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To cite this article: Hamid Amir, Yvon Cavaloc, Thomas Crossay, Alexandre Bourles, Simon Gensous, Alexandre Lagrange, Valérie Burtet-Sarramegna & Linda Guentas (2023) Importance and roles of arbuscular mycorrhizal fungi in New Caledonian ultramafic soils, Botany Letters, 170:3, 449-458, DOI: [10.1080/23818107.2022.2160808](https://doi.org/10.1080/23818107.2022.2160808)

To link to this article: <https://doi.org/10.1080/23818107.2022.2160808>



Published online: 28 Dec 2022.



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ARTICLE



Importance and roles of arbuscular mycorrhizal fungi in New Caledonian ultramafic soils

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ABSTRACT

Our knowledge about New Caledonian serpentine ecosystems has increased greatly during the past half-century, mainly thanks to Jaffré's group. However, research on soil microflora and plant symbionts started only in the nineties and was mainly published during the last two decades. We aim to synthesize these studies, focusing particularly on arbuscular mycorrhizal fungi (AMF). Research on AMF consists firstly of a global and inventory approach aiming to produce a basic but essential lacking knowledge. These studies showed that AMF are abundant in ultramafic soils and concerned nearly all plant species of these ecosystems. Even Ni-hyperaccumulator plants and sedges, generally considered non-mycorrhizal, were found to be functionally colonized by AMF in New Caledonian ultramafic soils. The adaptation of AMF communities to the extreme conditions of these soils led to high levels of metal tolerance (particularly to Ni) and noticeable originality of the taxa. The influence of these symbionts on plant growth and adaptation was assessed in greenhouse and field conditions. An accurate selection of AMF isolates that improve plant growth, and plant metal tolerance was performed. It was demonstrated that combinations of AMF isolates with complementary functional traits showed highly synergistic effects on plant development. Finally, a partnership with a biotechnological company led to the production of an efficient commercial inoculant now used in the ecological restoration of mine-degraded areas. Today studies are focused mainly on the additive effects of AMF and mycorrhiza-helper bacteria.

ARTICLE HISTORY

Received 20 October 2022
Accepted 15 December 2022

KEYWORDS

AMF; bacteria; serpentine ecosystems; abiotic stress; toxic metals; restoration ecology; New Caledonia

Introduction

Arbuscular mycorrhiza are among the most frequent plant-microbe mutualistic symbiosis, established with 80% of vascular plants (Wang and Qiu 2006; Smith and Read 2008; Strullu-Derrien et al. 2017). This symbiosis is also one of the most ancient, initiated probably when plants have colonized terrestrial areas more than 400 million years ago (Karatygin and Demchenko 2006; Humphreys et al. 2010; Strullu-derrien et al. 2014). Arbuscular mycorrhizal fungi (AMF) act fundamentally on different mechanisms of plant development, including mineral nutrition, drought resistance and toxic metal tolerance (Smith and Smith 2011; Amir et al. 2014; Augé et al. 2015; Ferrol et al. 2016). Their use in environmental remediation and ecological restoration is then particularly appropriate (Göhre and Paszkowski 2006; Amir et al. 2019; Valliere et al. 2020). Moreover, these targeted environmental applications are among the most advanced for large-scale mycorrhizal inoculation practices today (Hart et al. 2017).

Serpentine ecosystems developed in ultramafic soils are generally characterized by extreme conditions: macronutrient deficiency, unbalanced Ca/Mg ratio,

metal toxicity and frequent drought stress. These conditions have contributed to promoting original flora (Brooks 1987; Proctor 2003; Jaffré and L'Huillier 2010; Isnard et al. 2016). It is particularly the case in New Caledonia, a Pacific island biodiversity hot spot (Myers et al. 2000; Marchese 2015), characterized by an endemism of 96.7% of the ultramafic obligate flora (Isnard et al. 2016). This precious biodiversity is threatened by mining activities, fires, and other anthropogenic influences (Jaffré et al. 1998; L'Huillier et al. 2010).

The origin and pedological classification of new Caledonian ultramafic soils and their physicochemical features have been the subject of many studies since the seventies (Jaffré et al. 1971; Jaffré and Latham 1974; Latham 1975; Latham et al. 1978; Jaffré and L'Huillier 2010). Metal concentrations and their bioavailability in these soils were also investigated in relation to their potential toxicity on plants (L'Huillier and Edighoffer 1996; Quantin et al. 1997; L'Huillier et al. 1998). However, their microbiology was not investigated until the nineties, and this was also true for other countries, with rare exceptions (Lebedeva et al. 1978). In particular, AMF survival and activity, and their relationships with plants in these extreme conditions,

with very low phosphorus availability (Dubus and Becquer 2001; Jaffré and L'Huillier 2010) and high potentially toxic metal concentrations constituted an original unexplored research subject.

The first study on mycorrhizal associations in ultramafic soils worldwide concerned AMF spore densities and mycorrhizal colonization of 13 endemic plant species in different New Caledonian sites (Amir et al. 1997). From the year 2000, several publications showed the high interest of these extreme soils to investigate the role of mycorrhizal symbiosis in the adaptation to edaphic and environmental stresses of plants (Boulet and Lambers 2005; Jourand et al. 2010a; Lagrange et al. 2011; Orłowska et al. 2011; Amir et al. 2013). The adaptive traits of fungal symbionts were also highlighted (Turnau and Mesjasz-Przybyłowicz 2003; Amir et al. 2008; Jourand et al. 2010b; Branco and Ree 2010; Majorel et al. 2012).

Studies on ectomycorrhizas (EM) in New Caledonian ultramafic ecosystems were not detailed here. EM are important particularly in forests (Carriconde et al. 2019) and in maquis dominated by *Tristaniopsis* Brongn. & Gris and *Sannantha* Peter G. Wilson (Myrtaceae) species or *Acacia spirorbis* Labill. (Fabaceae) (Pillon et al. 2021). They are present on trees belonging to Myrtaceae, Fabaceae, Casuarinaceae and Nothofagaceae families (Perrier 2005; Amir and Ducouso 2010; Carriconde et al. 2019). A recent list of EM plants was reported in Pillon et al. (2021). Their role is then complementary to AMF, the root system of some plants (*Tristaniopsis* and *Nothofagus* Blume (Nothofagaceae) species, for example) being simultaneously colonized by the two symbiont groups (Perrier et al. 2006). EM also has good potential for their use in ecological restoration of mined areas (Houlès et al. 2022).

In New Caledonia, studies on AMF were taken over mainly by the University of New Caledonia. This review synthesizes those focused on ultramafic soils, particularly the ecological aspects and their practical consequences for the ecological restoration of mine-degraded areas. Are these symbionts able to maintain their spores and colonize root systems in these extreme soils, and how AMF diversity is shaped by these conditions? Are the most frequent plants in ultramafic maquis, particularly those used in restoration programs, arbuscular mycorrhizal? What are the main functions of AMF in plant nutrition, and how could they participate in plant adaptation to highly stressed conditions? These questions are relevant not only for science but also for their potential use in ecological restoration of mined areas.

Exploration and inventory studies

When research on ultramafic soil microbiology started in New Caledonia, the abiotic characterization of these

subtracts in relation to ecosystem functions was relatively advanced (Jaffré et al. 1971; Jaffré and Latham 1974; Lee et al. 1977; Becquer et al. 1995). Microbiological studies were then focused first on a global approach that can help to explain some ecological specificities of the studied ecosystems. Quantitative and qualitative analyses of soil microbiota and its activity in relation with plants and soil metal concentrations were assessed (Amir and Pineau 1998, 2003a, 2003b; Saintpierre 2001). These publications showed different specificities of ultramafic soil microbiology, with low level of activity but high metal tolerance of the microbiota, part of which being responsible for the release of different metals, including Ni and Co. *Frankia* symbiosis with Casuarinaceae is frequent in New Caledonian ultramafic ecosystems (Navarro et al. 1999; Gauthier et al. 1999) and may play an important role in nitrogen enrichment of these soils. A global approach on plant growth promoting rhizobacteria was initiated (Mercky 1999). More recently, it was shown that ultramafic soil properties do not limit their microbial diversity (Bordez et al. 2016; Carriconde et al. 2019). However, this rich diversity showed wide variations in relation to environmental conditions (Bordez et al. 2016; Gourmelon et al. 2016). The vegetation cover, particularly its density, seemed to play a major role. Among soil properties, pH, nitrogen and calcium influenced the distribution patterns of microbial communities.

After exploratory works on mycorrhizas (Amir et al. 1997; Perrier 2005; Perrier et al. 2006), it was clear that AMF are abundant in New Caledonian ultramafic soils. Most of the plant species tested were found to be arbuscular mycorrhizal, and AMF spore densities were globally similar to those of non-ultramafic soils (Perrier et al. 2006; Amir and Ducouso 2010). If AMF root colonization does not generally induce changes in root morphology, Duhoux et al. (2001) showed that *Gymnostoma* L.A.S. Johnson trees (Casuarinaceae) produce small root nodules called myconodules, colonized by AMF related to *Glomus*. Similar small nodules rich in AMF structures were found in the roots of *Podocarpus* L'Hér. ex Pers. trees (Podocarpaceae) in New Zealand (Russell et al. 2002) and were confirmed to be present with the same characteristics in *Araucaria* trees in New Caledonia (Amir, unpublished data). A correlation between AMF spore abundance and soil global activity was detected (Perrier et al. 2006) probably due to negative effect on AMF development of high phosphorus deficiency in the poorest soils (Lagrange et al. 2013; Amir et al. 2021). A list of over 60-studied plant species, particularly those used in ecological restoration, presenting their affinity with AMF or ectomycorrhizal fungi was then published (Amir and Ducouso 2010).

Adaptation of arbuscular mycorrhizal symbiosis to ultramafic soils

In the past, Ni-hyperaccumulating plants were generally assumed to be non-mycorrhizal (Leyval et al. 1997; Pawlowska et al. 2000). Amir et al. (2007) tested nine Ni-accumulating New Caledonian plants ranging from weak accumulators to hypernickelophore species. All species were more or less mycorrhized, but mycorrhizal colonization was reduced by high levels of Ni-hyperaccumulation (Figure 1). Indeed, for the same species, the level of mycorrhizal colonization was negatively correlated with Ni-concentration in plant leaves. The main reason for classically considering Ni-hyperaccumulators as non-mycorrhizal was that the plant species generally studied for this property in Europe and the USA belonged to non-mycorrhizal plant families (Brassicaceae, Caryophyllaceae).

Some studies on metal-polluted soils have revealed a high tolerance to Zn and Cd of AMF isolated from

this environment (Weissenhorn et al. 1994; Tullio et al. 2003). When tested for Ni tolerance, AMF from ultramafic soils were more tolerant than those from other origins (Amir et al. 2008). Moreover, isolates from roots of Ni-hyperaccumulating plants tolerated the highest Ni concentrations (Amir et al. 2007, 2008). This last study also reported that Ni-tolerance of AMF isolates could be induced by the presence of this metal in the substrate solution during host plant growth.

In New Caledonian ultramafic areas, the herbaceous stratum is mainly represented by Cyperaceae (sedges), a family generally considered non-mycorrhizal (Brundrett 2009). However, several endemic Cyperaceae species highly adapted to ultramafic soils were colonized at low levels by AMF (Perrier et al. 2006; Lagrange et al. 2011). Tested in greenhouse conditions and field experiment, *Tetraria comosa* (C. B. Clarke) T. Koyama, one of the most frequent and pioneer sedge species in New Caledonian maquis, was shown to be functionally mycorrhizal, even at

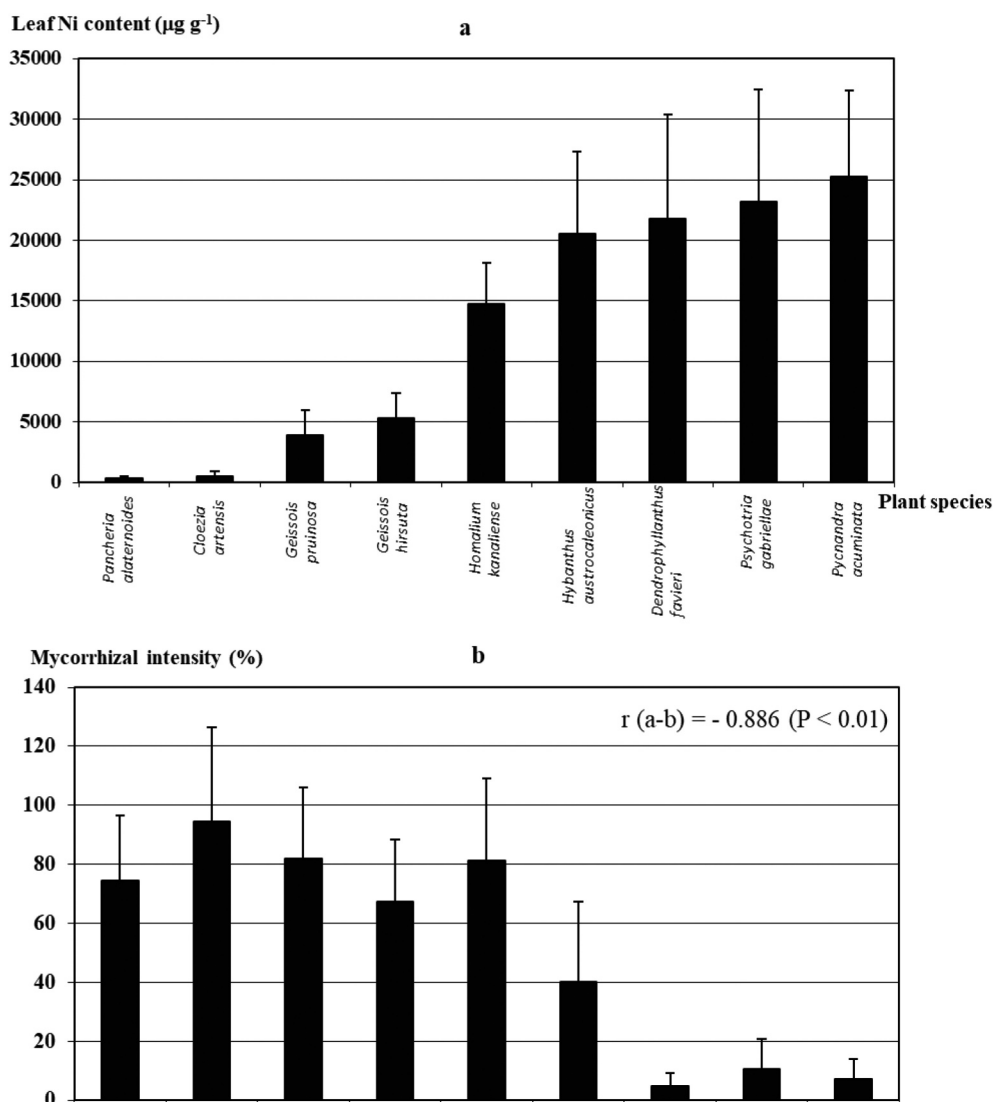


Figure 1. Relationships between leaf Ni content and mycorrhizal intensity of 9 Ni-accumulating plant species (means of 8–10 samples for each value). The coefficient $r(a-b)$ indicates the total linear correlation between the two parameters. From Amir et al. (2007), reprinted with the permission of Plant and Soil.

low levels of root colonization, with positive effects on plant survival rate and plant growth (Lagrange et al. 2011, 2013).

Importance and role of AMF on plant adaptation to ultramafic soils

AMF are obligate symbionts so their cultivation requires a host plant. Isolates from New Caledonian ultramafic soils were obtained in a greenhouse in association with sorghum. This grass was chosen not only because it has a good affinity with AMF but also because it can grow in difficult conditions with a relatively high rate, contrary to native species that grow slowly. The effects of AMF isolates on plant development have then been tested with sorghum and two endemic shrubs, *Alphitonia neocaledonica* Hillebr. (Rhamnaceae) and *Cloezia artensis* (Montrouz.) P.S.Green (Myrtaceae), currently used in restoration programs (Amir et al. 2013). The study showed that AMF not only stimulated the growth and phosphorus nutrition of these plants but also reduced nickel absorption and its toxicity (Figure 2). Similar but less important effects were obtained on *T. comosa* (Lagrange et al. 2011).

Ultramafic soils are often highly deficient in phosphorus (P), this element being moreover strongly adsorbed to iron oxides (Dubus and Becquer 2001; Jaffré and L'Huillier 2010). It is well known that the optimal level of available P in soil generally reduces AMF root colonization (Marschner 1995; Smith and Read 2008), but the effect of high P deficiency has

received less attention (Abbott et al. 1984; Lambers et al. 2009). Lagrange et al. (2011) suggested that P deficiency could explain low levels of AMF root colonization in New Caledonian ultramafic soils. A field experiment with *T. comosa* in an ultramafic area confirmed this hypothesis: it showed that the AMF root colonization and arbuscules' density of non-inoculated plants were clearly enhanced by phosphorus supply, with a correlatively better mineral nutrition (Lagrange et al. 2013).

In the latter cited study, plants were not inoculated with AMF. More recently, a field experiment with *Metrosideros laurifolia* hort. ex Dum.Cours. (Myrtaceae) plants inoculated in greenhouse with a mix of three AMF isolates was assessed in an ultramafic area in Goro (south of New Caledonia). Stored topsoil spread in this area a few years before, and characterized by a low density of AMF spores, was amended or not with sewage sludge and planted with *M. laurifolia* plantlets (Amir et al. 2019). After 528 days, the aerial dry biomass of AMF-inoculated plants was four times greater than the control ones (Figure 3). Mycorrhizal colonization was increased by sewage sludge inducing a complementary effect with AMF inoculation. This resulted in better plant growth and mineral nutrition, with plant biomass 7.7 times greater than control ones. The Ca/Mg ratio was also enhanced by AMF inoculation, and the translocation to aerial parts of potentially toxic metals (particularly Mn, Ni, and Co) was strongly reduced. The analysis of AMF diversity in *M. laurifolia* roots showed a higher number of operational taxonomic units (OTU) in AMF-inoculated plants grown on non-amended plots

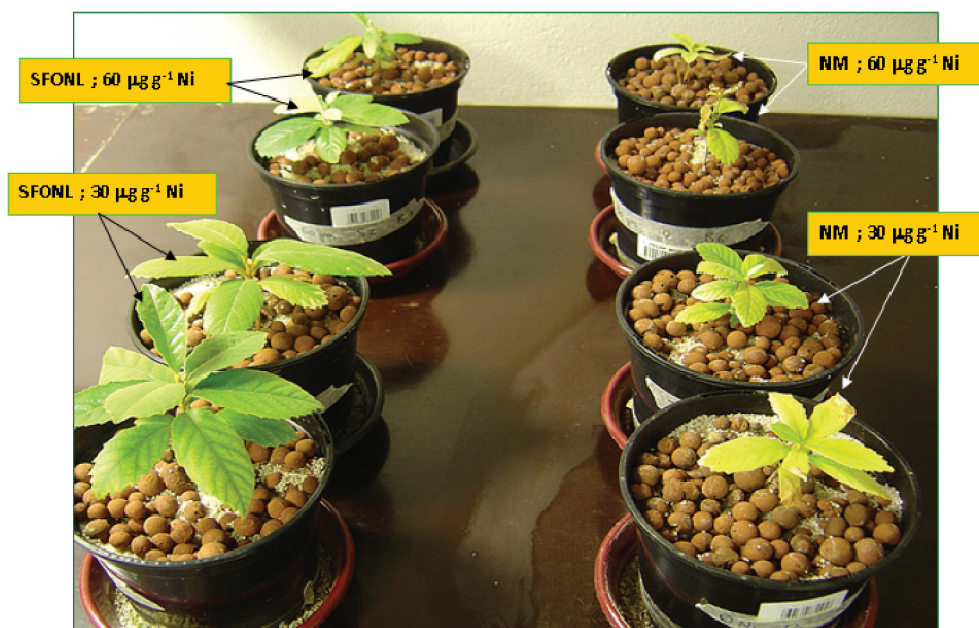


Figure 2. Aspect of *Alphitonia neocaledonica* plants in pots treated or not with nickel and inoculated or not with SFONL arbuscular mycorrhizal fungus isolate, showing Ni-toxicity symptoms. *Alphitonia neocaledonica* plants without Ni are not shown because they have the same aspect than SFONL $30 \mu\text{g g}^{-1}$ Ni. NM: non-mycorrhizal plants. From Amir et al. (2013), reprinted with the permission of Mycorrhiza.

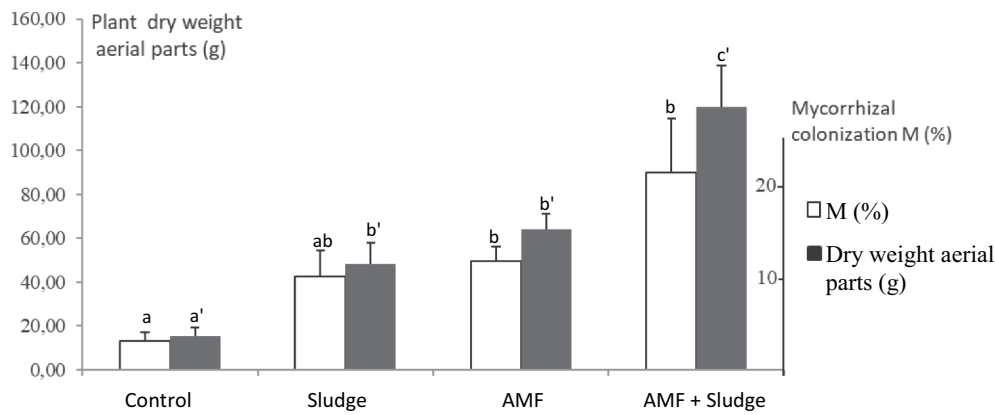


Figure 3. Influence of AMF inoculation, sewage sludge and their combination on growth (plant dry weight of aerial parts) and mycorrhizal colonization (M%) of *Metrosideros laurifolia* plants, 528 days after plantation (means values with standard error). Bars with the same letters are non-significantly different (post hoc Bonferroni corrected Mann-Whitney test). From Amir et al. (2019), reprinted with the permission of Science of the Total Environment.

compared to non-inoculated control. However, the introduced AMF isolates constituted at most only 9% of the detected OTUs. These results were explained by the strong increase in plant biomass of AMF-inoculated plants. This increase allowed more carbon allocation to AMF in roots, the competition between AMF communities, then inducing a relative reduction of inoculated isolates. However, the relative decrease of the introduced isolates did not weaken the positive effects of mycorrhizal inoculation on plant nutrition and growth, even after 3.5 years (Amir et al. 2019). This latter point is interesting for AMF biotechnologies, knowing that inoculum reduction after a few months to a few years is one of the drawbacks of this practice (Pellegrino et al. 2012; Janoušková et al. 2013).

Studies on AMF diversity of New Caledonian soils, quite recently initiated, revealed the originality and high richness of AMF communities of ultramafic soils (Gensous 2014; Amir et al. 2015; Cavaloc et al. 2019). A comparison between AMF communities associated with roots of *Psychotria* L. (Rubiaceae) and *Phyllanthus* L. (Phyllanthaceae) species from tropical rain forests developed on ultramafic and volcano-sedimentary soils, in four regions, was performed (Gensous 2014). The richness of AMF diversity did not differ significantly between the two types of forests, but the community composition was different. Ultramafic plants were associated mostly with the genera *Rhizophagus*, *Glomus*, *Diversispora* and *Archaeospora*, whereas plants from volcano-sedimentary soils were associated more frequently with *Acaulospora*, *Claroideoglomus*, and an unknown Glomeraceae. Moreover, in ultramafic forests, the AMF community composition differed significantly between Ni-hyperaccumulating and non-accumulating plants. Cavaloc et al. (2019) analyzed the diversity of AMF in soils of 4 ultramafic open, dense and bushy maquis in southern New Caledonia. They reported total number of 188 Amplicon Sequence Variants (ASVs), varying from 72 to 104 ASVs per

type of maquis, increasing with the vegetation density. Each analyzed plot contained about 10 to 30 ASVs. Shannon-Wiener AMF diversity index varied from 1.5 to 3.5. Amir et al. (2015) estimated the AMF diversity inside the roots of 4 endemic plant species collected from a dense maquis in Goro (south New Caledonia). They detected 427 sequences corresponding to 54 Operational Taxonomic Units (OTUs), varying from 13 to 20 per plant species. These AMF communities were dominated by the Glomeraceae family, the genera *Rhizophagus* and *Glomus* generally constituting more than 60% of the sequences (Gensous 2014; Amir et al. 2019; Cavaloc et al. 2019). The other most detected genera were *Sclerocystis*, *Acaulospora*, *Scutellospora*, *Claroideoglomus*, *Diversispora*, *Redeckera*, and *Paraglomus*. Five new AMF species were published (Błaszczkowski et al. 2017; Crossay et al. 2018).

This diversity has also been the object of functional experiments. With a larger collection of fungal isolates, greenhouse studies on the effects of different AMF mixes using the endemic plant *M. laurifolia* grown on ultramafic soil were assessed, assuming synergistic effects would be found. Indeed, combinations of co-inoculated isolates belonging to different families and having different functional traits were more efficient than single ones (Crossay et al. 2019). The best mix improved not only mineral nutrition with better absorption of major elements, particularly P and K, compared to single isolates, but also increased Ca/Mg ratio and reduced Ni and Co translocation more clearly. These effects resulted in a large growth improvement, with an aerial dry biomass 21.6 times larger than in non-inoculated plants. In contrast, the best single isolate induced a 12-fold increase in this biomass. These results comfort the hypothesis stating that synergistic effects of AMF on plant development are optimal when the phylogenetic distance between the mixed isolates is maximized (Maherali and Klironomos 2007), thus complementing

biological niches and reducing functional redundancy. Mathematical modeling of these AMF synergistic effects was produced (Crossay et al. 2019) explaining the experimental results with a high concordance ($R^2 = 0.90$, $p < 0.00001$).

AMF and mycorrhiza helper bacteria

Studies on bacteria and their communities in New Caledonian ultramafic soils have received less attention than fungal symbionts (Héry et al. 2003; Herrera et al. 2007; Bordez et al. 2016; Gourmelon et al. 2016). A few articles reported some of their growth promoting effects on plants (Mercky 1999; Gonin et al. 2013; Bourles et al. 2019; Bourles et al. 2020a). Complementary effects between bacteria and AMF have been addressed only recently (Bourles et al. 2020b). The latter studied the strain BE isolated from the rhizosphere of *Tetraria* plants and screened by Gonin et al. (2013) for its metal tolerance and plant growth promotion properties: phosphorus solubilization, and production of indole acetic acid (IAA), siderophores, ammonium and 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase). This bacterium belonging to the species *Curtobacterium citreum* was able to form a biofilm and produce an exopolysaccharide inducing Ni adsorption and inactivation capacities (Bourles 2019; Bourles et al. 2019). The strain reduced Ni, Co and Cr absorption by sorghum plants (Bourles et al. 2019) and strongly enhanced mycorrhizal colonization (Bourles et al. 2020b). The latter study reported complementary effects on the growth and nutrition parameters of *T. comosa* plants when the bacterium was co-inoculated with AMF in greenhouse conditions. A field experiment testing these effects is underway.

AMF and ecological restoration of ultramafic degraded areas

A part of AMF studies in New Caledonia concerned directly the ecological restoration of ultramafic mine-degraded areas. It was shown that AMF communities of revegetated subsoils in mine-degraded areas are different and functionally non-equivalent to AMF communities of non-degraded related ecosystems (Cavaloc et al., unpublished data). AMF diversity seemed to adapt to the new conditions of the restored ecosystem. The reuse of topsoil, generally not recuperated by mine companies until the nineties, was strongly recommended (Amir et al. 2003; Bordez et al. 2018), but in practice, this substrate was generally stored for years before being spread for revegetation. Studies have shown that topsoil storage not only reduces seed bank, soil activity and nutrients' reserve, but also AMF spore density and AMF diversity (Amir

et al. 2015, 2022). It was then recommended to reuse the topsoil for the revegetation as soon as possible, preferably no more than 6 months after its stripping (Bordez et al. 2018; Amir et al. 2022).

Considering the important role of AMF in plant development on ultramafic areas, a company partner of the University of New Caledonia recently developed a commercial inoculum, containing synergistic isolates, based on Crossay et al. (2019) results, after innovation of an aseptic method for AMF culture. Today, this inoculum is used to enhance growth and adaptation of plants for the revegetation of mined areas from an ecological restoration perspective. It is also envisaged to develop inoculants with isolates that are specific to particular lateritic soils to avoid reduction of native AMF biodiversity.

Ongoing greenhouse and field experiments aim to adapt the inoculation technique to seeding methods, by incorporating AMF inoculum into seed balls. These experiments also test the co-inoculation of AMF and MHB. Three to ten seeds of different native species, depending on their size, are incorporated with the AMF powder inoculum into 8 mm balls. Balls made with a mix of clay and organic matter are then sowed and followed-up for seed germination, plant growth, mycorrhizal colonization and inoculum behavior.

Conclusion

Research on mycorrhizas' role in New Caledonian ultramafic soils during the last two decades followed a progression dictated by the local context. The protection of the biodiversity of valuable ecosystems geared the studies toward the ecological restoration perspective. Yet, the originality of ultramafic environment and the absence of knowledge worldwide on the AMF symbiosis of these soils have made this subject particularly attractive to investigate plant adaptation in extreme environments.

The abundance and importance of these symbionts in New Caledonian ultramafic ecosystems were shown, and their diversity and relative originality in relation to the high plant endemism of this environment were then highlighted. The ability of AMF to improve plant mineral nutrition and metal tolerance in harsh conditions pointed out the central role of these symbionts in plant adaptation to multi-stress environments. Greenhouse and field experiments then revealed practical perspectives.

If an efficient AMF inoculant adapted to ultramafic mined areas is commercialized today, more research on microbial ecology is needed to improve restoration techniques in such extreme conditions. New microbe consortia containing AMF and bacteria constitute a particularly interesting target for deeper investigations.

Acknowledgments

The authors gratefully acknowledge for their contribution all of the research team, particularly, Laurent Bordez, Valerie Médevielle, Audrey Laurent, Monika Lemestre, Véronique Gaudichon, Clément Richert, Vincent Véron, Cyril Antheaume and all the trainees that worked with us from 1995 to 2020.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The research synthesized here was supported by different financial funds, particularly, Agence Nationale de la Recherche Scientifique (ANR), CNRT Nickel et son Environnement, the South Province of New Caledonia, Koniambo Nickel Society (KNS), and the University of New Caledonia.

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Author contributions

HA managed the research, designed the experiments and wrote the article; YC designed and followed up biomolecular studies; TC, AB, AL and SG contributed as PhD students to significant parts of the studies; TC worked as co-manager of a private company in partnership with the research team for the commercial use of selected AMF; VBS and LG followed up and designed biochemical and bacterial studies; all reviewed the article text.

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