreme temperatures and weather events, such as heatwaves and flooding, are increasing in frequency worldwide as CO_2 levels increase and thus our natural capital may require active management to protect its current condition (Fischer and Knutti 2015; Hailey and Percival 2015).

Climate change is predicted to have a profound impact on the distribution, abundance, physiology, productivity, phenology, behaviour and ecology of all plant species (Hughes 2000; Nooten et al. 2014). Forest species are particularly susceptible to climate change as the higher longevity of trees hinders rapid adaptation (Broadmeadow et al. 2005; Lindner et al. 2010). Moreover, climate change is known to impact plant-associated microbes some of which play critical, mutualistic roles in maintaining healthy environments. For example, climate change is likely to impact the dispersal of mycorrhizal fungi, key symbionts of trees, which may in turn limit tree migration and colonisation of novel habitats (Pickles et al. 2015). Warming may induce a decrease in arbuscular mycorrhizal fungal colonisation, as has been demonstrated in a manipulated Mediterranean climate, with a likelihood of significant impacts on plant communities and ecosystem function (Wilson et al. 2016).

It has also been recognised that changes in the environment or host can alter the nature of the host-endophyte interaction (Schulz and Boyle 2005). When a tree is subjected to physiological or environmental stress the intimate plant-endophyte relationship is altered and the endophyte may become pathogenic. For example, the fungal endophyte *Discula quercina,* which inhabits healthy *Quercus cerris* trees, causes damage to host structure and function when the tree experiences drought stress (Moricca and Ragazzi 2008; Ragazzi et al. 2001). *Picea abies* (Norway spruce) and other conifers are predicted to become unsuitable for forestry in the central regions of Europe due to rises in temperature (Breymeyer 1996; Fanta 1992), especially at lower elevations (Lexer et al. 2002), which may subject the present large spruce forests to severe stress in the future. Similarly, altered climates may affect BCA function and efficacy. Climate change may also change the lifecycles and feeding behaviour of phytophagous insects, with vector-mediated impacts on tree disease spread (Battisti 2008). It is therefore possible that we will observe an increasing incidence of disease in trees caused by endemic endophytic species, in addition to and potentially interacting with highly destructive pest invasions.

Numerous factors play a role in the under implementation of BCAs for control of diseases in trees and woody plants. These include the size, area, complex root system, inoculum size, and impact of release on the associated ecological system. Many of the difficulties are shared with conventional PPPs, such as reaching internal pests and diseases. Arthropod pests of crops and trees are extremely diverse like their hosts and thus can be notoriously hard to control. Rapid reproduction rates of some of these species (e.g. aphids, gypsy moth, and spruce budworm) mean dense infestations can arise rapidly, reaching levels damaging the plants that then leads to losses that impact both the environment and local and regional economies. Furthermore, different life cycle stages mean that one method of control may not be adequate to manage a pest population effectively, such as in the case of scale insects (Mansour et al. 2017). There is a general consensus that the detrimental effects of insect pests on crops and woody plants are set to worsen with accelerated climate change and control of these will be required for agriculture to keep up with the demands of a growing world population (Dukes et al. 2009).

Effects of introduction of ‘alien’ species. What are the consequences?

It is as yet unclear as to whether endophytes introduced as BCAs on plants may be effective in reducing disease, but another important aspect is to understand if they have adverse effects on the natural microbial community of the host when the plant is under environmental stress. The introduction of endophytes that have not co-evolved with the host plant may result in the loss of beneficial organisms and so negatively impact the host plant (Whipps 2001). Furthermore, it is important to consider whether the gains provided by the endophyte outweigh the costs associated with it. For example, gall wasps are a problematic species to trees. However, *Apiognomonia errabunda*, the dominant endophyte in beech leaves, has been found to cause abscission of galls by forming necrotic tissue around the affected area, but this may, in time, prove to be more harmful to the host than the gall would have been (Sieber 2007). Furthermore, there is also a risk that some endophytes may not be as useful as hoped in integrated pest management systems as they may affect the efficacy of other BCAs employed to combat pest species. Bultman et al. (2017) found that although endophytes proved effective against plant herbivores, they had repercussions higher up the trophic chain, significantly affecting the performance of parasitoids by reducing pupal mass, which would reduce the parasitoids’ success as a BCA.

Pros of using endophytes as BCAs

1. No known adverse environmental effects of native endophytic biological control agents as they are already present in the plant ecosystem.
2. Ability to colonize internal host tissues, the same ecological niche as pathogens, allowing persistence and competition for resources in addition to antagonism. The internal tissue also protects the biological control agent from dangerous UV rays and temperature fluctuations therefore they can persist for longer periods of time.
3. As well as controlling infection, endophytes may simultaneously promote plant growth, for example by increasing photosynthetic activity (Ren et al. 2013).
4. Narrow range of target specificity, less likely to be harmful to non-target organisms.
5. Endophytes may induce systemic resistance in the host and may consequently induce resistance against other pathogens and/or pests (Zamioudis and Pieterse 2012).
6. Pathogens may be less likely to acquire resistance to endophytic BCAs than they are to pesticides due to dynamic interactions.

Cons of using endophytes as BCAs

1. Most research to date has taken place in laboratory conditions, but it is unknown how the endophyte-pathogen interaction will alter in the presence of changing environmental conditions and competition with other organisms in the tree ecosystem.
2. More research must be conducted to find the optimum time for delivery of biocontrol agent inoculum, as seasonal changes in weather and tree physiology could alter efficacy (Brooks et al. 1994).
3. In some cases, resistance to pathogens is isolated only to the plant part that is inoculated with endophytic control. Delivery, and systemic transmission, of BCA to whole tree is likely to be difficult in many cases.
4. Possible changes in host-endophyte-pathogen interaction with climate change, could the endophyte itself become a pathogen? (Moricca and Ragazzi 2008; Ragazzi et al. 2001).
5. Endophytic BCA may alter the microbial community of the host tree, which may adversely affect the host or may have consequences at higher trophic levels.

Conclusion

With growing concern about environmental pollution and the harmful effects of chemicals, the use of biological control as an alternative environmentally friendly option is becoming necessary. The traditional breeding of trees for resistance remains one potential route, but it is a strategy that might be outpaced by the spread and introduction of pests and diseases, as well as being a time consuming and sometimes difficult task. Despite the challenges confronting biocontrol of tree diseases and pests, research shows that endophyte treatments can be successfully implemented and there is clear potential for endophytes to be applied to trees as BCA in the future. However, it is unclear how the endophyte enters the plant tissues and disperses throughout the plant. The efficacy of the biocontrol method can be enhanced by integrating it with complimentary cultural and environmental conditions to stimulate plant health and enhance inhibition of the pathogen or pest, but this still requires more attention in the future. Advancements in molecular techniques, such as NGS, are revealing more accurate community structures and, as new environments are studied, it is very likely that new bacterial and fungal species will be discovered and enable the dissection of community effects of individual organisms. Application of community analysis and metagenomics technologies in future studies will advance understanding in both plant-microbe associations and biological control science, with endophytes being prime candidates for use as BCAs.

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Compliance with Ethical Standards

Conflict of interest The authors confirm no conflict of interest.

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