

Rhizosphere microbiota interferes with plant-plant interactions

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Abstract Diversity, structure and productivity of above-ground compartment of terrestrial ecosystems have been generally considered as the main drivers of the relationships between diversity and ecosystem functioning. More recently it has been suggested that plant population dynamics may be linked with the development of the below-ground community. The biologically active soil zone where root-root and root-microbe communications occur is named “Rhizosphere” where root exudates play active roles in

regulating rhizosphere interactions. Root exudation can regulate the soil microbial community, withstand herbivory, facilitate beneficial symbioses, modify the chemical and physical soil properties and inhibit the growth of competing plant species. In this review, we explore the current knowledge assessing the importance of root exudates in plant interactions, in communications between parasitic plants and their hosts and how some soil microbial components could regulate plant species coexistence and change

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relationships between plants. This review will be focussed on several well documented biological processes regulating plant-plant communications such as exotic plant species invasions, negative root-root communication (allelopathy) and parasitic plant / host plant interactions and how some soil microbial components can interfere with signal traffic between roots. The reported data show that the overall effect of one plant to another results from multiple interacting mechanisms where soil microbiota can be considered as a key component.

Keywords Allelopathy · Rhizosphere · Plant invasions · Plant-soil feedbacks · Parasitic plant

Introduction

Plant biodiversity and species composition are regulated and maintained in terrestrial ecosystems by different biological processes such as competition between neighbouring plants (Aarsen 1990; Grace and Tilman 1990), spatial and temporal resource partitioning (Ricklefs 1977; Tilman 1982), disturbance creating new patches for plant colonization (Grubb 1977) and interactions with other organisms in the ecosystems (Bever et al. 1997). Diversity, structure and productivity of above-ground compartment of terrestrial ecosystems have been generally considered as the main drivers of the relationships between diversity and ecosystem functioning. There is also extensive knowledge on how abiotic and biotic soil factors interact with vegetation (Wardle 2002). For instance it is well known that at local scales the composition and activity of microbial communities are mainly subjected to plant factors such as species composition and formation age (Priha et al. 1999; Grayston et al. 2001) as well as environmental factors such as soil type, nutrient status, pH and moisture (Stotzky 1997). Recent studies have reported that local interactions between plants and microbial communities strongly influence both plant and soil community composition and ecosystem processes (Bever 2003). The biologically active soil zone where root-root and root-microbe communications occur is named “Rhizosphere” (Hiltner 1904). The rhizosphere is a densely populated area where root exudates play active roles in regulating rhizosphere interactions. Root exudation can regulate the soil microbial

community, withstand herbivory, facilitate beneficial symbioses, modify the chemical and physical soil properties and inhibit the growth of competing plant species (Bais et al. 2004). In terrestrial ecosystems, most of plant species are commonly associated with arbuscular mycorrhizal (AM) fungi that are considered as a key component of the microbial populations influencing plant growth and uptake of nutrients (Johansson et al. 2004). AM symbiosis generally increases root exudation (Graham et al. 1981), modifies carbohydrate metabolism of the host plant (Shachar-Hill et al. 1995) and influences rhizosphere microbial communities (Marschner and Timonen 2005). In addition, mycorrhizal fungi themselves can exude substances that have a selective effect on soil microbiota (Andrade et al. 1998; Marschner and Timonen 2005; Offre et al. 2007). Root function and microbial equilibrium changes in the rhizosphere following AM symbiosis establishment, lead to a new microbial compartment influenced by both the roots and the mycorrhizal fungus that is commonly named “mycorrhizosphere” (Linderman 1988). It also includes the more specific term “hyphosphere” which only refers to the zone surrounding individual fungal hyphae (Johansson et al. 2004). AM fungi and mycorrhizosphere microbial communities significantly act on soil bio-functioning and plant coexistence (van der Heijden et al. 1998; Kisa et al. 2007) and reciprocally plant genotypes affect the structure of the AM fungal community (Pivato et al. 2007).

Understanding the biological factors that govern the abundance and diversity of plant species remains one of the major goals in plant ecology. For instance, the opportunities of changes in ecosystem processes induced by invader plants might also be a feature of both their invasibility and the susceptibility of the recipient community to invasion as such mechanisms would have important ramifications for the management of invasions and restoration of native communities. Invaded communities often differ from native communities in organismal composition and may have altered ecosystem functions compared with native communities, including the rate and dynamics of biogeochemical processes (Vitousek and Walker 1989; Belnap and Phillips 2001; Evans et al. 2001; Ehrenfeld 2003; Wolfe and Klironomos 2005) and the suitability of habitat for other organisms (Roberts and Anderson 2001; Duda et al. 2003; Levine et al. 2003; Stinson et al. 2006; Chen et al. 2007).

In this review, we explore the current knowledge assessing the importance of root exudates in plant interactions, in communications between parasitic plants and their hosts and how some soil microbial components known to act on plant root exudation (i.e. Arbuscular mycorrhizal fungi, AMF) could regulate plant species coexistence and change relationships between plants. This review will be focussed on several well documented biological processes regulating plant-plant communications such as exotic plant species invasions, negative root-root communication (allelopathy) and parasitic plant / host plant interactions and on the biological processes from which some soil microbial components can interfere with signal traffic between roots.

Invasive exotic plant species and soil microbiota

Exotic-species invasions are among the most important global-scale problems facing natural ecosystems. Recent reviews of the extent of the homogenization of the world biota have shown that it is not only islands and disturbed sites that are affected but mainland areas and minimally disturbed ecosystems are also often invaded, even dominated, by newly established species originating from distant places. A general definition has been proposed by Shine et al. (2000): “*an invasive species is considered as an alien species that becomes established in natural or semi-natural ecosystems or habitat and is “an agent of change and threatens native biological diversity”*”. It is now well recognized that plant exotic invasions induce habitat destruction and the endangerment and extinction of native species (Vitousek et al. 1997; Wilcove et al. 1998; Simberloff 2003) and thus, drastically threatened the global biological diversity (Pimentel et al. 2000; Cabin et al. 2002; CBD 2006; Meiners 2007). Likewise, Vitousek et al. (1997) noted that for managers of parks and reserves, exotic species are “*ongoing threat to the persistence of native assemblages because they can consume native species, infect them with diseases to which they have no resistance, outcompete them, or alter ecosystem functions, making it difficult and expensive to return the ecosystem to its prior, often more desirable condition*”. Moreover, several well documented studies have shown that the species composition of communities can have far-reaching effects on ecosystem processes: changes in

overall species richness, in the type of species present (‘functional groups’), or in the presence of a ‘key-stone’ species change food-web architecture, leading to changes in standing stocks and flows of energy and nutrients. It has been also suggested that the species composition disturbances following exotic plant invasions should alter ecosystem processes, particularly their functioning and stability (Vitousek and Walker 1989; D’Antonio and Mahall 1991; D’Antonio and Vitousek 1992; Couto and Betters 1995; Hutchinson and Vankat 1997; Hamilton et al. 1999; Belnap and Phillips 2001; Hierro and Callaway 2003; Chen et al. 2007).

Invasive species also present an economic problem, costing the United States alone as much as U.S. \$137 million annually in loss ecosystem services control measures, and public health (Wilcove et al. 1998; Pimentel et al. 2000). Indeed, managers of many reserves estimated they spend a significant amount of their annual operating budget on control of non-indigenous species. For example, at Hawaii Volcanoes National Park, 80% of their annual budget has been spent in controlling exotic species activities (D’Antonio and Meyerson 2002).

Exotic plants may become aggressive invaders outside their home ranges for a number of reasons, including release from native, specialized antagonist (Mitchell and Power 2003), higher relative performance in a new site (Thébaud and Simberloff 2001), direct chemical (allelopathic) interference with native plant performance (Callaway and Ridenour 2004), and variability in the responses and resistance of native systems to invasion (Hobbs and Huenneke 1992; Levine and D’Antonio 1999).

Although soil organisms play important roles in regulating ecosystem-level processes (Wardle et al. 2004; Wolfe and Klironomos 2005) and contain most of the terrestrial ecosystems biodiversity (Torsvik et al. 1990; Vandenkoornhuysen et al. 2002), the effects of plant invasions have been mainly studied on aboveground flora and fauna (Levine et al. 2003). However, the composition and functioning of soil microbiota are closely linked with aboveground composition (Wardle et al. 2004) and exotic plant species can directly or indirectly disrupt these links after their invasion (Duda et al. 2003 ; Stinson et al. 2006 ; Kisa et al. 2007).

The large ecological and economic impacts of invasive plant species on terrestrial ecosystems and agrosystems has lead to a great interest in order to

elucidate the biological mechanisms that regulate the interactions between exotic plant species and soil microbiota (Pimentel et al. 2000). In this manuscript, we review some of the recent scientific advances on exotic plant species vs soil microbiota interactions with an emphasis on mycorrhizal fungi. These micro-symbiots, widely widespread in soil, form a key component of sustainable soil-plant interactions (Bethlenfalvay 1992; van der Heijden et al. 1998; Johansson et al. 2004) and indeed, might play a crucial role in plant invasion processes.

Effects of exotic plant invasions on soil microbiota

The soil immediately surrounding plant roots constitutes a particular physical, biochemical, and ecological environment that has been named “rhizosphere”. The rhizosphere is to a large extent controlled by the root system itself through chemicals exuded/secreted into the surrounding soil. Through the exudation of a wide variety of compounds, roots may regulate the functionalities and the structure of soil microbial communities in their immediate vicinity, encourage beneficial microbial symbioses, change the chemical and physical properties of the soil, and inhibit the development of competing plant species (Nardi et al. 2000; Bais et al. 2002).

Native plant influence soil communities but invasive plant-mediated modifications may be more pronounced, or may introduce novel biological mechanisms in the native community environment. In addition, more than one mechanism may involve in exotic plants invasion processes exacerbating their effects on soil communities (Wolfe and Klironomos 2005).

Main mechanisms involved in soil community alteration

Plants supply resources for soil communities by providing organic matter through leaf-litter inputs, through the release of root exudates, or through other ways of deposition of organic compounds into the soil environment (Grayston et al. 1996). Plants develop diverse ways of supplying these resources to the soil, and as a result, specific soil communities form under different plant species (Bever et al. 1996; Westover et al. 1997; Wolfe and Klironomos 2005; Pivato et al. 2007) and under plant communities that differ in

composition and abundance (Zak et al. 2003; Johnson et al. 2004). Hence it is well established that distinct microbial communities, in their structure as well as their function, might develop under different plants species (Roberts and Anderson 2001; Duda et al. 2003; Kourtev et al. 2003).

As an exotic plant species invades a community, it can alter links between native aboveground communities and belowground communities, including the timing, quality, quantity, and spatial structure of plant-derived soil inputs (Wolfe and Klironomos 2005). Kourtev et al. (2003) clearly showed that exotic invasive plants might induce drastic modifications in soil communities. Their results indicated that the structure and functional diversity of soil microbial communities (established by PhosphoLipid Fatty Acids (PLFA) profiles and substrate-induced respiration patterns) are strongly affected by the invasion processes. Moreover, these shifts are accompanied by alterations in soil chemical properties (soil pH and nitrogen content, nitrogen mineralization processes) as microbial communities are the drivers of main biogeochemical cycles. In addition, Ehrenfeld (2003) suggested that plant invasions-mediated shifts in soil salinity, moisture, pH, carbon and nitrogen content, are also susceptible to significantly modify belowground microbial communities.

Furthermore, Kourtev et al. (2002, 2003) investigated the effects of two exotic understory species, Japanese barberry (*Berberis thunbergii*) and Japanese stilt grass (*Microstegium vimineum*), on soil biota in northeastern hardwood forest of North America. In field conditions, the structure of the microbial community, determined by PLFA profiles, was different under these two invaders compared with the soil under native plant species. In barberry soils, there was an overall decrease in fungal abundance, indicating conversion to a community dominated by bacteria. In stilt grass soils, one of the most pronounced structural changes was an increase in the abundance of arbuscular mycorrhizal fungi (AMF). Using molecular biological tools (i.e. Terminal Restriction Fragment Length Polymorphism T-RFLP), some authors indicated a significant reduction of AMF diversity in soil samples collected in *Centaurea maculosa* Lam (spotted knapweed)-dominated areas compared to uninvaded ones. In addition, extraradical hyphal lengths exhibited a significant reduction in *C. maculosa*—versus native grass-dominated sites

(Mummey and Rillig 2006). Belnap and Phillips (2001) also found that most aspects of the vegetative and soil food-web communities changed after the introduction of *Bromus tectorum*, an invasive annual grass in western United States: a decrease in the overall soil biological diversity, fewer fungi and invertebrate abundance, and higher number of active bacteria, resulted from carbon and nitrogen availability-mediated by *B. tectorum* organic compound inputs.

Plants release secondary compounds into the soil environment from their roots as exudates, and if the compounds released by an exotic plant are newly represented in soil environment, they may alter the structure and function of soil community (Wolfe and Klironomos 2005). Allelochemicals released from plant roots have been widely used as an explanation of the success of exotic plants in the context of plant-plant interactions (Hierro and Callaway 2003), but evidence of allelochemicals altering the interactions between native plants and soil communities has only recently been established (Bais et al. 2002; Wolfe and Klironomos, 2005). Bais et al. (2002) investigated the allelopathic capacities of the noxious weed spotted knapweed (*Centaurea maculosa*) and they showed that this plant species exuded (\pm)-catechin in their rhizosphere; ($-$)-catechin enantiomer was phytotoxic whilst ($+$)-catechin had antibacterial activity against root-infesting pathogens, which ($-$)-catechin did not show. It suggests that the exudation of racemic catechin had a biological significance in giving different properties that are beneficial for plant growth and survival. Diffuse knapweed (*Centaurea diffusa*) is an Eurasian knapweed species that has invaded many natural ecosystems in western North America. This plant species could release the chemical 8-hydroxyquinoline from its roots. This chemical compound has been demonstrated to be an antimicrobial agent (Vivanco et al. 2004) and diffuse knapweed could cause shifts in the composition of the soil microbial community probably through the release of these allelochemicals (Callaway et al. 2004). Garlic mustard (*Alliaria petiolata*), another exotic species in North America and native from Europe, is a member of the Brassicaceae, a family of plants in which many species produce glucosinolates (Wolfe and Klironomos 2005). These compounds are deposited into the soil, through root exudation or litter production, and they may cause changes in soil microbial communities (Vaughn and Berhow 1999). The dominance of garlic mustard in North American forests has

been shown to cause significant alterations in AMF communities (Roberts and Anderson 2001; Mummey and Rillig 2006; Stinson et al. 2006). Stinson et al. (2006) highlighted that the antifungal activity of this invasive plant suppressed native plant growth. This exotic plant species acted by disrupting mutualistic associations between native canopy tree seedlings and belowground AMF. Their results elucidated an indirect mechanism by which invasive plants can impact native flora, and explain how this plant successfully invades relatively undisturbed forest habitat.

Other traits of exotic plants, such as novel nutrient acquisition strategies, could also have implications on the structure and function of soil communities (Wolfe and Klironomos 2005). A widely recognized example of an exotic plant altering the attributes of an ecosystem is the invasion of firetree (*Myrica faya*) in Hawaii. In this area, this plant species and its nitrogen-fixing root symbionts (*Frankia* spp.) have invaded nitrogen-limited communities, altering nitrogen cycling and native plant community composition (Vitousek and Walker 1989).

Some exotic plants cause increases in litter production that can lead to increases in fire intensity and frequency (D'Antonio and Vitousek 1992) and changes in fire regime could indirectly alter soil communities (Boerner and Brinkman 2003). Furthermore, as invasive plants affected soil physical properties and erosion processes, they could alter soil microbial communities through soil microorganism habitat perturbation (Rillig et al. 2002).

From these different studies, it remains apparent that belowground effects of exotic plant invasions can be highly variable. Studies have documented negative, neutral, or positive effects on soil composition and functionalities, depending on the exotic plant species, the community or ecosystem invaded, the methods used to assess changes in structure or functions, and the temporal and spatial scales considered (Wolfe and Klironomos 2005). In addition to variation in the effects of exotic invasion on soil communities across plant species and systems, the authors indicate that it is also interesting to note that different taxonomic groups within a soil community may not respond similarly to the presence of an invasive exotic. These complexities, sole or together, may thus limit researchers's ability to predict the effects of exotic plant species invasions on soil microbial communities.

Soil microbial communities in exotic plant invasion processes

Role of specific components of the soil community on exotic plant

To discuss exotic plant invasions in the context of aboveground vs belowground relationships, it is crucial to consider not only how exotic plants could affect soil microbiota but, conversely, how the structure and function of soil communities might play a role in exotic plant invasions (Wolfe and Klironomos 2005). Indeed, soil microbiota and their feedback effect on plant growth and survival can strongly influence the relative abundance of plant species within a community.

A main mechanism by which soil biota influence the invasion of plants into native plants communities is through direct effects (either positive or negative) of specific soil organisms on plant growth (Wolfe and Klironomos 2005). The view that biotic resistance determines invasion success or failure has been introduced by Chapman (1931) with the concept of “environmental resistance”. It describes the forces that oppose the establishment of species in a new location. This concept is principally based on biological factors (complex of native predators, pathogens, parasites, competitors, mutualists, etc) and it could be resumed as a “biotic resistance” (Simberloff 1974; Simberloff and Von Holle 1999). Several well-illustrative examples of how soil organisms, particularly mycorrhizal fungi, can play a major role in the establishment and dominance of an invading plant have already been described. The first situation is the facilitation of the invasion of pine (*Pinus* spp.) by ectomycorrhizal fungi in parts of the Southern Hemisphere. Most members of the genus *Pinus* symbiotically grow with ectomycorrhizal fungi. Nevertheless there were no or few ectomycorrhizal fungal symbionts of pine native to many regions of the Southern Hemisphere. Then, with the introduction of suitable fungal symbionts with introduced trees, exotic pine species have been able to invade many plant communities in the regions (Richardson et al. 1994). Similarly, Fumanal et al. (2006) also proposed that, with regards to the invasive status of the common ragweed *Ambrosia artemisiifolia* L., increases in growth and development resulting from AMF colonization might be the main factor facilitating the spread

of this plant species. Moreover, others studies (Marler et al. 1999; Callaway et al. 2001, 2003; Zabinski et al. 2002; Carey et al. 2004) indicated that the presence of AMF is a major factor to facilitate the invasiveness of the spotted knapweed, *Centaurea maculosa* Lam. The specificity of AMF-facilitated *C. maculosa* competitiveness could be due to a number of potentially interacting factors, including alteration of AMF functionalities resulting from differential host responses to AMF species and/or alteration of AMF community composition comprising mycelial networks (Mummy and Rillig 2006).

On the other hand, Stinson et al. (2006) found that the mechanism by which garlic mustard, *Alliaria petiolata* (Brassicaceae), invaded the mesic temperate forests in North America result from a disruption in belowground mutualisms, notably mutualistic associations between native plants and AM fungi. As this plant species is non-mycorrhizal, thus the presence of AM fungi propagules in the soil should promote plant coexistence by decreasing the competitive abilities of this dominant non mycotrophic plant (Zobel and Moora 1995; Moora and Zobel 1996), hindering *A. petiolata* invasion. The authors showed that garlic mustard inhibited AM formation in native tree species through phytochemical inhibition, by reducing germination rates of native AM spores (Stinson et al. 2006) and this remains the major strategy leading to *A. petiolata* invasion.

These two kinds of results (positive or negative relationships between the presence of AMF and the invasive plant species) may not necessarily be in conflict and the outcome may be highly dependent to the invasive plant mycorrhizal dependency in the local dominance hierarchy (Urcelay and Diaz 2003). In this context, some authors argued that if an otherwise less competitive plant species is infected by more AMF than is a highly competitive plant species, then AMF should promote plant coexistence by increasing the ability of less competitive species to access nutrients (Zobel and Moora 1995; Moora and Zobel 1996). Alternatively, if a highly competitive plant species is also more infected by AMF, then AMF would simply reinforce competitive dominance by that species (West 1996).

Feedbacks between exotic plants and soil biota

Although it is useful to understand the effects of specific soil biota to predict the relative importance of different

soil organisms in the invasion process, knowledge of the net effect of the soil community is more useful to understand the role of soil microbiota in the invasion process in field conditions (Wolfe and Klironomos 2005). Plants have different abilities to influence their abundance by changing the structure of their associated soil microbiota that is an important regulator of plant community structure (Klironomos 2002).

Soil microbes have profound negative or beneficial effects on plant growth and survival through pathogenic effects, root-fungus mutualisms and by driving the nutrient cycles on which plants depend (Newsham et al. 1994; Packer and Clay 2000; Mitchell and Power 2003). These effects, and the reciprocal effects of plants on soil microbes, contribute to two contrasting dynamic feedback interactions between plants and root soil microbiota (Bever et al. 1997). As a plant grows in a local soil community, it may modify the composition of the soil organisms by altering abiotic or biotic components of the soil environment. These modifications can lead to changes into the effects of soil microbiota on plant growth (either positive, negative, or neutral), leading to feedbacks between plants and soil biota (Bever et al. 1997; Bever 1994, 2003; Wolfe and Klironomos 2005). Positive feedbacks occur when a plant species promote microbes near their roots that have beneficial effects on the same plant species, such as mycorrhizal fungi and nitrogen fixers. Positive feedbacks are thought to lead to a loss of local community diversity (Bever et al. 1997; Bever 2003). Negative feedbacks occur when plant species accumulate pathogenic microbes in their rhizospheres, creating conditions that are increasingly hostile to the plants that favor the pathogens (Klironomos 2002; Bever 1994). Negative feedbacks are thought to enhance community diversity by increasing species turnover rates (Bever et al. 1997; Bever 2003).

Within a plant community, the feedback between plants and the soil microbiota can explain the relative abundance of plant species, with the most abundant species having positive or neutral feedbacks with soil microbiota and the least abundant species having negative feedbacks (Klironomos 2002; Wolfe and Klironomos 2005). Wolfe and Klironomos (2005) cultured five of North America's most notorious exotic invaders in soil that had been cultivated with each of the five species. A positive growth effect was observed compared with plant growth in soil that had been cultured by a different species. They argued that

changes in the soil microbiota resulting from the presence of these plants, would not result in negative growth effects on the same plant. But, when five rare native species were treated in the same way, a negative growth effect was observed when growing in their own soil compared with the growth of these plants in the soil of others species, suggesting that the plants accumulated pathogens in their local soil community. Hence, they concluded that exotic plants, and in some cases widespread native plants, could be abundant within native communities because they do not experience the same negative feedback with soil biota as do rare native species (Klironomos 2002).

These initial feedback studies suggested that exotic plant may escape the negative effects of soil pathogens in their novel ranges (Wolfe and Klironomos 2005), supporting the enemy-release hypothesis that has been demonstrated for some exotic plants with aboveground antagonists, such as herbivores (Reader 1998; Maron and Vila 2001) and fungal and viral pathogens (van der Putten et al. 1993; Mitchell and Power 2003). Several recent studies have followed up these previous works by comparing the soil feedbacks of exotic plants in their native and exotic ranges. Spotted knapweed (*Centaurea maculosa*), a major exotic plant that dominates many grasslands of western North America, is native from Europe. Callaway et al. (2004) indicated that *C. maculosa* was able to modify soil microbiota in invaded soils to its advantage, thus favouring its invasion process. In contrast, *C. maculosa* is inhibited by a negative feedback in its native soil, probably due to the accumulation of pathogens and potentially also due to adaptation of inhibitory microbial populations to antimicrobial compounds produced by the spotted knapweed. Otherwise, if plants and pathogens co-evolved locally, it would be expected that feedback between a plant species and soil microbes from its native range will be negative, and that exotic invaders may escape more pathogens than they acquire in their new habitat (Mitchell and Power 2003). In addition and in contrast to the host-specific tendency of pathogenic microbes, many mycorrhizal fungi tend to infect a broad range of hosts (Eom and Hartnett 2000). Hence it was possible for mycotrophic invaders to use the native AMF in their introduction area. Therefore, the feedback of soil microbiota from the invaded range of an exotic weed to the weed itself is likely to be neutral or positive because of the potential for the

invader to accumulate mutualistic fungi in the absence of host-specific soil pathogens (Callaway et al. 2004). These results indicated that soil organisms and their feedback effects on plants could strongly drive plant species relative abundance within a community.

Positive feedback responses were also found between black cherry (*Prunus serotina*) and soil microbiota in its introduced range (Europe) and negative responses to soil microbiota in its home range (North America) (Reinhart et al. 2003).

Overall, these combined findings support the hypothesis that feedback between plants and soil communities may strongly determine the ability of a plant to establish, invade and persist in a local habitat (Klironomos 2002). Thus, feedback could be an important mechanism for coexistence and/or invasion, and the regulation of plant biodiversity in communities. Beyond this evident effect of feedback mechanisms in invasion processes, conflicting studies on the release of exotic plants from negative soil feedbacks in invasive ranges make it difficult to generalize how important this mechanism may be in explaining the success of invasive plant (Wolfe and Klironomos 2005). These authors cited the example of European beachgrass (*Ammophila arenaria*) which was introduced into California in the 1800s. In its native range (Europe), this plant is an early-successional dune species that is replaced by others species as it accumulates soil organisms that negatively affect its growth (van der Putten et al. 1993). In California, soil microbiota was found to have similar negative effects on this species (Beckstead and Parker 2003), suggesting that European beachgrass did not escape the negative effects of soil biota in its invasive range (Wolfe and Klironomos 2005). However, escape from negative feedback from soil microbiota was observed in populations in South Africa, another region where European beachgrass has invaded plant communities (Knevel et al. 2004). These discrepancies suggested that soil communities will not have the same magnitude or direction (positive versus negative) effect on the invasion of all exotic species in all novel ranges (Levine et al. 2004; Wolfe and Klironomos 2005).

Soil microbiota and ecological restoration following plant invasion

A major goal of restoration practitioners is to return a habitat to more desirable conditions involving a particular species composition, community structure,

and/or set of ecosystem functions (Noss 1990). They are several reasons why both ‘natural’ and direct human disturbances are known to promote invasive exotic species in plant communities (Huenneke et al. 1990; Hobbs and Huenneke 1992; Hughes and Vitousek 1993; Maron and Connors 1996; Lozon and MacIsaac 1997; Baskin and Baskin 1998; Tardiff and Stanford 1998; D’Antonio et al. 1999), and an understanding of these processes may provide insight into management options.

After the establishment of an invasive species that begins to dominate in an area, land managers try to stop the spread of the invasive plant, to remove plants that have established, and to restore attributes of the pre-invaded community. Traditionally, these restoration approaches have been ‘aboveground-focused’, only considering the components of the community that can be easily seen and monitored over time as the restoration progresses (Wolfe and Klironomos 2005). A variety of processes have been used to remove exotic species from reserves or restoration sites. These most commonly include hand or mechanical removal, herbicides, fire, planned disturbance, biological control, or some combinations of the above techniques (Masters and Nissen 1998; D’Antonio and Meyerson 2002) but soil microbiota has generally been ignored (Wolfe and Klironomos 2005).

More recently, the opportunity of using microbial control has been investigated. In this context, selective manipulation of soil fertility through soil microorganisms may be used for control of some undesired species (D’Antonio and Meyerson 2002). Although application to natural areas may be difficult, this approach may potentially be useful in a restoration project where the particular nutrient requirements of an invader are known. Where high N-demanding exotic species are present, several investigators have suggested the addition of sawdust or a carbon ‘cocktail’ to decrease soil-available N (Wilson and Gerry 1995; Reeve-Morghen and Seastedt 1999; D’Antonio & Meyerson 2002). The underlying reasoning behind this cultural approach is that labile C will stimulate microbial population growth and increased microbial populations will then immobilize soil N. The resulting lower soil N will differentially affect the faster growing more N-demanding plant species, decreasing their competitive advantage over native species for at least a brief window of time (D’Antonio and Meyerson 2002). Likewise, it has

been demonstrated that the spread of the annual meadow grass, *Poa annua* L., was controlled by the bacterial species *Xanthomonas campestris* pv. *poae* (Zhou and Neal 1995; Imaizumi et al. 1997, 1998). Furthermore, others authors successfully used AMF to reduce the growth and the invasion of golf putting greens by annual meadow grass (Gange et al. 1999); this weed grass is generally considered to be undesirable in putting greens because its shallow root system makes it particularly susceptible to abiotic stress, especially water availability (Adams and Gibbs 1994) and this is important because water use is an expensive and often controversial aspect of golf course management (Kneebone et al. 1992). It has been previously reported that the abundance of *P. annua* in one golf course was negatively related to the amount of AMF in the soil (Gange 1994). In others respects, when the abundance of AMF was very low then *P. annua* was common, and *vice versa*. Accordingly, in a manipulative experiment, Gange et al. (1999) added mycorrhizal inoculum to a golf green soil and observed that mycorrhizal inoculation could eventually decrease the abundance of *P. annua* contrary to the abundance of *Agrostis stolonifera*, one of the most widely sown and desirable species in golf greens.

Parasitic plant—host plant interactions

Intra and interspecific plant chemical signaling is of great importance in biology and more particularly in non-beneficial underground interactions (Hirsch et al. 2003). One example of plant-plant underground communication is the recognition by the parasitic plants (*Orobanchae* spp. and *Striga* spp.) of chemical signals exuded by the roots of susceptible plant species. Broomrapes (*Orobanchae* spp.) and witchweeds (*Striga* spp.) can heavily infest crops with a large negative impact on agriculture in many countries. Since the life cycle of *Striga* and *Orobanchae* spp. are essentially similar, the knowledge of rhizosphere mediated parasitic host plant interaction will be reviewed on the *Striga* genus.

Striga spp. belong to the hemiparasites whereas *Orobanchae* spp. are holoparasites (both *Scrophulariaceae*) which largely depend on a host plant to obtain their nutrients and water (Parker and Riches 1993). More than thirty species has been described

and eighty percent have been found in Africa. Nine species are indigenous to Africa and three to Australia (Musselman 1987). The majority of *Striga* species does not impact agriculture production, but those which parasitize crops are extremely harmful. The main species that have an important economical impact is *Striga hermonthica* (Del.) Benth, *S. asiatica* (L.) Kuntze and *S. gesneroides* Benth (Berner et al. 1995). *Striga hermonthica*, causes extensive damage in sub-Saharan dry areas, particularly West Africa (Olivier 1995). In sub-Saharan area, this obligate root hemiparasite can cause important yield losses in cereals such as maize (*Zea mays* L.), sorghum (*Sorghum bicolor* L.) and millet (*Pennisetum typhoides* L.) (Parker 1991). *Striga* is considered as the largest biological constraint on food production in sub-Saharan Africa and crop losses resulting from *Striga* infestation are estimated to more than 7 billions US\$ (Lenné 2000).

Botanical description and physiological aspects

Striga plant can reach a height of 80 cm and is characterized by green, rigid and rough stems and by bright irregular flowers. The seeds are light and tiny (250 µm x 150 µm), and 40000 to 100000 seeds per plant are produced according to the species. They are covered with a hard and brownish integument with typical ornamentations. These characteristics allow an easy dissemination and a seed protection in the soil for many years. Seeds can keep their germination potential for more than 15 years in the soil until suitable environmental conditions are reached (Sallé and Raynal-Roques 1989). *Striga* is well adapted to climatic conditions encountered in semi-arid tropical regions (Salle and Aber 1986). The seeds require a period of after-ripening (4 to 6 months) and need a period of pre-treatment or conditioning (2–4 weeks) before they have the potential to germinate. The seeds need to be water imbibed and stocked at 30°C in the dark. Then they become responsive to the stimulant signals secreted by host plant roots (Worsham 1987). These stimulants induce seed germination within 3 to 6 mm around the host plant root. *Striga* radicles grow towards the host plant roots by chemotropism and some papilla develop at their tip facilitating their attachment (Sallé and Raynal-Roques 1989). At that time, a factor inducing the development of the haustorium is excreted by the host plant roots to allow their attachment. Once xylem connection

established between both plant partners, the parasitic plant develop an underground vegetative form and draws its nutritive elements from its host (Fig. 1) (Joel et al. 1995).

The parasitic plant emerges after 4 or 5 weeks. The strongest morphological and physiological perturbations of the host plant are expressed at this stage. The *Striga* plant develops chlorophyllian structures but remains dependent of the host root for its mineral and water nutrition. The parasitic plant reaches to its maturity, flowers and produces mature seeds (Fig. 1).

Chemical communications regulating *Striga* development

In many of the steps of the life cycle of *Striga* development (germination, attachment, penetration and nutritional demand by the parasite), chemical communication occur between the host plant and the parasite. It begins by the exudation of secondary metabolites from the roots of the host that induce the germination of the seeds of the parasite. Then other host-derived secondary metabolites regulate the plant-plant interactions. It has been suggested that the *Striga* radicle is oriented towards the host root by the concentration gradient of the germination stimulant or other host plant secondary metabolites (Dube and

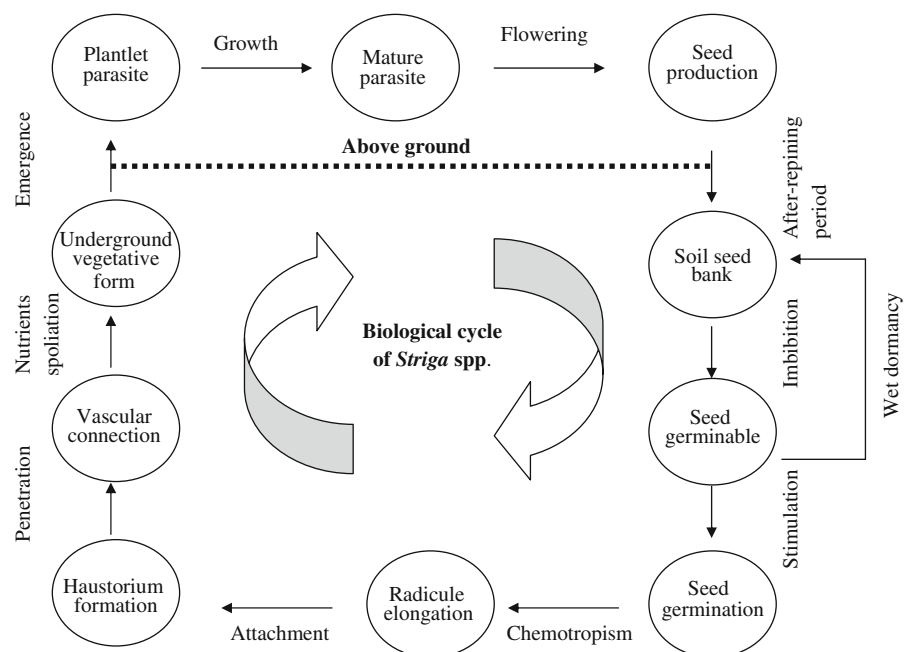
Olivier 2001). Hausterium formation that allows the attachment of *Striga* radicle to the host plant root and the host-parasite xylem connection is initiated by host-derived metabolites, more particularly phenolic compounds (Hirsch et al. 2003). *Striga* seeds need phenolic compound (2,6 -dimethyl-p-benzoquinone) as signal for haustorium induction (Kim et al. 1998). Finally, hydrolytic enzymes produced by the parasite facilitate the penetration of intrusive cells into the host root xylem (Losner-Goshen et al. 1998) and the transition from vegetative to flowering stage can be induced by phenolic compounds (Albrecht et al. 1999).

Germination stimulants

As described above, parasitic weed seeds require a chemical signal to initiate germination. Hence the germination stimulants play a crucial in the life cycle of parasitic plants and are generally considered as an important target to ensure the control of parasitic plants.

It has been demonstrated that germination stimulants were mainly synthesized and exuded from the apex of the root. The first naturally occurring germination stimulant identified was “Strigol” (Fig. 2), an unstable tetracyclic sesquiterpene isolated from non host root exudates (*Gossypium hirsutum* L.) (Cook et al. 1966).

Fig. 1 Biological cycle of *Striga* spp



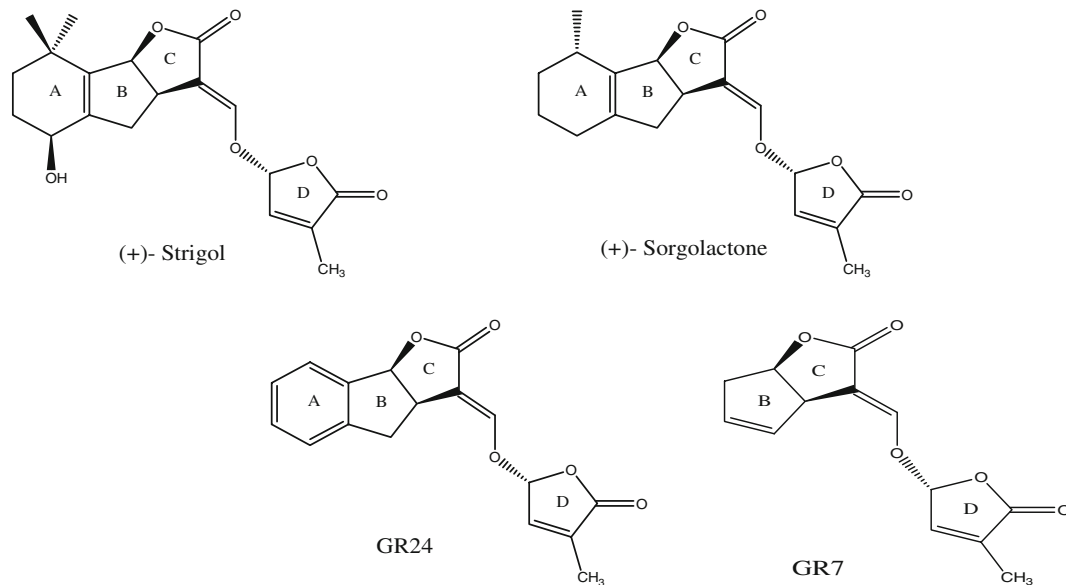


Fig. 2 Chemical structure of natural [(+)- Strigol and (+)- Sorgolactone] and synthetic (GR24 and GR7) germination stimulants of *Striga* seeds

In 1992 “Sorgolactone” (Fig. 2), an analogous of “Strigol”, was isolated from sorghum (*Sorghum bicolor* L. Moench) roots (Hauck et al. 1992).

During the ten last years, several synthetic compounds analogous of Strigol were artificially synthesized and the most potent and active, currently used, compounds are GR7 (Gerry Roseberry 7, Fig. 2) and GR24 (Wigchert et al. 1999). These molecules are unstable, widely distributed in the plant kingdom and active at very small concentrations. For example, seedlings of cotton produce about 14 pg of strigol per plant per day (Sato et al. 2005).

Factors affecting *Striga* development

Low nitrogen availability in the soil promotes *S. hermonthica* infection (Farina et al. 1985). Generally, nitrogen fertilizer application reduces the crop damage caused by these parasitic plants (Khan et al. 2002). It has been established that reduced forms of nitrogen, exogenously applied, affected the biosynthesis and/or leakage of germination stimulants from the host root (Raju et al. 1990) and had a negative influence on the attachment and development of *Striga* seedlings (Cechin and Press 1993). With *Orobanche spp.*, nitrogen in ammonium form inhibits the elongation of seedling radicles by half (Westwood and Foy 1999).

In addition, some amino acids cause severe physiological disorders in germinating seeds (inhibiting germination, germ tube elongation). Among the amino acids tested, methionine was able to inhibit almost totally the germination of *Orobanche* seeds by reducing strongly the number of *Orobanche* plantlets (Vurro et al. 2006).

Nitrogen metabolism in *Striga* is characterized by a very high level of asparagine accumulation. This amino acid seems to be a storage form of the supra-optimal nitrogen amounts derived from xylem sap and the important nitrogen uptake appears to be one of the main factors responsible of the drastic effect of *Striga* on its host plant (Pageau et al. 2000).

The use of *Azospirillum spp.* to biologically control parasitic plant development

Importance of plant growth promoting rhizobacteria (PGPR) *Azospirillum*

This Gram negative diazotrophic bacterium (α -subclass of proteobacteria) able to fix atmospheric nitrogen, lives in close association with plant roots and forms associative symbioses. *Azospirillum* are isolated from the rhizosphere of many grasses and cereals all over the world, in tropical as well as in temperate climates.

Agronomic applications of these beneficial effects have been recorded in many studies (from 1997 to 2003) listed by Bashan et al. (2004). In many cases, inoculation reduced the utilization of chemical fertilizers from 20 to 50%, particularly nitrogen fertilization. In many developing countries, PGPR inoculation has improved the cost / benefit ratio of crops. The main effect of these inoculations was recorded on the morphological modifications of the host root system which increased in volume, weight and surface (Bashan and Levanony 1990). They also improved other plant growth parameters such as height, total biomass and nitrogen level in the stem and the seeds of the host plant (Jacoud 1997). Indeed, *Azospirillum* is mainly known by its capacity to produce and to exude plant hormones, polyamines and amino acids (Thuler et al. 2003). Among the hormones, auxins like IAA (indole acetic acid) and gibberellins play the most important roles.

The bacterium *Azospirillum* can also protect its host against phytopathogenic stresses *via* an antagonism phenomenon or by changing the host plant susceptibility, for example, by induced resistance (Dobbelaere et al. 2003). This protection was not limited to deleterious microorganisms and soil-borne pathogens, but also to the parasitic plants such as *Striga*. Several authors have demonstrated that some strains of *Azospirillum* can inhibit the germination of *Striga* seeds (Miché et al. 2000; Dadon et al. 2004). Therefore, the plant growth-promoting effect of *Azospirillum* in fields infested by *Striga*, could result from a direct effect on the plant growth but also from an indirect effect (*Azospirillum* antagonistic effect against *Striga* development). Many studies focused on the molecular basis of plant growth promotion and biocontrol by *Azospirillum* (Dobbelaere et al. 2003; Bashan et al. 2004) but none so far on the potential control by PGPR bacterium of parasitic plants development.

Potential effects of Azospirillum metabolites on Striga seed germination and infestation

Many hypotheses have been suggested on the potential role of substances secreted by *Azospirillum* strains against *Striga* infestation (Fig. 3). Indeed, it was already shown that *Azospirillum*, through chemical signals, could inhibit *Striga* invasion by reducing its germination rate and by blocking its radicle elongation (Miché et al. 2000).

Phytohormones and Striga germination

The influence of auxins on root elongation is well known, as well as the production of this hormone by *Azospirillum*. Al-Menoufi et al. (1986) have demonstrated that auxins have not a direct role in seed germination of the *Orobanche* parasitic plant. If the application of auxin alone does not stimulate germination, the application of the germination stimulant (GR24) strongly increases the seed germination rate (Al-Menoufi et al. 1986). The same effect of root elongation inhibition could also occur in the case of germinated *Striga* seeds.

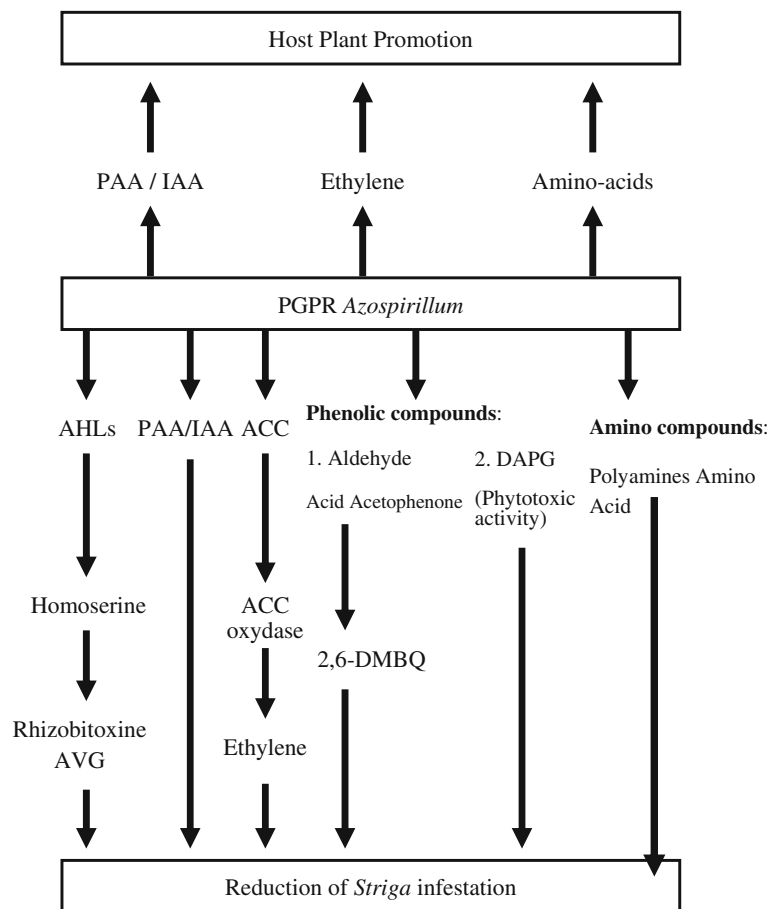
Ethylene is involved in seed germination (Babiker et al. 2000). It was reported that germination induced by the germination stimulants, natural or synthetic, depends on the endogenous synthesis of ethylene (Logan and Stewart 1991). These stimulants induce the biosynthesis of ethylene that is a mediator of a biochemical cascade leading to seed germination (Babiker et al. 2000). Conversely, the addition of exogenic ethylene reduced the germination of the seeds in the presence of GR24, in particular with *Orobanche* spp. (Zehhar et al. 2002).

Ethylene production by *Azospirillum* spp is related to the phytohormones released into the medium and on the presence or absence of ACC (1-aminocyclopropane-1-carboxylate) desaminase. Indeed, it has been reported that a synergistic action of auxin and cytokinin on the stimulation of ethylene production (Babiker et al. 1994).

Striga germination and aminoethoxyvinyl glycine (AVG)

It has been showed that *Striga* germination was inhibited by an inhibitor of ethylene biosynthesis, the Aminoethoxyvinyl Glycine (AVG) known to inhibit the 1-amino-cyclopropane-1-carboxylate (ACC) synthase (Adams and Yang 1979). Babiker et al. (2000) showed that AVG inhibits the induction of ethylene carried out by GR24. Sugimoto et al. (2003) mentioned the inhibition of *Striga* germination by the inhibitor of the ethylene biosynthesis “AVG”. Zehhar et al. (2002) confirmed the same significant decrease of germination when AVG and GR24 were applied simultaneously. These results led to the hypothesis that the AVG or similar compound acting in the same way could be produced by *Azospirillum* to protect its

Fig. 3 Compounds secreted by *Azospirillum spp.* potentially antagonistic against *Striga spp.* 1-amino-cyclopropane-1-carboxylate (ACC), Acyl-homoserine lactone (AHLs), Aminoethoxyvinyl Glycine (AVG), Diacetylphloroglucinol (DAPG), 2,6-dimethyl-p-benzoquinone (2,6-DMBQ), Indole acetic acid (IAA), Phenylacetic acid (PAA)



host against *Striga*. Nevertheless, the production of AVG-type compounds has not yet described in *Azospirillum* species.

Allelopathy and soil microbiota

Plant interactions result from the product of complex interactions based on combinations of specific mechanisms (Chapin et al. 1994). Allelopathy effect is generally considered as a competition by interference (Mahall and Callaway 1992) but its relative contribution to the total negative effect of one species on another remains poorly evaluated (Nilsson 1994). Allelopathy refers to the harmful effects of one plant on another plant by the release of chemicals from plant parts by leaching, root exudates, volatilization, residue decomposition and other biological processes in both natural and agricultural systems. In the present review, the role of root secretions in interactions among plants

will be explored as well the effects of rhizosphere microbes on such biological relationships. Here we will particularly review our own work performed on *Eucalyptus camaldulensis* and on the effects of AM fungi against the allelopathy effect of this exotic tree species on native plant cover in West Africa.

Negative root-root communication

Root synthesises and accumulates a great diversity of micro- and macromolecular metabolites that are secreted into the rhizosphere as root exudates (Bais et al. 2004). Although recognition of the importance of root exudates in plant interactions has increased with recent studies of inter- and intraspecific root communication (Mahall and Callaway 1991), there were a few studies that had separated the effects of competition and allelopathy in plant interferences.

Root-mediated allelopathy has been suggested since the early 1800s by De Candolle (1832). This

author suspected that plants could exude some chemical compounds that are detrimental for other plant species. Other studies have reported that these deleterious substances to plant growth were excreted into the soil by growing roots and they have found that “carbon black” soil amendment decreases soil toxicity (Schreiner and Reed 1908). The use of “carbon black” (charcoal powder) led to a decrease in the ability of *Larrea* roots to inhibit the elongation of neighboring roots (Mahall and Callaway 1991). More recently, the relative importance of allelopathy and resource competition in plant-plant interactions has been clearly assessed (Ridenour and Callaway 2001). Using “carbon black” to manipulate the effects of root exudates of *Centaurea maculosa* (noxious weed in western North America) on the development of native bunchgrass *Festuca idahoensis*, they found that the decrease of *Festuca* growth resulting from *Centaurea* was modulated by the “carbon black” soil amendment. They concluded that allelopathy was of great importance in the mechanisms of interference between both plant species. However these results have been obtained under controlled conditions and the mechanisms could be more complex in natural conditions. In the field, the secretion of root allelochemical compounds depends on many factors such as plant densities, root distributions, root densities and microbial activity.

Interferences between rhizosphere microbes and root-mediated allelopathy

Eucalyptus camaldulensis, one of the most widely planted eucalypts in the world, is extremely damaging ecologically to many native plant species. The annual vegetation adjacent to naturalized stands of *E. camaldulensis* is severely inhibited and annual herbs rarely survive to maturity when *Eucalyptus* litter accumulates. In addition, it is generally observed that the introduction of this tree species leads to a depletion of soil nutrients, acidification and to an excessive water utilization (Couto and Betters 1995). A study was conducted in controlled conditions to evaluate the impacts of *E. camaldulensis* on bacterial community structure and functional diversity and to determine the effects of arbuscular mycorrhizal inoculation on this exotic plant species effect in a sahelian soil (Kisa et al. 2007). The results showed that this plant species clearly modified the soil

bacterial community. Both microbial community structure and microbial functions were significantly affected. These changes were accompanied by disturbances in the composition of the herbaceous plant species layer and mycorrhizal soil infectivity (reduction of the total number of mycorrhizal spores and of the mycelial network). However the negative impact of this exotic tree species was significantly moderated when it was inoculated with an efficient arbuscular mycorrhizal (AM) fungus. Beside a significant promoting effect on *E. camaldulensis* tree growth, the inoculation of *Glomus intraradices* (an AM fungus species) tended to return the soil to its initial conditions with a similar bacterial community structure and soil mycorrhizal potential. In addition AM inoculation has increased the development of herbaceous plant species under AM inoculated *E. camaldulensis* plants. The well-developed mycelial network measured under inoculated *E. camaldulensis* trees could explain this positive effect by equalizing the distribution of soil resources among competitively dominant and sub-dominant species (Wirsal 2004). But it has been also reported that soil microbes can act against allelochemical mediators, inactivating or metabolizing toxic compounds (Renne et al. 2004). In particular, it has been suggested that AM fungi could protect seedlings from allelopathy (Renne et al. 2004).

More recently, this biological property of AM symbiosis has been studied with an invasive plant species, *Amaranthus viridis*, in Senegal (Sanon et al., unpublished data). The experiment was conducted in Senegal at two sites: (i) one invaded by *A. viridis* and the other covered by other plant species but without *A. viridis*. Additionally, five sahelian *Acacia* species were grown in (1) soil disinfected or not collected from both sites, (2) un-invaded soil exposed to *A. viridis* plant aqueous extract, (3) soil collected from invaded and un-invaded sites and inoculated or not with the AM fungus *Glomus intraradices*. The results showed that the invasion of *A. viridis* increased soil nutrient availability, bacterial abundance and microbial activities. In contrast symbiotic microorganisms (AM fungi, Rhizobia) development and *Acacia* species growth were severely reduced in the *A. viridis* invaded soil. However, the inoculation of *G. intraradices* was highly beneficial to the growth and nodulation of *Acacia* species irrespective to the soil origin. Hence this negative impact of the invasive plant species was modified when *Acacia* species were inoculated by an

efficient AM fungus. These results highlight the role of AM symbiosis in interacting with root–root communication and modifying plant coexistence.

Conclusion

All these results show that microbial soil communities are of great importance the biological processes driven plant co-existence. Hence it also shows that specific management regimes could be used to favour the development of target soil communities that are compatible with the development of desired above-ground communities. This approach will probably not become practical until the technical challenges and costs of current soil microbial community analyses are reduced and until we obtain a better understanding of what measures of microbial community structure and function can serve as reliable and meaningful indicators (Harris 2003; Wolfe and Klironomos 2005). It shows that the overall effect of one plant to another result from multiple interacting mechanisms where soil microbiota can be considered as a key component. It highlights the need to consider soil microbiota in future management practices in order to maintain plant diversity in terrestrial ecosystems and improve the productivity in agrosystems.

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