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Effects of nickel on growth and nutrient concentrations of *Cunonia macrophylla*, an endemic New Caledonian Cunoniaceae

Efectos del níquel en el crecimiento y las concentraciones de nutrientes de *Cunonia macrophylla*, una Cunoniaceae endémica de Nueva Caledonia

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SUMMARY

One of the main characteristics of New Caledonian ultramafic soils is their relatively high Ni concentrations. The objective of this study was to evaluate the Ni tolerance of *Cunonia macrophylla* Brongniart & Gris, an endemic species of New Caledonian ultramafics. A greenhouse experiment was conducted to study the effects of addition of Ni solutions (from 5 to 1000 $\mu\text{g Ni g}^{-1}$) on growth and on organic and mineral composition of *C. macrophylla*. Growth was improved with the addition of 50 $\mu\text{g Ni g}^{-1}$, whereas 1000 $\mu\text{g g}^{-1}$ reduced growth. The results also showed decreased NO_3^- concentrations in roots at 50 $\mu\text{g Ni g}^{-1}$ treatment, whereas leaf Cu and Zn concentrations increased with the same treatment. However, Ni applied at 1000 $\mu\text{g g}^{-1}$ had an antagonistic effect on K concentrations in all parts and induced greater sugar and protein concentrations in shoots. Concentrations of Ni increased in all parts with increasing concentrations of applied Ni, with an accumulation in roots. This study revealed the possible beneficial effect of Ni at 50 $\mu\text{g g}^{-1}$ on *C. macrophylla* development, probably stimulating the transfer of nitrogen from roots to shoots and increasing concentrations of two cofactors of enzymes, Cu and Zn. We also demonstrated the capacity of *C. macrophylla* to accumulate Ni in roots when it is at high concentrations in the soil environment.

RESUMEN

Una de las características más importantes de los suelos ultramáficos de Nueva Caledonia es su relativamente alta concentración de níquel. El objetivo de este trabajo es evaluar la tolerancia al Ni de *Cunonia macrophylla* Brongniart & Gris, una especie endémica de las ultramafitas de Nueva Caledonia. Se llevó a cabo un experimento en condiciones controladas para estudiar el efecto de la adición de soluciones de Ni (desde 5 hasta 1000 $\mu\text{g g}^{-1}$) en el crecimiento y en las concentraciones de compuestos minerales y orgánicos en *C. macrophylla*. El crecimiento mejoró con la adición de 50 $\mu\text{g Ni g}^{-1}$, mientras que 1000 $\mu\text{g g}^{-1}$ redujo el crecimiento. Los resultados también muestran un decrecimiento en las concentraciones de NO_3^- en las raíces bajo el tratamiento de 50 $\mu\text{g Ni g}^{-1}$, mientras que las concentraciones de Cu y Zn de las hojas se incrementaron con el mismo tratamiento. Sin embargo, el Ni aplicado a 1000 $\mu\text{g g}^{-1}$ tiene efecto antagónico sobre los niveles de K en todas las partes e inducen grandes concentraciones de azúcares y proteínas en los brotes. Las concentraciones de Ni se

incrementaron en todas las partes de la planta con el incremento de la concentración de Ni aplicado, acumulándose en las raíces. Este estudio reveló el posible efecto beneficioso de concentraciones de Ni de 50 $\mu\text{g g}^{-1}$ en el desarrollo de *C. macrophylla*, probablemente estimulando la transferencia de nitrógeno de las raíces a los brotes e incrementando las concentraciones de dos cofactores de enzimas, Cu y Zn. Además demostramos la capacidad de *C. macrophylla* de acumular Ni en las raíces cuando los niveles de este metal en el suelo son altos.

INTRODUCTION

One-third of the largest island of New Caledonia (Grande Terre) is covered with outcrops of ultramafic rocks on which mining sites have been established for Co, Cr, Fe and Ni extraction (Jaffré *et al.*, 1997). Industrial activities very quickly denude soil, causing gully erosion during torrential rains (Jaffré & Rigault, 1991), wind erosion, high insolation and compaction of horizontal surfaces (Jaffré *et al.*, 1997). These impacts are normally reduced by vegetation. Environmental protection involves revegetation programmes, which require the use of pioneer plants able to develop on poor soils to make possible the recovery of at least some of the original vegetation (Jaffré & Rigault, 1991).

The principal plant formation of the New Caledonian ultramafics contains 92% endemic species and is heliophilous and shrubby, with a cyperaceous herbaceous layer (Jaffré & Veillon, 1994). These species grow very slowly and their mineral composition usually reflects that of the soil they colonize: with low concentrations of some macronutrients (N, P, K, Ca) and relatively high concentrations of Ni (Jaffré, 1977). New Caledonian ultramafic soils present an ionic imbalance due to high Mg concentrations that accentuate the unfavorable conditions for plant development (Brooks, 1987; Jaffré *et al.*, 1997).

A family well-represented in the mining maquis is the Cunoniaceae, including six genera and more than 90 species. We study one species of this family, *Cunonia macrophylla*, to examine its potential for revegetation programmes. This species is resistant to drought in its natural environment and is common on ultramafic areas at low altitude. It also synthesizes biomolecules of pharmacological interest (Fogliani *et al.*, 2002a; Fogliani *et al.*, 2002b). Nickel is defined as an essential element for plants at low concentrations (Eskew, 1983; Brown *et al.*, 1987), but the great Ni content of many ultramafic soils can be toxic. The critical toxic concentration in soil depends on environmental factors such as temperature and aeration of the soil, presence or absence of organic inhibitors and chelates, ionic composition

and the pH of the soil solution, as well as species-specific factors (*e.g.* phenologic stage, presence of mechanisms for Ni tolerance) (Gabbrielli, 1991). Some Cunoniaceae in the genera *Geissois* and *Pancheria* accumulate Al or Ni (Jaffré *et al.*, 1979).

The objective of this study was to examine morphological, biochemical and mineral changes in young *Cunonia macrophylla* as induced by Ni added to the soil during a greenhouse experiment.

MATERIALS AND METHODS

Culture and harvest of plants

Seeds of *Cunonia macrophylla* were collected in the Koghis Mountains (ultramafic area in the south of La Grande Terre, New Caledonia) in March 2000 and kept in closed bottles at room temperature for 3 months. Seeds were sown at a rate of five seeds per pot (square pots, 9 cm each side) on a homogeneous mixture (1:1) of compost (Grignon U44551; made from blond and brown peat, heath mould; 42% dry matter; organic matter 42%; pH=6.8) and vermiculite (3–6 mm particles of Mg-Al iron silicate). The substratum was sterilised to limit algae and fungi development. Plants were grown in a greenhouse, with automatic daily watering for 5 min. After 9 months young plants were transferred to separate pots (15 cm each side) using the same substrate. In addition to the automatic watering, each pot was watered manually once a week with aqueous $\text{NiCl}_2 \cdot (6\text{H}_2\text{O})$ solutions containing 5, 10, 50, 100, 500, or 1000 $\mu\text{g Ni g}^{-1}$. However, the actual Ni concentration to which roots were exposed was uncertain. Plant-available Ni was probably lower in our substratum than in a hydroponic culture. This fact must be recognized in comparison to plants of the same species which grow on ultramafic soils, which are very low in organic matter.

Each treatment was repeated 3 times. After 6 months the fresh leaf and stem matter was weighed and leaf number and stem length were noted. Stem length was defined as shoot height from soil level to apical meristem. Fresh weight of roots was not measured

because many of their ends were lost due to strong adhesion to the substrate. The various parts (stems, leaves, roots) were frozen in liquid nitrogen and preserved at -18°C . Frozen samples were then crushed manually with liquid nitrogen and dried in a lyophilisator on a cycle of 48 h at -55°C . Dried samples were preserved at -18°C in sealed flasks.

Biochemical analysis

To extract water-soluble material, 200 mg of dry sample and 10 ml of distilled water were incubated for 1 h at 45°C in a water bath. The aqueous suspension was agitated for 10 min (Agitest 86212), then centrifuged at 5000 rev min^{-1} for 15 min. The supernatant (aqueous extract) was recovered by filtration (Laurent Trat-Dumas filter no. 1) and frozen at -18°C .

For analysis of total water-soluble sugars, 2 ml of anthrone reagent (92 mg of thiourea and 92 mg of anthrone in 100 ml of 70% H_2SO_4) and 100 μl of water were added to 100 μl of aqueous sample. After mixing, tubes were incubated for 10 min in a water bath at 95°C and the reaction was then terminated in an ice bath. The optic density was read at 635 nm with a reference of D+glucose (1 to 10 mg l^{-1}). Nitrate was measured by the method of Cataldo *et al.* (1975) in which a range of KNO_3 solutions (0.1 to 15 mM) was used as a reference. Total soluble proteins were measured according to the Folin Lowry method using a range standard of bovine albumin serum (3 to 30 $\mu\text{g ml}^{-1}$).

Mineral analysis

A Digesdahl Hach model 23130–21 mineralisator was used for the mineral analysis. Three hundred mg of dry matter were deposited in the mineralisator, 5 ml of 95% H_2SO_4 were added and then the hotplate was turned on at 440°C . After opening the vacuum system and when the backward flow was started, 17 ml of H_2O_2 were added. After total evaporation of the H_2O_2 and addition of 15 ml distilled water, the system was heated for 15 min at 204°C . The suspension was then collected in a 25 ml volumetric flask and analysed by the Analytical Chemistry Laboratory of the Institute of Research for Development in Nouméa for the determination of Al, Ca, Co, Cu, Fe, K, Mg, Mn, Ni and Zn concentrations using an ICP plasma spectrophotometer (Perkin Elmer 3300DV).

Statistical analysis

Results presented in graphs are the means of three replicates. Data were analyzed by one-way analysis of variance (ANOVA) (SigmaSTAT). Bars denoted by different letters are significantly different as determined by a t-test. Linear regression was conducted for some experimental results: R^2 values for these analyses are reported in figures.

RESULTS

Morphological study

A Ni addition of $50\text{ }\mu\text{g g}^{-1}$ (Fig. 1) increased leaf number. Shoot and leaf fresh weight, and stem fresh weight:length ratio, reached a maximum at $50\text{ }\mu\text{g Ni g}^{-1}$ but these trends were not statistically significant. The stem fresh weight:length ratio indicated thickening of stems. All morphological features measured were equivalent to the control at a Ni addition of $1000\text{ }\mu\text{g g}^{-1}$. However shoots of plants treated with $1000\text{ }\mu\text{g Ni g}^{-1}$ were less green and necrotic areas appeared.

Biochemical study

Addition of $50\text{ }\mu\text{g Ni g}^{-1}$ induced a rise in the nitrate concentrations (Fig. 2A) of stems and a reduction of nitrate in roots and leaves. At $1000\text{ }\mu\text{g Ni g}^{-1}$, the nitrate concentration decreased in stems and remained equivalent to the control in roots and leaves. Correlations between the nitrate concentration of roots and the fresh weight of different shoot parts (Fig. 3) indicated that the less the nitrate concentration in roots the more shoot fresh weight was produced.

Soluble sugar concentration (Fig. 2B) was constant in roots until $500\text{ }\mu\text{g Ni g}^{-1}$, then increased quickly at $1000\text{ }\mu\text{g Ni g}^{-1}$. The sugar concentration in stems increased proportionally with Ni applied ($R^2=0.93$) but did not vary significantly in leaves.

The leaves:stems ratio for soluble protein concentration (Fig. 2C) remained unchanged regardless of treatment, showing that Ni treatments have the same effects on all shoot parts. Stems:roots and leaves:roots soluble protein concentration ratios strongly increased at $1000\text{ }\mu\text{g Ni g}^{-1}$.

Mineralogical study

Macronutrients and Fe: Shoot and root concentrations (Fig. 4A, B) of K decreased when Ni increased. Calcium,

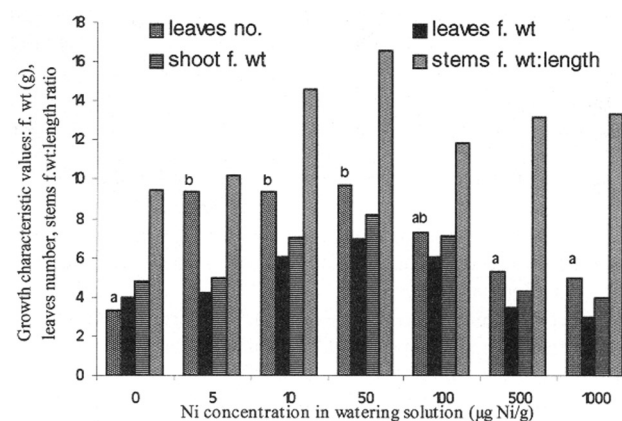


Figure 1 Effects of Ni treatment on shoot f. wt. (n.s.), leaves f. wt. (n.s.), leaves number ($P<0.01$) and stem f. wt.:length (n.s., values on y-axis should be multiplied by 100).

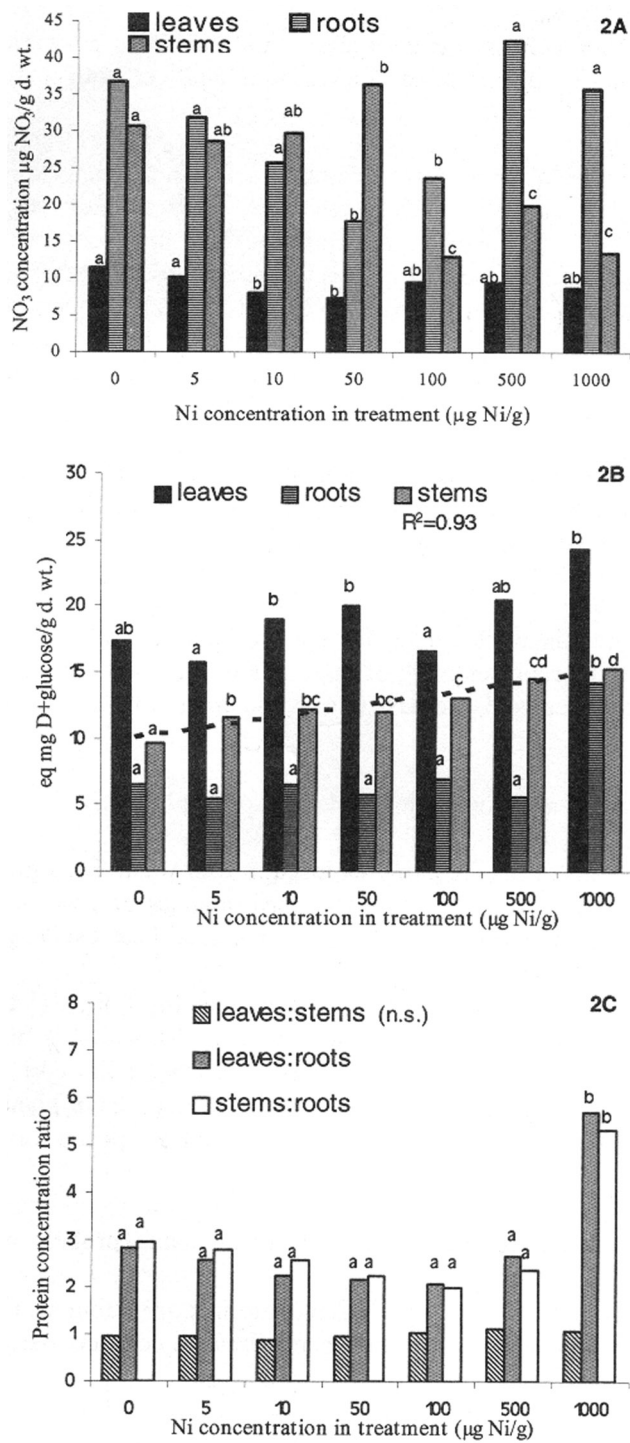


Figure 2 Effects of Ni treatments on: 2A, nitrate concentrations; 2B, water soluble sugar concentrations (dotted line shows linear tendency for stem values); and 2C, soluble protein concentration ratios of plant parts ($P < 0.05$).

Fe, and Mg concentrations did not vary with treatment in leaves, but decreased greatly in roots with increased Ni (Ca decreased 51%, K 65% and Fe 84% in the 1000 $\mu\text{g Ni g}^{-1}$ treatment as compared with the control).

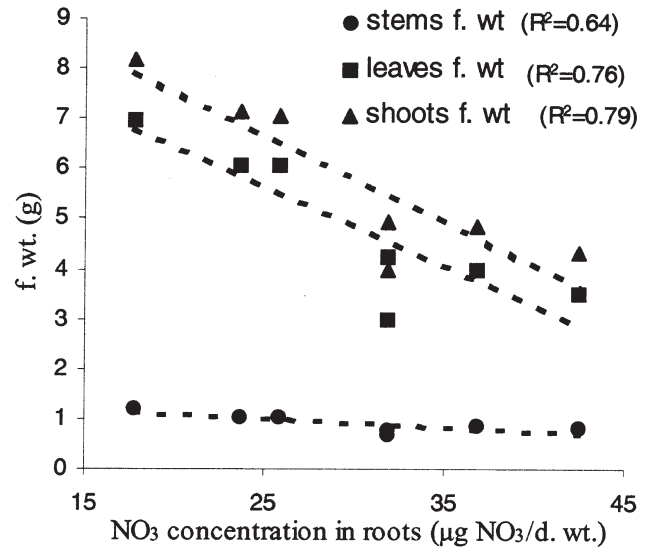


Figure 3 Correlation between root NO_3^- concentration and shoot f.wt.

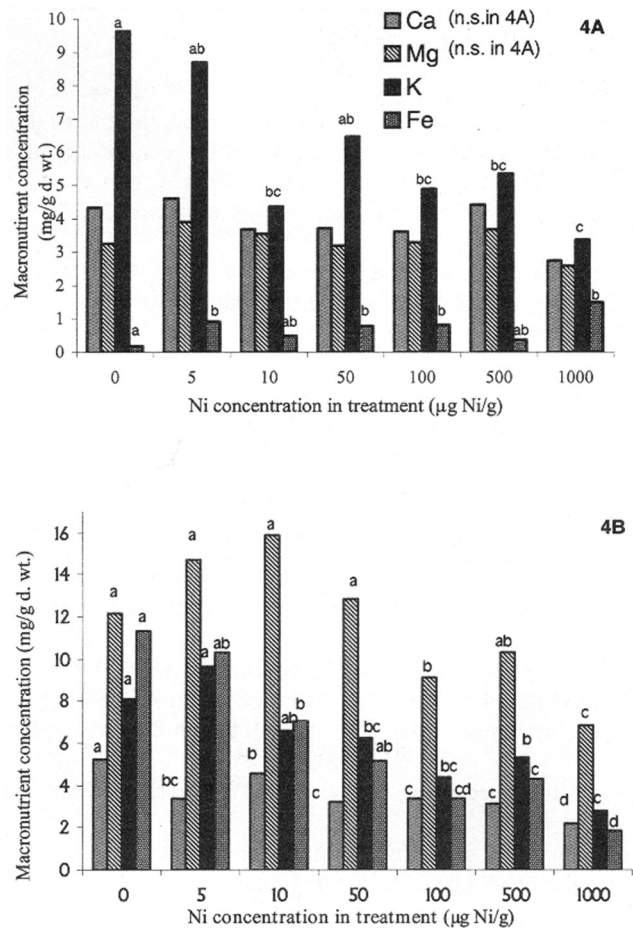


Figure 4 Effects of Ni treatment on macronutrient and Fe concentration in leaves (4A) and roots (4B) ($P < 0.05$).

Micronutrients, Co and Al: To represent the micronutrient concentration, we present the leaves:roots ratio (Fig. 5). At $50 \mu\text{g Ni g}^{-1}$, this ratio increased 11-fold compared to the control for Cu, 4-fold for Zn, 2.5-fold for Mn and 2-fold for Co (n.s.). Aluminum concentration increased with increasing Ni application.

Nickel: Nickel concentrations in leaves, stems and roots increased proportionally to Ni applied to the substratum (Fig. 6). Figure 6 shows that Ni concentrations in roots were greater than in stems, and in stems were

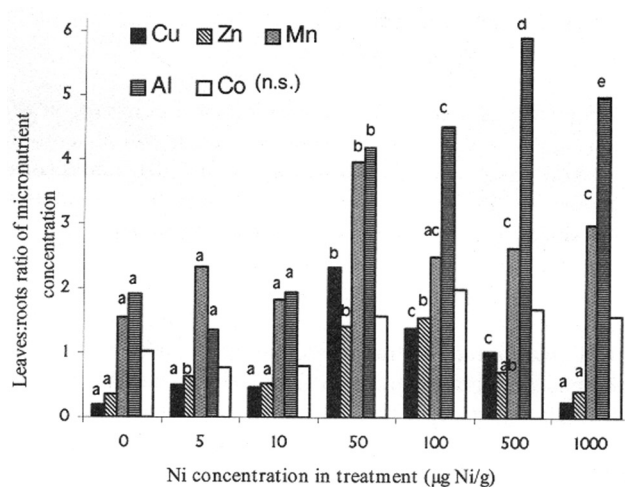


Figure 5 Effects of Ni treatment on micronutrient leaves:roots ratios. Ratios were divided by 10 to simplify y-axis scale when graphed ($P < 0.05$).

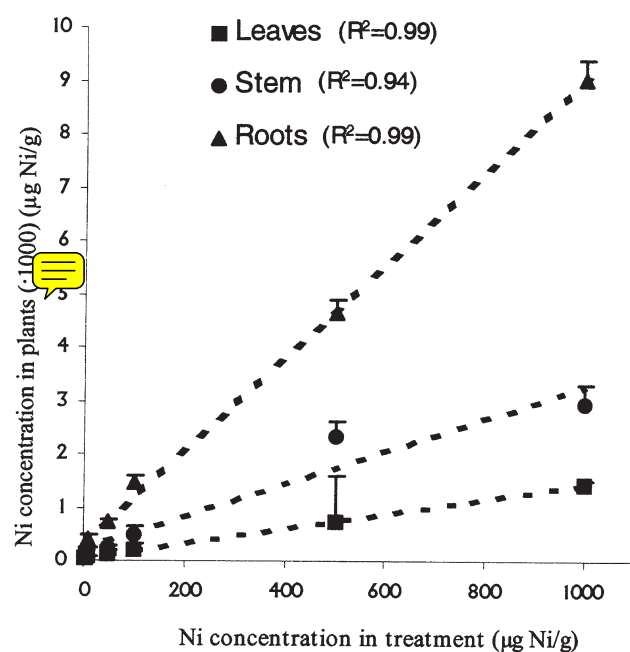


Figure 6 Effects of Ni treatments on Ni concentrations (values on y-axis should be multiplied by 1000) in plant parts ($P < 0.01$).

greater than in leaves. This suggested that Ni diffuses in the plant along a gradient, decreasing from the roots towards the leaves, and accumulating in roots. The Ni concentration was greater in plants than in the watering solutions ($9022 \mu\text{g Ni g}^{-1}$ in roots treated with $1000 \mu\text{g Ni g}^{-1}$).

DISCUSSION

Morphological study

Growth of *Cunonia macrophylla* was improved by Ni addition. Beneficial effects of low Ni levels on plant growth have previously been observed. Homer *et al.* (1991) noted a 2-fold increase in biomass produced with *Alyssum troodii* (a Ni hyperaccumulator) in the presence of $212 \mu\text{g Ni g}^{-1}$, and an increase of 15% for *Aurinia saxatilis* (a non-hyperaccumulator) with $94 \mu\text{g Ni g}^{-1}$. *Pisum sativum* seedlings had a 20% increase in growth with 0.01 and $1 \mu\text{g Ni g}^{-1}$ applied to a non-enriched natural calcareous substrate (Kevresan *et al.*, 2001). Küpper *et al.* (2001) also noted a significant increase in dry weight produced in culture on compost enriched with $500 \mu\text{g Ni g}^{-1}$ (NiSO_4) of *Alyssum lesbiacum*, *Alyssum bertolonii* and *Thlaspi goesingense*. In our study, nickel toxicity appeared only beyond $500 \mu\text{g Ni g}^{-1}$. This suggested that the behaviour of *C. macrophylla* could be similar to a Ni-tolerant species in this experiment, indicating its potential usefulness in revegetation programmes at Ni mines.

Biochemical study

The decrease in nitrate concentration in roots and leaves with $50 \mu\text{g Ni g}^{-1}$ was related to the increase in shoot biomass production. We assumed that a possible translocation of nitrate from roots towards leaves favored shoot metabolism and enhanced growth. The enhancement of stem thickness with $50 \mu\text{g Ni g}^{-1}$ could be explained by a slight increase of nitrate. Zornoza *et al.* (1999) suggested that N assimilation from nitrates could be partially inhibited by Ni, whereas N assimilation from ammonium seems insensitive to Ni. Singh *et al.* (1990) noted that the presence of $200 \mu\text{g Ni g}^{-1}$ in a loam soil (not limestone) induced a 20% decrease in the total nitrogen concentration of *Triticum aestivum*.

Nickel added in great concentration induces an increase in sugar concentration in the whole plant. It is possible that the latter are protective sugars of the cell walls. In addition, protein concentration increased with Ni addition. Considering the symptoms of toxicity observed with this strong treatment, these proteins could be produced in reaction to metal stress.

Mineral analysis

Nickel applied to the substrate modified the mineralogical composition of *Cunonia macrophylla*. Nickel induced decreases of K in leaves and Mg, K, Ca and Fe

in roots. A decrease in cellular turgidity, causing escape of K ions, is often observed with metal toxicities (Barcelo & Poschenrieder, 1990). Ahonen-Jonnarth & Finlay (2001) observed a reduction in K concentration in the roots of *Pinus sylvestris* when hydroponic culture solutions were enriched with 85 and 170 $\mu\text{g Ni g}^{-1}$. Since K and Ni can be combined with organic acids (Mazliak & Laval-Martin, 1995; Yang *et al.*, 1997), Ni can compete for binding sites on the organic acids if the concentration is too high. The application of 15 $\mu\text{g Ni g}^{-1}$ ($\text{NiCl}_2 \cdot 6\text{H}_2\text{O}$) to *Zea mays* induced membrane lipidic peroxidation, probably due to contact between Ni and the root cell membranes (Baccouch *et al.*, 2001). Membranes damaged by successive oxidations induce a leakage of K, then a loss of cellular turgidity. Gabbrielli *et al.* (1990) observed in *Silene italica* (a Ni tolerant species) a stimulation of peroxidase activities under Ni treatment. Baccouch *et al.* (2001) observed a reduction in root Ca concentration. Nickel could be involved in membrane destruction by weakening of the pecto-cellulose wall (Ca-pectin chain) and thus can slow down cell division.

The Fe concentration decreased in roots with increasing Ni treatment, while the Fe concentration in leaves remained constant regardless of treatment. The same results have already been observed (Singh *et al.*, 1990) with *Triticum aestivum*. The decrease in Fe concentration in roots was in accordance with previous research (Homer *et al.*, 1991; Yang *et al.*, 1996b). Antagonistic effects between Ni and Fe uptake have been reported (Kukier & Chaney, 2004). Indeed, roots secrete chelating amino acids capable of making ferric oxide soluble, thus allowing Fe uptake by roots. Nickel can inhibit this by competing with iron for the chelating ligands. The unchanged Fe concentration in the leaves suggested that Fe deficiency in roots in the presence of Ni induced the translocation of Fe from roots towards shoots. When plants are not protected against Ni, competition between Fe and Ni could inhibit photosynthesis, because of the role of Fe in chlorophyll synthesis (Nagy & Proctor, 2001). In the case of *C. macrophylla*, translocation of Fe from the roots towards the shoots under Ni stress revealed strategies which protected the shoots from the indirect depressive effects of Ni on photosynthesis. To explore this assumption, further study should be directed towards the processes which produce Fe transporters in plants.

It appears that 50 $\mu\text{g Ni g}^{-1}$ in solution induced in *C. macrophylla* an enrichment of Mn, Cu and Zn in leaves. Zinc is a constituent of the enzyme carbonic anhydrase, which facilitates the diffusion of CO_2 in chloroplasts and thus acts to improve photosynthetic activity. It is also a cofactor of glutamate synthetase for the assimilation of nitrate. Bernal *et al.* (1994) showed an increase in the foliar concentration of Zn and Cu in *Alyssum murale* (a Ni hyperaccumulator species) and

Raphanus sativus (a non-accumulating species) cultivated on a compost enriched with 400 $\mu\text{g Ni g}^{-1}$. Yang *et al.* (1996b) showed an increase in the flow of Zn ions from the soil toward the roots of *Lolium perenne* and *Zea mays* with Ni treatment of 1.5 and 15 $\mu\text{g Ni g}^{-1}$, as well as a similar increase in Cu concentration in *Lolium perenne*. However, Singh *et al.* (1990) reported that Ni decreases trace elements such as Zn, Cu and Mn in *Triticum aestivum*. The effects of Ni on the level of Cu and Zn in shoots are thus not elucidated. Aschmann & Zasoski (1987) showed that Ni, Zn and Cu have a similar K_m and V_{max} in *Avena sativa* for low Ni concentrations (to 1.25 $\mu\text{g Ni g}^{-1}$) in hydroponic solutions. Thus, the ionic balance in the rhizosphere when plants are watered with 50 $\mu\text{g Ni g}^{-1}$ may be favorable for the assimilation of Mn, Cu and Zn in *C. macrophylla*. Increased Mn, Zn and Cu concentrations appeared for the 50 $\mu\text{g Ni g}^{-1}$ treatment, which had greater fresh biomass production. The assumption was that these micronutrients played a role in the better growth observed under the stimulation of Ni treatment. However this hypothesis has to be confirmed by further experiments and greater number of replicates.

Strong chemical and physiological similarities between the mechanisms of control of the assimilation of Co and Ni in higher plants have been suggested (Jaffré, 1977; Homer *et al.*, 1991) and this could explain the increase in the Co concentration.

Nickel concentration in roots and shoots of *C. macrophylla* increased in proportion to Ni treatments. This assumed a passive uptake of Ni into all parts and a lack of Ni exclusion mechanisms in the roots. Our results assumed that *C. macrophylla* is not a Ni-excluder species, like many ultramafic species. Nickel concentration increased linearly in leaves and roots in *Triticum aestivum* cultivated with increasing Ni concentrations (Singh *et al.*, 1990). In the results we suggested that Ni diffused in the plant along a gradient, decreasing from the roots towards the leaves, and having a favourable Ni accumulation in roots. High Ni concentrations in the roots are probably due to a large exchange capacity between the roots and the soil solution (Singh *et al.*, 1990). Some authors (Yang *et al.*, 1996a; Kovacevic *et al.*, 1999) have suggested that traits that induce weaker transfers of Ni toward shoots, which seems to be the case for *C. macrophylla*, result in Ni tolerance. The flow of Ni from soil towards shoots is thus reduced and the photosynthetic parts are protected from the depressive effects of Ni. However, Ni tolerance and hyperaccumulation in *Alyssum tenium* are not necessarily dependent on translocation of the metal through the plant (Nedelkoska & Doran, 2001). Further experiments are required to characterise the processes of Ni translocation from roots to shoots and the location of Ni in the various tissues of *C. macrophylla*. The Ni concentration was higher in the plants

than in the watering solution, which suggested an accumulation of Ni in the plants. This does not mean that *C. macrophylla* is a hyperaccumulator species, because the accumulation in tissues could result from an accumulation of Ni in the substrate during the culture and not from hyperaccumulation by *C. macrophylla*. However the high concentrations throughout the plant suggested that *C. macrophylla* was able to support strong accumulation of Ni without damage to growth. Several hypotheses may explain the presence of mechanisms of Ni accumulation in plants (Sagner *et al.*, 1998): a strategy of adaptation to survive on soil rich in Ni, but also a means of protecting plants against predation by herbivores and microorganisms.

CONCLUSIONS

Cunonia macrophylla seemed to be Ni tolerant in our experiment. The beneficial effect of 50 $\mu\text{g Ni g}^{-1}$ on growth and changes in micronutrient and macronutrient concentrations are the most obvious effects of Ni on this species. A study of nitrate-reductase, glutamine-synthetase and glutamate-synthetase activities could refine these conclusions. Moreover, an endemic hyperaccumulator species of the Cunoniaceae, *Geissois pruinosa*, has shown similarly beneficial effects of addition of 50 $\mu\text{g Ni g}^{-1}$ solution to soils (Fogliani, 2002). That research showed adaptation of *C. macrophylla* to a high-Ni environment and the potential use of this species for revegetation programmes on Ni-rich soils.

All the assumptions exposed in the present work have to be confirmed by the use of a greater number of replicates coming from different ultramafic areas. Indeed, the location and date of seed collection are very important factors controlling the physiological responses of plants to Ni stress. This work could serve as a model for further studies in the field of Ni tolerance of New Caledonian ultramafic species.

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