Journal of Soil Science and Plant Nutrition
https://doi.org/10.1007/s42729-021-00626-6

ORIGINAL PAPER

Phosphorus Fertilization of an Ultramafic Soil Reduced Effects of Arbuscular Mycorrhizal Fungi but not Mycorrhizal Colonization

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Received: 8 July 2021 / Accepted: 20 September 2021

Abstract
Arbuscular mycorrhizal fungi (AMF) are generally involved in the adaptation of native plants to ultramafic soils, especially in New Caledonia. These soils are deficient in major elements, particularly in phosphorus (P), and are rich in potentially toxic metals such as nickel, chromium, cobalt, and manganese. We aimed to test the effects of increasing P doses on mycorrhizal functions of plants grown on P-deficient ultramafic soil. We analyzed the effects of soil P fertilization on growth, mineral nutrition and potentially toxic metal absorption of plants inoculated or not with AMF native isolates. Three endemic plants frequently used in the ecological restoration were tested: *Metrosideros laurifolia* (Myrtaceae), *Alphitonia neocaledonica* (Rhamnaceae), and *Tetraria comosa* (Cyperaceae). They were grown in pots supplied with different doses of P, after being inoculated or not with AMF. P fertilization increased greatly the growth rate of all three species. In pots non-supplied with P, only *M. laurifolia* showed a higher growth rate when inoculated with AMF, but all plant species showed different positive effects of mycorrhizal symbiosis, such as better mineral nutrition, particularly for potassium (K) and calcium and a higher calcium/magnesium values (Ca/Mg). Mycorrhizal colonization was not reduced by P supply, but the specific positive effects of AMF on growth and mineral nutrition were reduced or suppressed. Negative effects of P fertilization on mycorrhizal functions were induced without reduction of mycorrhizal colonization. As the adaptive traits of the three plants to ultramafic soils were obtained by a reduction of their growth rate, we hypothesized that the high increase of this growth rate induced by P fertilization could have altered this adaptive structure.

Keywords Ultramafic soil · Arbuscular mycorrhiza · Phosphorus fertilization · Mineral nutrition · Metal absorption

1 Introduction

Ultramafic soils are generally characterized by low levels of major elements and high concentrations of different potentially toxic metals (Brooks 1987). The low calcium/magnesium values (Ca/Mg < 1) of these soils is also a limiting factor for plant growth, because Ca absorption is restricted by the competition with Mg cations (Proctor 2003; Jaffré and L'Huillier 2010a). New Caledonia ultramafic soils are generally highly deficient in phosphorus (P) and potassium (K) and the availability of potentially toxic metals such as nickel (Ni), chromium (Cr), cobalt (Co), and manganese (Mn) can be very high in some soils, particularly in the rhizosphere (Jaffré 1980; Amir and Pineau 2003). In addition, New Caledonian ultramafic maquis are subject to large fluctuations of water availability inducing water stress (Jaffré and L'Huillier 2010a).

In these extreme conditions, mycorrhizal symbioses can have a great importance (Amir and Ducousso 2010; Jourand et al. 2010; Amir et al. 2013). Arbuscular mycorrhizal fungi (AMF) have been reported to improve particularly P and K absorption in these soils (Amir et al. 2013, 2019; Crossay et al. 2019). They also improve the unbalanced Ca/Mg value (Amir et al. 2019; Crossay et al. 2019) and enhance plant tolerance to metal toxicity (Khade and Adholeya 2007; Amir et al. 2014; Crossay et al. 2019). These AMF effects have been considered important traits of plant adaptation to ultramafic conditions (Amir et al. 2019; Crossay et al. 2019).

Phosphorus is central in mycorrhizal symbiosis because it is generally weakly available for plant and AMF contribute to its absorption (Smith and Read 2008). High levels of available P (when > 100 mg kg^{-1}) generally reduce

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Published online: 29 September 2021

mycorrhizal colonization and AMF efficiency (Schubert and Hayman 1986; Marschner 1995; Smith and Read 2008). Indeed, the plant may not need fungal symbionts when P is not a limiting factor and can control AMF colonization through the C efflux to the roots (Marschner 1995; Smith and Smith 2013). The effect of P deficiency (particularly when available P < 10 mg kg^{-1}) is less documented. However, some studies have reported that low levels of available P limit AMF symbiosis by inducing weak root colonization (Abbott et al. 1984; Amir and Ducousso 2010; Lagrange et al. 2013). Lambers et al. (2009) suggested that mycorrhiza symbiosis may not be effective for the plant in P-deficient soils, particularly when P is strongly sorbed onto soil particles. In these conditions, plant anabolism is weak affecting the C transfer. Lagrange et al. (2013), working on *Tetraria comosa*, have shown a clear increase of AMF colonization in field conditions after soil fertilization with 218 kg ha^{-1} of P.

P enrichment of the substrate is necessary for ecological restoration of mining-degraded areas in New Caledonia. However, it is important to assess the effects of this enrichment on ecosystem functions, particularly on AMF symbiosis. We studied the effects of mineral phosphorus fertilization on this symbiosis in a Ferralsol (lateritic ultramafic soil) characterized by a very low concentration of available P (3.5 mg kg^{-1}). We aimed to determine the approximate level of P supply which could be used to increase plant growth, without disturbing plant adaptation processes. Since plant species endemic to New Caledonian ultramafic soils are tightly adapted to this environment, we hypothesized that there could be a threshold of P supply beyond which AMF functions would be disturbed. The experiment was conducted in greenhouse conditions with three endemic pioneer species having different mycorrhizal statuses and frequently used for ecological restoration of degraded areas. The shrub *Metrosideros laurifolia* (Myrtaceae) has been tested as having a good affinity with AMF (Crossay et al. 2019); *Alphitonia neocaledonica* (shrub, Rhamnaceae) was considered an arbuscular mycorrhizal, but moderately colonized by these symbionts (Amir et al. 2013). *Tetraria comosa* (syn. *Costularia comosa*) is a sedge (Cyperaceae). This family is generally considered a non-mycorrhizal, but *T. comosa* has been reported as functionally mycorrhizal at a low level of AMF colonization (Lagrange et al. 2011; 2013). This sedge is also considered oligotrophic, with lower P requirements than other plants (Jaffré and L'Huillier 2010a, b). Different positive effects of AMF inoculation have been reported for the three species (Amir et al. 2013; Lagrange et al. 2013; Crossay et al. 2019). We aimed to test the effects of increasing P doses on these mycorrhizal functions. The clear differences between these three species were assumed to induce different responses to P fertilization.

We analyzed the effects of P supply on parameters related to AMF functions: mycorrhizal colonization; P, K, and Ca absorption; Ca/Mg value; and potentially toxic metal alleviation.

2 Materials and Methods

2.1 Soil Used

The soil used is a highly weathered Geric Ferralsol (Becquer et al. 2001) collected from an ultramafic ligno-herbaceous maquis in the Plum area (22°16′59″S, 166°39′12″E). Its physicochemical characteristics are as follow: organic carbon (C) 4.56%; total nitrogen (N) 0.22%; C/N 20.0; pH (H2O) 5.34; total P 192.4 mg kg^{-1}; available P (Olsen) 3.5 mg kg^{-1}; total Ca 0.09%; KCl-extractable Ca 79 mg kg^{-1}; total Mg 0.72%; total sodium (Na) 93.6 mg kg^{-1}; total K 682.7 mg kg^{-1}; total iron (Fe) 37.8%; total Mn 1.43%; total Ni 0.54%; total Co 0.12%; total Cr 3.67%; dimethylenetriaminopentaacetic acid (DTPA) extractable elements: K 40.1 mg kg^{-1}; Mg 170 mg Kg^{-1}; Mn 1,116 mg kg^{-1}; Fe 106 mg $kg^{-1} - 1$; Ni 116 mg kg^{-1}; Co 79 mg kg^{-1}; Cr 0.6 mg kg^{-1}.

2.2 Plant Species

Three endemic plant species frequently used for ecological restoration of mining-degraded areas (Wulff et al. 2010) were chosen for greenhouse experiment: two shrubs *Metrosideros laurifolia* (Myrtaceae) and *Alphitonia neocaledonica* (Rhamnaceae) and one of the most abundant species in herbaceous stratum in ultramafic maquis, *Tetraria comosa* (ex-*Costularia comosa*, Cyperaceae).

The seeds of *A. neocaledonica* having dormancy were heat-treated by 5 min immersion in a hot water (80 °C). Then the seeds of the three species were surface disinfected in a 1.25% solution of sodium hypochlorite (12° chlorometric) for 15 min and rinsed with distilled water in sterilized Petri dishes. After disinfection, the seeds were sown on sterilized vermiculite (autoclaved for 60 min at 120 °C), before transferring to experimental pots in ultramafic soil.

2.3 Pots Preparation for Greenhouse Experiment

The transfer of the seedlings from vermiculite to soil was performed after 1 month for *A. neocaledonica*, 4 months for *M. laurifolia*, and 5 months for *T. comosa* (the seedlings of the two latter species are fragile and cannot be transferred successfully at an earlier stage). *A. neocaledonica* and *M. laurifolia* were transferred in 2-L pots and *T. comosa* in 1-L pots. As the growth of these species is very slow in pure ultramafic soil, a mixture of 75% 2 mm sieved ultramafic soil and 25% (v/v) commercial compost (Terreau universel, AgrofinoFrance) was used. The composition of the

commercial compost was as follows: N 1.7 mg g^{-1}, P total 150 mg kg^{-1}, P Olsen 7 mg kg^{-1}, and K 139 mg kg^{-1}. If we consider the concentration of P in this compost, the increase in available P of the initial soil would be low (1.75 mg kg^{-1}). This mixture was autoclaved 3 times for 1 h at 120 °C, with an interval of 24 h. For each treatment and each species, 10 pots containing one individual plant were prepared. A plastic cup was placed under each pot to avoid losing elements by draining water.

2.4 Plant Inoculation with AMF

We used a mix of three selected isolates of AMF from ultramafic soils, previously tested in greenhouse conditions and described (Gensous 2014). They were selected for their tolerance to Ni, their spore production, and their positive effect on sorghum growth. These isolates have been characterized by sequence analysis of a part of the SSU rDNA: PSB1 (98% of similarity with *Claroideoglomus etunicatum*), PSO1, and RARC (the two showed 98% of similarity with *Acaulospora rugosa*). Their morphological characteristics confirmed this identification. The accession numbers are as follow: PSB1, Gb_MH424515; PSO1, Gb_MH424516; RARC, Gb_MH424517. Spores of each AMF isolate were produced separately on a sorghum culture grown for 5 months, on a non-ultramafic soil, autoclaved three times at 120 °C for 1 h, with an interval of 24 h. The spores were isolated by wet sieving (36 µm) and centrifugation using a 50% sucrose solution, and then thoroughly rinsed with water. They were immediately transferred to Petri dishes and counted under stereomicroscope. The plants were inoculated with a mix of spore suspensions of the three isolates at the following proportions (according to the spore production of each isolate): PSB1, 60%; PSO1, 25%; and RARC, 15%. For each plant, 2 mL of suspension containing about 100 spores was applied on the root system when transferred into the pots. Non-inoculated pots received 2 mL of the same suspension filtered through a 20-mm mesh size sieve.

2.5 Mineral Fertilization

To avoid the limitation effects of N and K deficiency when P was added, it was necessary to fertilize the soil with these two elements. They were added as Azolon 38 N (slow-release granules of methylene urea with 38% nitrogen) and potassium sulfate (K_2O 50%) at the same dose for all treatments for a given plant. The P was added as triple superphosphate (48%). The doses were chosen, in relation to the needs of these plants given by Jaffré and L'Huillier (2010a, b) and Wulff et al. (2010). For each plant species inoculated or not, five treatments differing only for P supply were tested. Table 1 gives the different doses used expressed in mg kg^{-1} of each of the three elements. For *T. comosa* (oligotrophic herbaceous with a slow growth rate), the doses of P, N, and K were lower than the two other species because a preliminary experiment revealed lower needs for these elements. In particular, the dose P4 used for the two other species induced high mortality of the plantlets during the first month in the greenhouse (Gensous 2014). The mineral supply was added only 45 days after the beginning of the experiment and was completed progressively, with 25% per week during four weeks, to avoid any toxicity for the small seedlings (this toxicity was observed on a preliminary experiment, particularly for *T. comosa*).

Table 1 P, N, and K fertilization doses used for the greenhouse experiment for *A. neocaledonica* and *M. laurifolia* and for *T. comosa*

P doses	N (mg kg^{-1})	K (mg kg^{-1})	P (mg kg^{-1})
A. neocaledonica and *M. laurifolia*			
P0	300	163.48	0
P1	300	163.48	82.74
P2	300	163.48	206.78
P3	300	163.48	413.57
P4	300	163.48	827.30
T. comosa			
P0	234.42	81.74	0
P1	234.42	81.74	86.23
P2	234.42	81.74	172.37
P3	234.42	81.74	258.51
P4	234.42	81.74	430.80

The pots (10 per treatment for each plant) were maintained under greenhouse conditions (23–28 °C day; 17–24 °C night), with daily watering to field capacity and partial shading.

2.6 Plant Growth and Mycorrhizal Colonization

The experiment ended 442, 367, and 440 days after the transfer to the pots respectively for *A. neocaledonica*, *M. laurifolia*, and *T. comosa*. The plants were then recovered with all their roots and washed to remove the soil. The root system and the aerial parts were separated and put in a dry chamber at 60 °C for 3 days to obtain the dry biomass.

Mycorrhizal colonization was estimated at the end of the experiment. For each treatment, about 0.5 g of fine roots of 5 randomly sampled plants were taken for mycorrhizal colonization assessment (for each pot, the roots were collected from three different points of the root system which colonized the pot without being very tight). The roots were stained with Trypan blue (Koske and Gemma, 1989). Root fragments were placed in a 10% potassium hydroxide (KOH) bath at 90 °C for 90 min. The roots were then rinsed in distilled water, soaked for few hours in 1% hydrochloric acid (HCl), and stained with Trypan blue (15 min at 90 °C). For

each plant, at least 25 root segments of 1–2 cm length were mounted on glass slides in 10% glycerol and observed under an optical microscope. A root segment was considered to be colonized by AMF when typical vesicles or intracellular hyphal coils were identified. The intensities of arbuscular mycorrhizal colonization, i.e., mycorrhizal density (M %) and mycorrhizal frequency (F%), were determined according to Trouvelot et al. (1986). The abundance of arbuscules was not quantified because they were not clearly visible (it is frequently the case in New Caledonian ultramafic soils).

2.7 Chemical Analyses

Before and at the end of the experiment, available P in soil was estimated using Olsen method, even if it has drawbacks in acidic soils. According to Fardeau et al. (1988), this method is better for agronomic uses than Dyer method which generally overestimates the biologically available P. At the end of the experiment, the plants were collected; the roots were separated from the shoots, and the organs were thoroughly washed. As the analyses need to have a total of at least 0.5 g of dry biomass to assess the plant mineral nutrition, the plant weight was not sufficient for some treatments (in pots non-supplied with P). It was then necessary to gather the samples of roots and shoots by two or three to obtain sufficient quantities of dry matter, and this was done for all treatments. Thus, only four samples of roots and shoots were finally obtained and analyzed. The samples were dried and ground to determine P, K, Ca, and Mg concentrations. Ca/Mg value was also calculated. Potentially toxic metal concentrations (Co, Ni, Cr) in shoots and roots were determined. The translocation factor (TF) defined as the ratio of metal concentration in shoots to that in roots was then calculated. All the analyses were done by ICP spectrophotometer at the chemistry laboratory of IRD (LAMA IRD Noumea) as described in Perrier et al. (2006).

2.8 Data Analyses

The effects of two factors and their interaction were tested: inoculation with AMF and P supply. A significant interaction indicates that the effect of inoculation depends on the level of P supply. As the distribution of most of the variables was not homoscedastic, we used two-way PERMANOVAs fixed models to identify the significant effects, using 999 unrestricted permutations of the raw data. If PERMANOVA test was found to be significant ($p \leq 0.05$), pair-wise post hoc permutation tests were used to identify the source of differences between groups. We also tested the effect of P supply on mycorrhizal colonization for all three species pooled together. A standardization within species was performed before the test to get comparable data. The same analysis was performed to test globally the effect of AMF inoculation and P supply on Ca/Mg value with the values of the three species considered together. A multiple correlation test was used to assess the links between mycorrhizal colonization and metal concentrations in shoots and roots.

All analyses were performed using Statgraphics v19 and Primer v7 softwares.

3 Results

3.1 Plant Growth

P supply had a strong effect on the growth of all species (Fig. 1). For *A. neocaledonica* and *T. comosa*, the biomass increased in proportion to the P dose. In pots non-inoculated with AMF, the smallest dose (P1) induced respectively 880% and 100% more shoot biomass for these two species, whereas P4 dose increased the shoot biomass by 2000% and 330% respectively. For *M. laurifolia*, a 28-fold increase of shoot biomass was observed for the P1 dose in comparison to P0. However, there were no significant differences between the different P doses in terms of plant biomass for non-inoculated plants, with the exception of the root biomass in P4 pots, which was significantly higher than that of the other treatments.

AMF inoculation did not have the same effect on the plant growth of the three plant species. In pots without P supply (P0), *A. neocaledonica* and *T. comosa* shoot and root biomasses were not significantly different at the end of the experiment, whether they were inoculated or not. On the contrary, *M. laurifolia* shoot and root growth was significantly improved by AMF symbiosis for P0 treatment (a 5.8-fold increase of shoot biomass). AMF inoculation did not influence *A. neocaledonica* and *T. comosa* biomasses for all P doses, except for *A. neocaledonia* P4 dose, which showed a significant increase of shoot biomass in presence of AMF. The growth of *M. laurifolia* was not changed by AMF at P1 and P2 doses but was reduced for P3 and P4 doses, respectively, for shoots and roots. P dose globally influenced the AMF effect for *M. laurifolia* and *A. neocaledonica*, but not for *T. comosa.*

3.2 Mycorrhizal Colonization

Mycorrhizal colonization of the plants not inoculated with AMF was nil or lower than 1%. Overall, *M. laurifolia* showed the highest levels of mycorrhizal colonization of the fine roots (15% at P0), whereas *A. neocaledonica* and *T. comosa* had lower levels (7–8% at P0) (Fig. 2). No significant differences were detected between the P treatments for the three plants taken separately, because of the high variability of the values and their distribution.

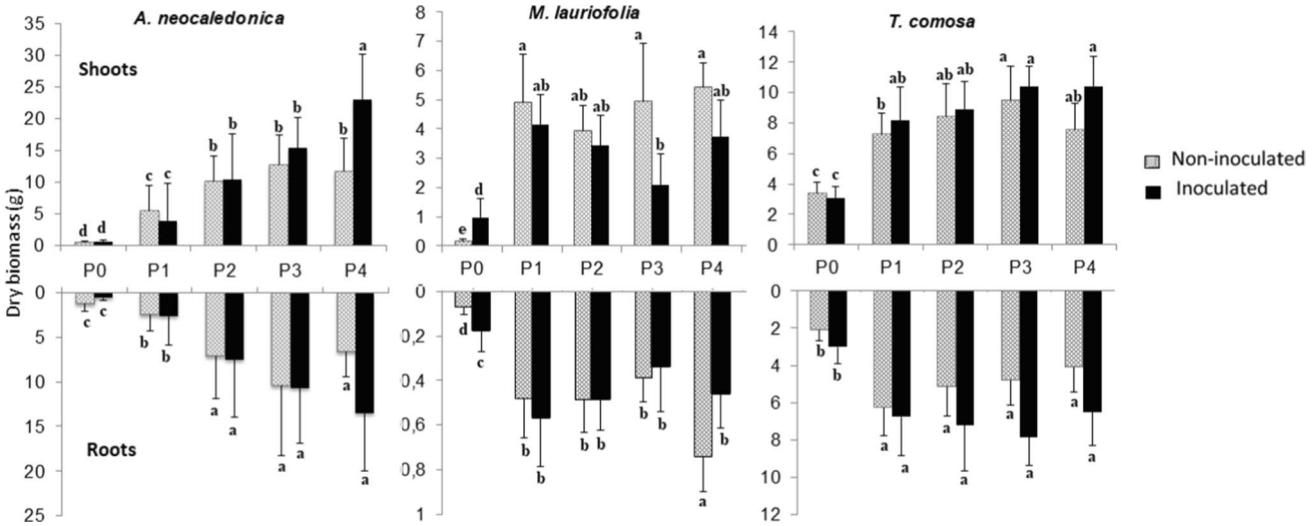

Fig. 1 Dry biomass (mean ± SE) for shoots and roots of *A. neocaledonica*, *M. laurifolia* and *T. comosa* at the end of the experiment (442, 367, and 440 days after inoculation with arbuscular mycorrhizal fungi, respectively for the three species). Effects of increasing doses of phosphorus supply (P0, P1, P2, P3, P4) and AMF inoculation. For each graph, means followed by the same letter do not differ significantly (two-way PERMANOVA followed by pair-wise permutation test; $n = 10$). The statistical significance of global effects and their interaction are given under the graphs. Significant interaction means that the effect of inoculation depends on P supply. NS: non-significant

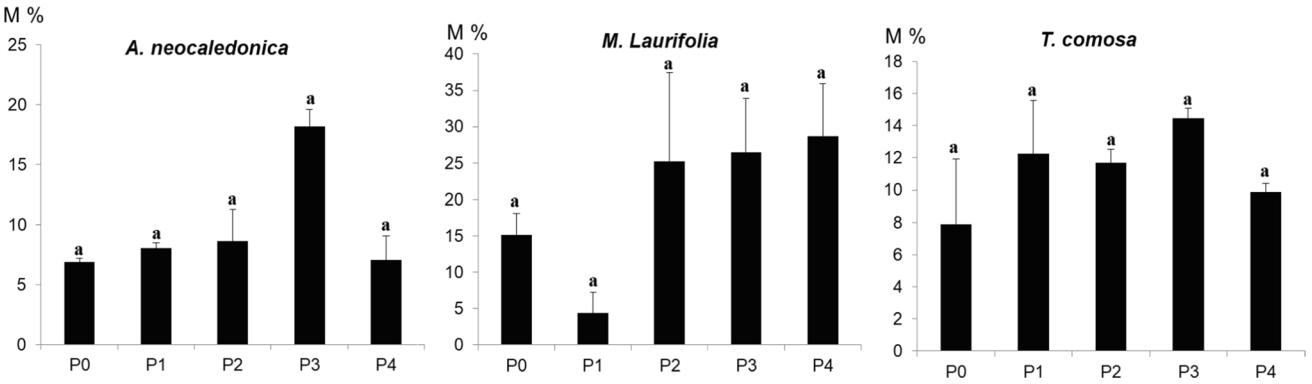

Fig. 2 Effects of increasing doses of phosphorus supply (P0, P1, P2, P3, P4) on mycorrhizal colonization, M% (mean ± SE), of inoculated plants of *A. neocaledonica*, *M. laurifolia*, and *T. comosa* at the end of the experiment (442, 367, and 440 days after inoculation with arbuscular mycorrhizal fungi, respectively for the three species). For all non-inoculated plants, mycorrhizal colonization was nil or lower than 1%. For each graph, means followed by the same letter do not differ significantly (two-way PERMANOVA followed by pair-wise permutation test; $n = 5$)

The values of mycorrhizal frequency (F%) varied from 64 to 81% but without any significant differences between the three plants and between the different treatments (data not shown).

3.3 Mineral Nutrition

P supply increased not only P absorption for the three plant species, but also K and Ca nutrition for *A. neocaledonica* and K nutrition for *M. laurifolia and T. comosa* (Table 2). For these two latter species, Ca concentration in shoots seemed to be reduced by P enrichment ($p = 0.001$ and $p = 0.005$).

The influence of AMF inoculation on the mineral nutrition of *A. neocaledonica* was not significant for all P doses when taken separately (Table 2). However, a global positive effect of AMF was detected for K concentrations ($p = 0.041$). For *M. laurifolia*, in absence of P supply, mineral nutrition was improved by AMF inoculation: K and Ca concentrations in shoots were significantly higher than those of non-inoculated plants. P concentration was not significantly enhanced, but the amounts of P absorbed by each plant were higher in presence of AMF because of their bigger volume enhanced by AMF (P absorbed per plant in presence of AMF was 0.57 g which was 6.3 times more than the control, 0.09 g).

Table 2 P, K, and Ca concentrations in shoots of *A. neocaledonica*, *M. laurifolia*, and *T. comosa* (mean ± SE) at the end of the experiment (442, 367, and 440 days after inoculation respectively for the three species) in relation to P supply (P0 to P4) and arbuscular mycorrhizal fungi (AMF) inoculation. The stars indicate significant differences with the non-inoculated corresponding treatment for the same P dose; the PERMANOVA could not give all the significances two by two because of uncertainty (two-way PERMANOVA followed by pair-wise permutation test; $n = 4$). Significant interaction means that the effect of AMF inoculation depends on P supply

P doses	AMF inoculation	*A. neocaledonica*			*M. laurifolia*			*T. comosa*		
		P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})
P0	Non-inoc[a]	0.13 ± 0.03	3.03 ± 0.41	3.10 ± 1.21	0.41 ± 0.07	2.22 ± 0.84	9.04 ± 0.96	0.32 ± 0.06	4.94 ± 0.80	1.73 ± 0.13
	Inoc	0.28 ± 0.14	5.07 ± 0.76	6.72 ± 0.01	0.52 ± 0.06	8.01 ± 0.83*	20.22 ± 3.06*	0.31 ± 0.01	5.03 ± 0.35	1.16 ± 0.02*
P1	Non-inoc	0.22 ± 0.05	5.97 ± 1.69	7.73 ± 1.02	1.47 ± 0.09	4.33 ± 0.46	6.55 ± 1.65	1.20 ± 0.03	4.99 ± 0.38	1.57 ± 0.15
	Inoc	0.24 ± 0.02	4.96 ± 0.28	5.93 ± 0.21	1.45 ± 0.09	4.60 ± 0.56	14.89 ± 2.59*	1.01 ± 0.18	5.09 ± 0.88	0.85 ± 0.02*
P2	Non-inoc	0.32 ± 0.06	6.04 ± 0.65	6.97 ± 1.05	1.71 ± 0.06	4.48 ± 0.31	6.29 ± 0.70	2.10 ± 0.12	6.29 ± 0.45	1.30 ± 0.13
	Inoc	0.35 ± 0.06	6.41 ± 0.02	8.26 ± 0.07	1.92 ± 0.18	5.81 ± 0.46	8.63 ± 2.39	1.95 ± 0.26	6.22 ± 0.53	0.96 ± 0.10
P3	Non-inoc	0.45 ± 0.03	6.68 ± 0.83	8.26 ± 0.19	2.22 ± 0.25	4.12 ± 0.03	5.76 ± 0.39	2.50 ± 0.39	5.64 ± 0.57	1.25 ± 0.01
	Inoc	0.56 ± 0.15	8.15 ± 0.24	7.19 ± 0.19	2.53 ± 0.15	6.45 ± 0.70	6.96 ± 1.18	2.05 ± 0.13	5.49 ± 0.20	1.11 ± 0.06
P4	Non-inoc	0.74 ± 0.21	6.76 ± 1.05	7.21 ± 0.79	2.81 ± 0.21	5.11 ± 0.36	6.60 ± 1.12	4.06 ± 0.32	7.08 ± 0.59	1.47 ± 0.07
	Inoc	0.40 ± 0.05	8.43 ± 0.46	5.91 ± 0.69	2.34 ± 0.12	8.84 ± 0.81	11.14 ± 0.77	2.87 ± 0.44	5.82 ± 1.04	1.09 ± 0.06*
Global effect of inoculation		NS	$p = 0.041$	NS	NS	$p = 0.001$	$p = 0.001$	$p = 0.006$	NS	$p = 0.001$
Global effect of P supply		$p = 0.001$	$p = 0.001$	$p = 0.002$	$p = 0.001$	$p = 0.029$	$p = 0.001$	$p = 0.001$	$p = 0.002$	$p = 0.005$
Interaction significance		NS	NS	$p = 0.001$	$p = 0.03$	$p = 0.001$	$p = 0.006$	NS	NS	$p = 0.044$

[a]*Inoc* AMF inoculated plants, *non-inoc* non-inoculated plants, *NS* non-significant

Overall, P supply reduced the effects of AMF on K and Ca concentrations in shoots of *M. laurifolia*: Only Ca concentration at P1 dose was significantly higher in presence of AMF when compared to non-inoculated plants. For *T. comosa*, no clear improvement of mineral nutrition was observed; a significant reduction of Ca concentration was even noted for P0, P1, and P4 doses, and a global reduction of P concentration in shoots was noted in P amended soils ($p = 0.006$).

Available P in soil, at the end of the experiment, increased from P0 to P4 dose (Table S1), reaching about 200 mg kg^{-1} for P4 dose in *A. neocaledonica* pots, 350 mg kg^{-1} in *M. laurifolia* pots, and 60 mg kg^{-1} in *T. comosa* pots. No differences were detected between AMF-inoculated and non-inoculated pots for *A. neocaledonica* and *M. laurifolia*. P-amended soil of *T. comosa* showed globally lower available P in AMF-inoculated pots when compared to non-inoculated ones ($p = 0.011$), as also revealed by interaction significance ($p = 0.007$).

AMF inoculation showed a global positive effect on Ca/Mg value for *A. neocaledonica* and *M. laurifolia* ($p = 0.001$ and 0.006) (Fig. 3). This effect is higher in absence of P supply (P0), with Ca concentrations two times higher than in non-inoculated plants (Table S2). For *C. comosa* at P0, the value of Ca/Mg in AMF inoculated pots was two times higher than the control (Mg uptake was lower), but the difference was not detected as significant. However, P supply globally reduced this ratio for this plant species ($p = 0.001$) and interacted with the effect of the AMF ($p = 0.012$). When considering the Ca/Mg values of the three species altogether, the global effect of AMF inoculation was significant ($p < 0.05$); and P0 values were found significantly higher for inoculated plants than all the P supplied pots taken together ($p < 0.01$).

3.4 Metal Concentrations in Plant

The effects of tested treatments on Ni, Co, and Cr shoot concentrations were mostly not significant when taken separately (Table S3). However, P supply globally reduced Ni concentrations for *A. neocaledonica* ($p = 0.002$). AMF inoculation significantly increased Co concentrations in P2, P3, and P4 amended soils. Cr concentrations were also globally increased by AMF ($p = 0.001$). For *M. laurifolia*, AMF inoculation globally enhanced Co concentrations ($p = 0.004$). For *T. comosa*, Ni concentration was globally reduced by AMF ($p = 0.045$), particularly in pots non-amended with P.

In roots, for *A. neocaledonica*, Ni and Cr concentrations were reduced by AMF inoculation at P0 and P1 doses, and Co was reduced only at P1 dose (Table S4). For *M. laurifolia*, AMF inoculation globally reduced Ni and Cr concentrations ($p = 0.023$; $p = 0.019$ respectively). Ni concentration in roots of *T. comosa* was globally decreased ($p = 0.017$), and Cr concentration was globally enhanced ($p = 0.001$); Co concentration was increased at P1 dose.

Metal translocation factors did not reveal significant effects (data not shown). Correlations tests were not able to detect significant links between mycorrhizal colonization and metal contents in shoots and roots of the three plants.

4 Discussion

The three endemic plant species already studied for their mycorrhizal status (Lagrange et al. 2011; Amir et al. 2013; Crossay et al 2019) were affected differently by P fertilization when grown in a highly P deficient ultramafic soil.

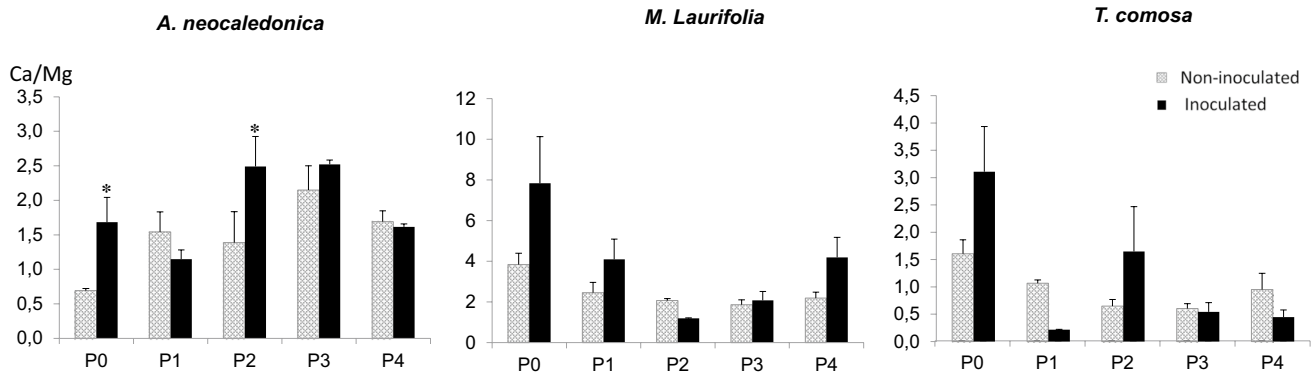

Fig. 3 Calcium/magnesium (Ca/Mg) values (mean ± SE) of aerial parts of *A. neocaledonica*, *C. laurifolia*, and *T. comosa* at the end of the experiment (442, 367, and 440 days after inoculation respectively for the three species). Effects of increasing doses of phosphorus supply (P0, P1, P2, P3, P4) and arbuscular mycorrhizal fungi (AMF) inoculation. The stars indicate significant differences with the non-inoculated corresponding treatment for the same P dose; the PERMANOVA could not give all the significances two by two because of uncertainty (two-way PERMANOVA followed by pair-wise permutation test; $n = 4$). The statistical significance of global effects and their interaction are given under the graphs. Significant interaction means that the effect of AMF inoculation depends on P supply. NS: non-significant

4.1 Effects of P Supply on Plant Growth

P deficiency appeared to be clearly limiting to plant growth rate. Indeed, plant biomass has been highly enhanced by P mineral supply for the three species, even at the lower dose used (P1) corresponding to about 80 mg kg^{-1} of total P added to the soil. This dose represented an increase of 43% in the total P. Available P concentration at the beginning of the experiment represents about 5% of the total P in the non-fertilized soil. At the end of the experiment, available P in soil for non-inoculated P1 pots were as follows: 22 mg kg^{-1} for *A. neocaledonica* (11% of the total P), 8 mg kg^{-1} M. *laurifolia* (4% of the total P), and 3 mg kg^{-1} for *T. comosa* (1.5% of the total P). Even if a part of the available P was absorbed during plant growth, as shown by the increase of P concentrations in plant organs, it seems that moderate levels of available P induce important increases of plant biomass, particularly for *A. neocaledonica* and *M. laurifolia* (respectively tenfold and 28-fold increase of aerial biomass). This clear effect of P fertilization on plant productivity of serpentine ecosystems has already been reported in a 10-year field experiment (Chiarucci and Maccherini 2007) and in field culture of maize on New Caledonian ultramafic area (L'Huillier et al. 1998). Overall, our results indicate that mineral P fertilization is suitable to enhance plant growth for ecological restoration of mining-degraded ultramafic areas. However, P supply had consequences in AMF symbiosis.

4.2 Effects of P Supply on Mycorrhizal Colonization

The relatively low levels of mycorrhizal colonization, as obtained here in non-fertilized pots, are frequently observed in New Caledonian ultramafic maquis, with values of M varying generally between 1 and 30% (Perrier et al. 2006), and have been related to the low productivity of the plants in these ecosystems (Amir et al. 2019). This low productivity means low energy produced by photosynthesis and then fewer carbon nutrients for AMF.

P mineral fertilization did not reduce mycorrhizal colonization; the values were even higher for P2, P3, and P4 doses, but not significant. An increase of mycorrhizal colonization after P fertilization (dose equivalent to P2 used here) has been observed for *T. comosa* in field conditions (Lagrange et al. 2013) confirming that P deficiency in ultramafic soils is limiting to AMF symbiosis. Other studies have shown a positive effect of P supply on mycorrhizal colonization in P deficient soils (Abbott et al. 1984; Bolan et al. 1984). At the end of the experiment, P available concentrations in soil non-supplied with P was low (1 to 9 mg kg^{-1} depending on treatment) confirming that the addition of 25% commercial compost did not change the low availability of P (3.5 mg kg^{-1} in the same soil without compost).

Schubert and Hayman (1986) considered that mycorrhizal development in onion plants was optimal at 50 mg kg^{-1} of available P in agricultural soils. However, this concentration can vary depending on soil characteristics. In New Caledonian Ferralsols, P is strongly adsorbed to iron oxides (Dubus and Becquer 2001; Jaffré and L'Huillier 2010b). L'Huillier et al. (1998), trying to grow maize on a New Caledonian ultramafic area, reported that the ability of these soils to adsorb P is exceptional; it was necessary to add more quantities of mineral P, in comparison with other soils, to obtain the same results. This means therefore that levels of available P higher than 50 mg kg^{-1} are needed to obtain the same effect on mycorrhizal colonization, than those obtained on agricultural soil. This can explain why mycorrhizal colonization was not inhibited, even for the higher doses of P. For example, P available concentrations in the soil of P3 non-mycorrhizal treatment at the end of the experiment were 79 mg kg^{-1} and 113 mg kg^{-1}, respectively, for the two shrubs *A. neocaledonica* and *M. laurifolia* and 65 mg kg^{-1} for the sedge *T. comosa*.

4.3 Effects of P Supply on Mycorrhizal Functions

The three plant species responded differently to AMF inoculation in pots supplied with different doses of P. For *A. neocaledonica* and *T. comosa* in non-fertilized pots, no significant mycorrhizal growth response (MGR) was observed. This was true also in P fertilized pots, with the exception of the P4 dose which induced a significant MGR on *A. neocaledonica* shoots. However, as stressed by Smith and Smith (2012) plants can obtain benefits from mycorrhizal symbiosis even in absence of MGR, particularly in P deficient soils. Indeed, some aspects of mineral nutrition were improved by AMF inoculation. K concentration was globally increased by the symbionts in shoots of *A. neocaledonica*. For *M. laurifolia*, in absence of P supply, an important MGR was noted on shoots and roots. Correlatively, K and Ca concentrations in shoots were enhanced. Ultramafic soils are mostly deficient for K and Ca (Jaffré and L'Huillier 2010b), and it was particularly the case for the soil tested in our experiment. Orlowska et al. (2011) also reported an increase of K and Ca concentrations in shoots of *Berkheya coddii* inoculated with AMF in ultramafic soil from South Africa. Doubkova et al. (2012) showed that inoculation of plants grown in ultramafic soils with a native AMF isolate increased shoot Ca concentrations. According to Doubkova et al. (2013), plants subjected to extreme nutrient limitation had markedly higher uptake efficiency of different elements, particularly Ca, in presence of AMF. In our experiment, Ca/Mg rose in pots non-supplied with P. Since low values of this ratio constitute a limiting factor in ultramafic soils (Proctor 2003; Jaffré and L'Huillier 2010a), higher values induced by AMF symbiosis enhance plants adaptation to ultramafic

constraints. AMF positive effects on Ca/Mg values of *M. laurifolia* shoots have been recently shown in a greenhouse and in field conditions (Amir et al. 2019; Crossay et al. 2019). Doubkova et al. (2011) reported a significant positive correlation between mycorrhizal colonization and Ca/Mg ratio of *Knautia arvensis* plants in different ultramafic areas. All these effects can be related to the increase of the exchange surface between soil and roots due to AMF extraradical mycelium, with selective uptake of the elements (Smith and Read 2008; González-Guerrero et al. 2016).

P supply appeared to reduce significantly mycorrhizal effects on mineral nutrition of the plants. P fertilization suppressed the positive effect of AMF inoculation on plant growth of *M. laurifolia*, with even a negative MGR for doses P3 and P4. K and Ca concentrations were not significantly enhanced at P2, P3, and P4 doses. Furthermore, P supply significantly reduced the effect of AMF inoculation on Ca/Mg ratio. Generally, high available P concentrations in soil reduce mycorrhizal colonization and then mycorrhizal functions (Smith and Read 2008; Yang et al. 2014). However, in our experiment, P supply did not reduce mycorrhizal colonization. These effects could then be related to the regulation of direct and indirect (AMF) pathways of P uptake, and its influence on the transfer of the other elements (Javot et al. 2007; Smith and Smith 2012).

The effects of AMF on potentially toxic metals are not as clear as reported before for *A. neocaledonica* and *M. laurifolia* (Amir et al. 2013; Crossay et al. 2019), probably due to lower mycorrhizal colonization. However, a significant reduction of Ni, Co, and Cr concentrations was observed in roots of *A. neocaledonica* in pots non-supplied with P or in pots of P1 dose. This reduction was not observed for the other P doses. Inversely, for the same plant, in P fertilized pots (particularly P2 and P3), an increase of Co concentration was induced by AMF inoculation in shoots of this species. For *T. comosa*, AMF inoculation reduced globally Ni concentrations in shoots but increased Co and Cr concentration in roots particularly in P fertilized pots. Studies on the influence of P fertilization on metal absorption did not show uniform conclusions. Nkrumah et al. (2021) supplied an ultramafic soil with different concentrations of P and did not find any significant influence of this fertilization on metal absorption by two Ni-hyperaccumulating plants. Contrastingly, Nafady and Elgharably (2018) reported that P fertilization decreased Cd and Zn concentrations in shoots of maize and this reduction was reinforced by AMF inoculation. According to Pigna et al. (2014), P fertilization did not influence arsenic (As) absorption but reduced As translocation to leaves of escarole when combined with AMF inoculation, in As-polluted soil. The authors suggested that suppression of the activity of high-affinity phosphate transporters linked to loss of the direct uptake pathway in AMF colonized roots could increase As tolerance. More generally, the reduction of metal uptake by AMF has been related to their downregulation of membrane transporters (Ferrol et al. 2016; González-Guerrero et al. 2016).

Overall, these results indicate that studied mycorrhizal functions seemed to be disturbed by P supply for the three plant species, the benefits observed in P0 pots being reduced or eliminated by P fertilization, without reduction of mycorrhizal colonization. To explain these results, we hypothesize that the negative effect of P fertilization on mycorrhizal functions could be related to the high adaptive structure of these plant species to ultramafic stresses. This adaptation was obtained by a reduction of their growth rate (Jaffré and L'Huillier 2010a; Bini and Maleci 2014), which help them to invest more energy to cope with the multiple stresses of this environment. A sharp increase of P availability, inducing a faster growth, may then disrupt this adaptive structure. As mycorrhizal colonization was not reduced, we can speculate that these symbionts contributed to P uptake even in highly P fertilized pots because of its strong adsorption in soil, but with hidden benefits when compared with non-inoculated plants (Smith and Smith 2012). However, as plant energy was mostly redirected towards the growth due to high P absorption, the other adaptive functions of the symbiosis were then lost or reduced in these conditions.

5 Conclusion

Our results showed that mycorrhizal symbiosis responded differently to P fertilization for the three tested plant species, in terms of growth, mineral absorption, and metal alleviation. However, it seems that in all cases, mycorrhizal functions were disturbed by P supply without reduction of mycorrhizal colonization. As the adaptive traits of the three plants to ultramafic soils were obtained by a reduction of their growth rate, we hypothesized that the high increase of this growth rate induced by P fertilization could have altered this adaptive structure.

To further test this hypothesis, it could be interesting, for example, to compare the behavior of plants adapted to ultramafic conditions with non-native plant species having a higher growth rate, such as sorghum. Sorghum is able to grow in compost-amended ultramafic soils and showed benefits from AMF inoculation in such conditions, particularly for metal alleviation (Amir et al. 2013; Crossay et al. 2020). Such a comparison, in soil supplied with different concentrations of P, could then highlight the perturbation of the adaptive traits of native plants inoculated with AMF.

New experimentations are also necessary to test P doses lower than P1 used here, particularly to determine what level of P supply could be used without having any disturbance in AMF functions. However, considering that the growth rate of the three plant species was highly increased by P1 and P2

doses, it seems clear that P3 and P4 doses are not suitable. This is especially advisable given that high mineral fertilization of New Caledonian ultramafic topsoils can induce the development of invasive plant species after revegetation (L'Huillier et al. 2010).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42729-021-00626-6.

Acknowledgements The authors thank the LAMA laboratory (LAMA-US IMAGO-IRD, New Caledonia) for the chemical analyses.

Author Contribution H.A. supervised and designed the research, provided the funding, and wrote the manuscript. S.G. conducted the experiment and corresponding analyses and treated the data. Y.C. contributed to the research supervision, particularly the molecular aspects. L.W. (statistician biologist) realized and corrected the statistical analyses and wrote the corresponding parts of materials and methods.

Funding The authors gratefully acknowledge CNRT "Nickel et son Environnement" for providing the financial support. The results reported in this publication are partly taken up from the CNRT report "Ecomine BioTop." We also are grateful to the South Province of New Caledonia for providing the PhD grant of Simon Gensous.

Declarations

Conflict of Interest The authors declare no competing interests.

References

Abbott LK, Robson AD, de Boer G (1984) The effect of phosphorus on the formation of hyphae in soil by the vesicular-arbuscular mycorrhizal fungus, *Glomus fasciculatum*. New Phytol 97:437–446

Amir H, Pineau R (2003) Relationships between extractable Ni, Co and other metals and microbiological characteristics of different ultramafic soils from New Caledonia. Aust J Soil Res 41:215–223

Amir H, Ducousso M (2010) Les bactéries et les champignons du sol sur roches ultramafiques. In : L'Huillier L, Jaffré T, Wulff A (eds) Mines et environnement en Nouvelle-Calédonie : les milieux sur substrats ultramafiques et leur restauration. IAC Ed, Noumea, pp 129–145

Amir H, Hassaine N, Lagrange A, Cavaloc Y (2013) Arbuscular mycorrhizal fungi, from New Caledonian ultramafic soils, improve tolerance to nickel of endemic plant species. Mycorrhiza 23:585–595. https://doi.org/10.1007/s00572-013-0499-6

Amir H, Jourand P, Cavaloc Y, Ducousso M (2014) Role of mycorrhizal fungi on the alleviation of heavy metal toxicity on plant. In: Solaiman ZM, Abbott LK, Varma A (eds) Mycorrhizal fungi: use in sustainable agriculture and land restoration. Springer, New York, pp 241–258. https://link.springer.com/chapter/10.1007/978-3-662-45370-4_15

Amir H, Cavaloc Y, Laurent A, Pagand P, Gunkel P, Lemestre M, Médevielle V, Pain A, McCoy S (2019) Arbuscular mycorrhizal fungi and sewage sludge enhance growth and adaptation of *Metrosideros laurifolia* on ultramafic soil in New Caledonia: a field experiment. Sci Total Environ 651:334–343. https://doi.org/10.1016/j.scitotenv.2018.09.153

Becquer T, Petard J, Duwig C, Bourdon E, Moreau R, Herbillon A (2001) Mineralogical, chemical and charge properties of Geric Ferralsols from New Caledonia. Geoderma 103:291–306

Bini C, Maleci L (2014) The « serpentine syndrome » (H. Jenny, 1980): a proxy for soil remediation. Environ Qual 15:1–13

Bolan NS, Robson A, Barrow NJ, Aylemore LAG (1984) Increasing phosphorus supply can increase the infection of plant roots by vesicular arbuscular mycorrhizal fungi. Soil Biol Biochem 16:419–420

Brooks RR (1987) The serpentine factor. In: Brooks RR (ed) Serpentine and its vegetation. A multidisciplinary approach. Discorides press, Portland, pp 32–59

Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77. https://doi.org/10.1007/s11104-008-9877-9

Crossay T, Cavaloc Y, Majorel C, Redecker D, Medevielle M, Amir H (2020) Combinations of different arbuscular mycorrhizal fungi improve fitness and metal tolerance of sorghum in ultramafic soil. Rhizosphere 14:100204. https://doi.org/10.1016/j.rhisph.2020.100204

Crossay T, Majorel C, Redecker D, Gensous S, Medevielle V, Durrieu G, Cavaloc Y, Amir H (2019) Is a mixture of arbuscular mycorrhizal fungi better for plant growth than single-species inoculants? Mycorrhiza 29:325–339. https://doi.org/10.1007/s00572-019-00898-y

Chiarucci A, Maccherini S (2007) Long-term effects of climate and phosphorus fertilization on serpentine vegetation. Plant Soil 293:133–144. https://doi.org/10.1007/s11104-007-9216-6

Doubkova P, Suda J, Sudova R (2011) Arbuscular mycorrhizal symbiosis on serpentine soils : the effect of native fungal communities on different Knautia arvensis ecotypes. Plant Soil 345:325–338. https://doi.org/10.1007/s11104-011-0785-z

Doubkova P, Suda J, Sudova R (2012) The symbiosis with arbuscular mycorrhizal fungi contributes to plant tolerance to serpentine edaphic stress. Soil Bio Biochem 44:56–64. https://doi.org/10.1016/j.soilbio.2011.09.011

Doubkova P, Vlasakova E, Sudova R (2013) Arbuscular mycorrhizal symbiosis alleviates drought stress imposed on Knautia arvensis plants in serpentine soil. Plant Soil 370:149–161. https://doi.org/10.1007/s11104-013-1610-7

Dubus IG, Becquer T (2001) Phosphorus sorption and desorption in oxide-rich ferrasols of New Caledonia. Aust J Soil Res 39:403–414. https://doi.org/10.1071/SR00003

Fardeau JC, Morel C, Boniface R (1988) Pourquoi choisir la méthode Olsen pour estimer le phosphore « assimilable » des sols ? Agronomie 8:577–584. hal-00885137

Ferrol N, Tamayo E, Vargas P (2016) The heavy metal paradox in arbuscular mycorrhizas: from mechanisms to biotechnological applications. J Exp Bot 67:6253–6265. https://doi.org/10.1093/jxb/erw403

Gensous S (2014) Les champignons mycorhiziens à arbuscules des sols ultramafiques de Nouvelle-Calédonie. Diversité, rôle dans l'adaptation des plantes à la contrainte ultramafique et interaction avec des rhizobactéries promotrices de la croissance des plantes. PhD thesis, Université de la Nouvelle-Calédonie, Noumea

González-Guerrero M, Escudero, V, Saéz A, Tejada-Jiménez M (2016) Transition metal transport in plants and associated endosymbionts: arbuscular mycorrhizal fungi and rhizobia. Front Plant Sci 7. https://doi.org/10.3389/fpls.2016.01088

Jaffré T (1980) Étude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle Calédonie. Travaux et documents de l'ORSTOM 124, ORSTOM, Paris.

Jaffré T, L'Huillier L (2010a) La végétation des roches ultramafiques ou terrains miniers. In : L'Huillier L, Jaffré T, Wulff A (eds) Mines et environnement en Nouvelle-Calédonie : les milieux sur substrats ultramafiques et leur restauration. IAC Ed, Noumea, pp 45–103

Jaffré T, L'Huillier L (2010b) Conditions de milieu des terrains miniers. In : L'Huillier L, Jaffré T, Wulff A (eds) Mines et environnement en Nouvelle-Calédonie : les milieux sur substrats ultramafiques et leur restauration. IAC Ed, Noumea, pp 33–44

Javot H, Pumplin N, Harrison MJ (2007) Phosphate in the arbuscular mycorrhizal symbiosis: transport properties and regulatory roles -. Plant Cell Environ 30:310–322. https://doi.org/10.1111/j.1365-3040.2006.01617.x

Jourand P, Ducousso M, Reid R, Majorel C, Richert C, Riss J, Lebrun M (2010) Nickel-tolerant ectomycorrhizal *Pisolithus albus* ultramafic ecotype isolated from nickel mines in New Caledonia strongly enhance growth of a host plant at toxic nickel concentrations. Tree Physiol 30:1311–1319. https://doi.org/10.1093/treephys/tpq070

Khade SW, Adholeya A (2007) Feasible bioremediation through arbuscular mycorrhizal fungi imparting heavy metal tolerance: a retrospective. Bioremediat J 11:33–43. https://doi.org/10.1080/10889860601185855

Koske RE, Gemma JN (1989) A modified procedure for staining roots to detect VA Mycorrhizas. Mycol Res 92:486–505. https://doi.org/10.1016/S0953-7562(89)80195-9

Lagrange A, Ducousso M, Jourand P, Majorel C, Amir H (2011) New insights into the mycorrhizal status of Cyperaceae from ultramafic soils in New Caledonia. Can J Microbiol 57:21–28. https://doi.org/10.1139/W10-096

Lagrange A, Amir H, L'Huillier L (2013) Mycorrhizal status of Cyperaceae from New Caledonian ultramafic soils: effects of phosphorus availability on arbuscular mycorrhizal colonisation of *Tetraria comosa* in field conditions. Mycorrhiza 23:655–661. https://doi.org/10.1007/s00572-013-0503-1

Lambers H, Mougel C, Jaillard B, Hinsinger P (2009) Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. Plant Soil 321:83–115. https://doi.org/10.1007/s11104-009-0042-x

L'Huillier L, Dupont S, Dubus I, Becquer T, Bourdon E, Laubreaux P, Bonzon B (1998) Carence et fixation du phosphore dans les sols ferrallitiques ferritiques de Nouvelle-Calédonie. In: Congrès Mondial de la Science du Sol : Actes = World Congress of Soil Science: Proceedings. Montpellier : ORSTOM, 8 p. Congrès Mondial de la Science du Sol, 16., Montpellier (FRA), 1998/08/20-26

L'Huillier L, Wulff A, Gateblé G, Fogliani B, Zongo C, Jaffré T (2010) La restauration des sites miniers. In : L'Huillier L, Jaffré T, Wulff A (eds) Mines et environnement en Nouvelle-Calédonie : les milieux sur substrats ultramafiques et leur restauration. IAC Ed, Noumea, pp 147–230

Marschner H (1995) Mineral Nutrition of Higher Plants. Academic Press, London

Nafady NA, Elgharably A (2018) Mycorrhizal symbiosis and phosphorus fertilization effects on Zea mays growth and heavy metals uptake. Int J Phytorem 20:869–875. https://doi.org/10.1080/15226514.2018.1438358

Nkrumah NI, Echevarria G, Erskine PD, Chaney RL, Sumail S, van der Ent A (2021) Contrasting phosphorus (P) accumulation in response to soil P availability in 'metal crops' from P-impoverished soils. Plant Soil in Press. https://doi.org/10.1007/s11104-021-05075-9

Orłowska E, Przybyłowicz W, Orlowski D, Turnau K, Mesjasz-Przybyłowicz J (2011) The effect of mycorrhiza on the growth and elemental composition of Ni-hyperaccumulating plant Berkheya coddii Roessler. Environ Pollut 159:3730–3738. https://doi.org/10.1016/j.envpol.2011.07.008

Perrier N, Amir H, Colin F (2006) Occurrence of mycorrhizal symbioses in the metal-rich lateritic soils of the Koniambo Massif, New Caledonia. Mycorrhiza 16:449–458. https://doi.org/10.1007/s00572-006-0057-6

Pigna M, Caporale AG, Cartes P, Cozzolino V, Mora M, Sommella A, Violante A (2014) Effects of arbuscular mycorrhizal inoculation and phosphorus fertilization on the growth of escarole (Cichorium endivia L.) in an arsenic polluted soil. J Soil Sci Plant Nut 14:199–209. https://doi.org/10.4067/S0718-95162014005000016

Proctor J (2003) Vegetation and soil and plant chemistry on ultramafic rocks in the tropical Far East. Perspect Plant Ecol 6:105–124. https://doi.org/10.1078/1433-8319-00045

Schubert A, Hayman DS (1986) Plant growth responses to vesicular-arbuscular mycorrhiza: XVI. Effectiveness of different endophytes at different levels of soil phosphate. New Phytol 103:79–90

Smith SE, Read DJ (2008) Mycorrhizal Symbiosis, 3rd edn. Academic Press, New York. https://doi.org/10.1016/B978-0-12-370526-6.X5001-6

Smith SE, Facelli E, Pope S, Smith F (2010) Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. Plant Soil 326:3–20. https://doi.org/10.1007/s11104-009-9981-5

Smith SE, Smith FA (2012) Fresh perspectives of the roles of arbuscular mycorrhizal fungi in plant nutrition and growth. Mycologia 104:1–13. https://doi.org/10.3852/11-229

Smith FA, Smith SE (2013) How useful is the mutualism-parasitism continuum of arbuscular mycorrhizal functioning? Plant Soil 363:7–18. https://doi.org/10.3389/fpls.2020.606472

Trouvelot A, Kough JL, Gianinazzi-Pearson V (1986) Mesure du taux de mycorhization VA d'un système radiculaire. Recherche de méthodes d'estimation ayant une signification fonctionnelle. In: Gianinazzi-Pearson V, Gianinazzi S (eds) Physiological and Genetical Aspects of Mycorrhizae. INRA Press, Paris, pp 217–221

Wang B, Qiu YL (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363. https://doi.org/10.1007/s00572-005-0033-6

Wulff A, L'Huillier L, Véa C, Jaffré T (2010) Espèces indigènes utilisables en revégétalisation. In : L'Huillier L, Jaffré T, Wulff A (eds) Mines et environnement en Nouvelle-Calédonie : les milieux sur substrats ultramafiques et leur restauration. IAC Ed, Noumea, pp 231–344

Yang G, Liu N, Lu W, Wang S, Kan H et al (2014) The interaction between arbuscular mycorrhizal fungi and soil phosphorus availability influences plant community productivity and ecosystem stability. J Ecol 102:1072–1082. https://doi.org/10.1111/1365-2745.12249