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Understanding Root Uptake of Nutrients, Toxic and Polluting Elements in Hydroponic Culture

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1. Introduction

The understanding of plant uptake (nutrients, toxic and polluting elements) is crucial for the future food needs of humanity given the explosive growth of the world population and the anthropogenic pressure on the environment which significantly modify the homeostasis of the balanced global cycles. Rice and banana are of fundamental interest for development policy since they are two major foods for the world population. The understanding of the mechanisms and the optimal conditions of nutrient uptake by these plants is thus important to ensure biomass production. Furthermore, the transfer of toxic and polluting elements in the soil-plant system can influence the nutrient uptake and plant growth, and thus has strong agronomic consequences, in addition to the large environmental consequences.

Cultivation of plant in mineral nutrient solution rather than in soil allow scientists to study the relationship between nutritional status and plant growth, but also the impact of biotic and abiotic factors on the plant development. Besides its usefulness for agricultural industry, hydroponic is an ideal culture device to isolate factors affecting plant growth and better understand the essential, beneficial, toxic and polluting effects of the chemical elements, and the chemical transfer of the elements from hydro/pedosphere to biosphere. The understanding of nutrient transfer is indeed crucial for the productivity of the Earth's biosphere in order to (i) maintain the homeostasis of elements between lithosphere, atmosphere and biosphere, (ii) produce sufficient food well-allocated between north and south hemisphere, and (iii) constrain the mobility of toxic and polluting elements in the soil-plant systems and their transfer in the hydrosphere. The chemical elements present in the soluble phase of soil are very reactive with the interfaces of roots in the rhizosphere, and their transfer in the biosphere clearly depends on the activity of other elements in the aqueous phase. Furthermore, in soil-plant systems, the activity of one element in soil solution depends also on many other environmental factors than its own activity in the interfaces of roots: acidity and redox potential of solution, the equilibrium between aqueous and solid phases (neoformation, adsorption, complexation, co-precipitation...), temperature, humidity, enzymatic activity, type of microorganisms, ...

Aluminium toxicity is a primary factor limiting the growth and yield of the majority of plants grown in mineral acid soils of tropical and subtropical areas (Horst, 1995; von Uexküll & Mutert, 1995). This toxicity occurs when soil acidification causes Al solubilization (Lindsay, 1979) and thereby increases the concentration of Al^{3+} ion, the most phytotoxic Al

form in the soil solution (Kochian, 1995). Numerous studies have demonstrated the marked depressive effects of soluble aluminium (Al) on water and nutrient uptake, root and shoot growth, and mineral content in different plant species (Quang et al., 1996; Voigt et al., 1999). In addition, since 1945, the toxic radioisotope ^{137}Cs has been released in the environment by nuclear weapons testing, controlled discharge of waste effluents from nuclear plants, and accidental release (Avery, 1996). A general consensus emerged that radiocesium exhibits a biogeochemical behavior rather similar to that of potassium. In this regard, radiocesium displays a relative mobility in various soil-plant systems through uptake by plants and organisms (Carter, 1993), threatening the food chain. The close link between soil solution and roots strongly controls the solubility of nutrients but also of toxic metals, which can cause severe losses in agricultural yield. It is thus crucial to better constrain the root-solution interface through hydroponic culture experiment in order to offer the current better practices for land use management. The dynamic of elements in soil-plant systems depends on ion exchange reactions between soil matrix, solution phase and root. These processes can be assessed by hydroponic studies (Dufey et al., 2001), which demonstrate that the release of protons and organic substances in the rhizosphere strongly influence the mobilization of nutrients and toxic elements (Hinsinger, 1998).

In this chapter, we develop hydroponic devices to study both **root-solution interface**, and **soil-solution-root reactions**. We report hydroponic solutions developed for banana, rice and tree seedlings (Douglas fir and Black pine) as close as possible to the actual concentrations of the soil solution. We also describe a culture medium including solid minerals as a source of nutrients and polluting elements. We focus on the use of hydroponic studies to better understand the dynamics of nutrients (Ca, Mg, K, Na), beneficial (Si), toxic (Al) and polluting (^{137}Cs) elements in the solution-root interfaces, but also the uptake mechanisms, assimilation and translocation of these elements by plants and their subsequent role on plant growth. Finally, we develop the use of geochemical tracers such as stable silicon isotopes and Ge/Si ratios as promising tools to understand plant physiological mechanisms through the quantification of Si isotope and Ge-Si fractionations between dissolved Si source and banana plant, between roots and shoots, and within shoots.

Combining hydroponic culture studies and knowledge in soil science and biogeochemistry, we then point the importance of hydroponic culture to suggest agronomic and environmental advices for plant growth in Earth's Critical Zones characterized by a very poor nutrient stock in old and weathered tropical soils, and largely influenced by global change processes.

2. Hydroponic culture devices

Numerous devices are reported in literature to conduct plant growth experiments in hydroponics. In this section, we describe the principles of the devices that we regularly used in our laboratory in the last forty years.

2.1 Growth conditions and composition of nutrient solutions

Prior to hydroponic culture in controlled conditions, seeds are surface-sterilized with 5% H_2O_2 and rinsed five times with demineralized water. The seeds are germinated, and then weaned in an adequate nutrient solution tanks before selecting uniform seedlings for the

experiments. Batches of seedlings are grown in separate pots and placed on a perforated plate of expanded polystyrene which limits water loss by evaporation (Fig. 1).

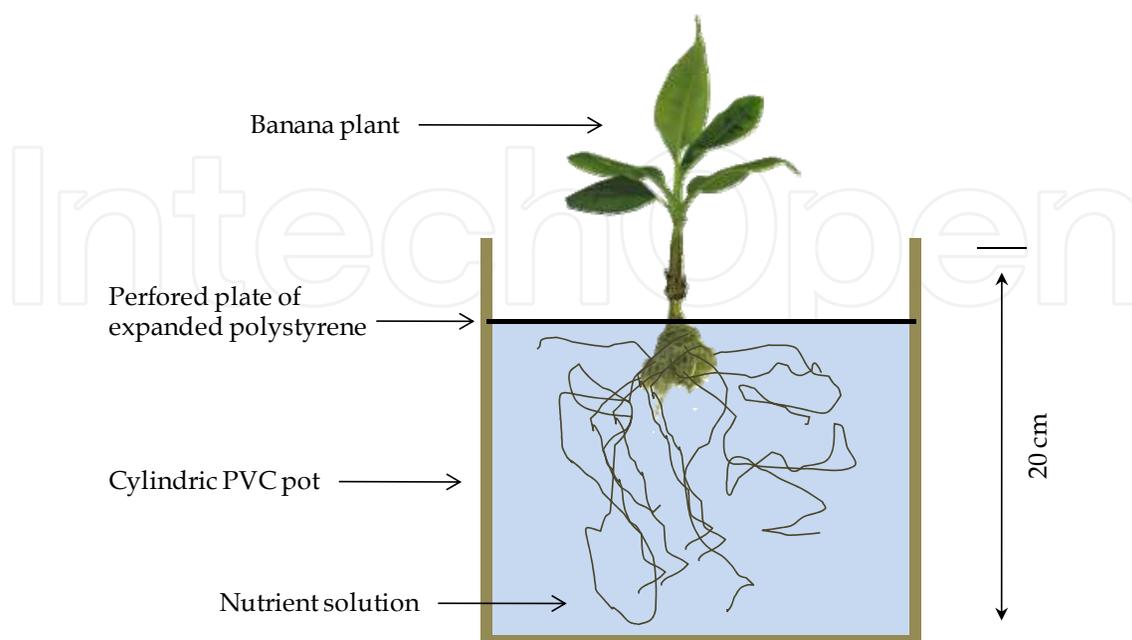


Fig. 1. Hydroponic culture device with the main compartments (only aqueous medium).

The hydroponic experiments are conducted in growth chambers at a specific photon flux density, relative humidity, day/night temperature for each specific plants and environments (Table 1). Depending on genus, plants are supplied with a solution obtained by mixing salts, boric acid and FeEDTA to reach realistic concentrations and match common plant nutrient requirements. In table 1, we describe hydroponic solutions as close as possible to the actual concentrations of the soil solution for banana, rice and coniferous tree seedlings. For banana, the nutrient solution composition is determined from (i) the nutrient requirements and the mineral equilibria as established for young bananas, and (ii) the realistic ion concentrations in solutions of tropical acid soils (Rufyikiri et al., 2000b). The composition of the nutrient solution for rice mimicks soil conditions, *i.e.* is very dilute with respect to most of the nutrient solutions used in plant physiological work (Tang Van Hai et al., 1989). The nutrient solution for the cultivation of Douglas fir and Black pine (Cornelis et al., 2010b) matches common tree seedling nutrient requirements (Ingestad, 1971), using the optimum $\text{NH}_4\text{-N}/\text{NO}_3\text{-N}$ ratio of 40/60.

In most hydroponic devices, there is no support for the plant roots (only aqueous medium; Fig. 1), while some hydroponic systems have a solid medium of support. With an aqueous medium, the hydroponic culture device can be (i) static where the nutrient solution is not renewed, or (ii) dynamic where the nutrient solution is continuously renewed at a specific rate with a peristaltic pump. A solid medium in the device (Fig. 2) allows to study the origin of the mobilization of elements.

The choice of the devices is thus adapted to the purpose of the research. We describe here the principles of the hydroponic devices that we regularly used in the last forty years to study the soil-plant relations. They will be refer to as Device 1, 2 and 3, respectively, throughout the Chapter.

	Banana	Rice	Douglas fir Black pine		
	Nutrient solution			Hoagland solution	Yoshida solution
macroelements (mM)					
Ca(NO ₃) ₂	0.9	/	4.8	6.8	/
CaSO ₄	0.05	/	1.6	/	/
CaCl ₂	0.05	0.25	1.6	/	1
KCl	0.5	0.2	4.0		/
K ₂ SO ₄	0.25	/	4.0	/	0.35
KH ₂ PO ₄	/	0.2	/	0.5	/
KNO ₃	/	/	/	5	/
MgCl ₂	0.05	/	0.4	/	/
MgSO ₄	0.05	0.4	0.4	3.3	1.6
NH ₄ Cl	0.1	/	3.2	/	/
(NH ₄) ₂ SO ₄	0.05	/	3.2	/	/
NH ₄ NO ₃	/	0.7	/	1	2.8
NaH ₂ PO ₄	0.05	/	0.2	/	0.3
NaOH	/	/	/	/	/
microelements (μM)					
H ₃ BO ₃	80	46	90	46	18.5
FeEDTANa	80	65	80	65	/
FeCl ₂ .6H ₂ O	/	/	/	/	35.8
MnCl ₂	8	12	8	12	9
ZnSO ₄	0.8	1	0.8	1	0.2
CuSO ₄	0.8	0.3	0.8	0.3	0.2
(NH ₄) ₆ Mo ₇ O ₂₄	5.6	/	5.6	/	0.5
Na ₂ MoO ₄ .2H ₂ O	/	0.5	/	0.5	/
Growth chamber conditions					
Luminosity	446 μE/m ² s ⁻¹ for 12h day light	250 μE/m ² s ⁻¹ for 12h day light	448 μE/m ² s ⁻¹ for 8h day light		
Temperature	28/25 °C day/night	30/22°C day/night	20/18 °C day/night		
Relative humidity	90%	80% day 90% night	75%		

Table 1. Nutrient solution and phytotron chambers conditions used for banana (Rufyikiri et al. 2000), rice (Tang Van Hai et al. 1989) and tree seedlings (Cornelis et al. 2010b) cultivation. Hoagland solution (1950) and Yoshida solution (1976) are given for comparison.

2.2 Static nutrient solution device (Device 1)

When the nutrient solution is not renewed (Fig. 1), the ion concentrations are calculated to maintain an optimum nutrient status during the experiment. Twice a week, the volumes of the remaining solutions are weighed to estimate water loss, which is immediately balanced by adding demineralized water. Water loss through evaporation is measured in six control pots. Cumulative water uptake is calculated as the difference between water loss and evaporation. The potential nutrient uptake by mass flow (MFU) is defined by the product of water uptake and nutrient concentration in the hydroponic solution.

2.3 Continuous nutrient flow device (Device 2)

Nutrient solution can be continuously renewed at a rate of $104 \text{ ml h}^{-1} \text{ pot}^{-1}$, corresponding to an expected residence time of the solution in the pot close to 24 h. The replacement solution ("input solution") is supplied at the bottom of the pot and the solution in excess ("output solution") is released and collected via an overflow pipe. Water uptake is assessed by weighing input and output solutions of each pot over 1 day. Nutrient uptake is calculated as the difference between daily input and output quantities for each pot (*i.e.*, the difference between the product of concentration and solution volume at input and output).

2.4 Culture device with substrate (Device 3)

A special culture vessel device developed by Hinsinger et al. (1991, 1992) allows to simulate a macroscopic rhizosphere in one-dimensional geometry. Thanks to this experiment, the sources of nutrients for plants can be identified and quantified. Three experimental designs were developed with differing substrate constitution and differing type of contact between roots and substrate:

1. Agarose-clay substrate in contact with a linear rhizosphere through a planar surface (Fig. 2a).
2. Agarose-soil mixture in contact with a linear rhizosphere through a planar surface (Delvaux et al. 2000)
3. Quartz-clay substrate in contact with the entire roots to simulate a real situation in soils (Fig. 2b).

3. Uptake of nutrient and toxic elements by banana and rice

Crop yields in very acidic soils are often limited by increasing aluminium concentrations in the soil solution. However, in field conditions, we are not able to vary the Al concentration in soil solution since the dynamic equilibrium between solid and aqueous phases imply modifications of soluble and exchangeable Al concentrations, and then modifications of pH and availability of other nutrients. The interpretation of the specific Al effect on the crop yields is thus impossible. This explains why most studies on the toxicity/resistance to Al have been conducted on nutrient solutions, which allow varying the total concentration of Al regardless of the concentration of other elements, provided that they remain undersaturated with respect to solid phases involving Al (Tang Van Hai, 1993).

3.1 Banana

The production of bananas and plantains in the tropics is of prime importance both for local consumption and for export market. Despite the fact that acid soils are common in the

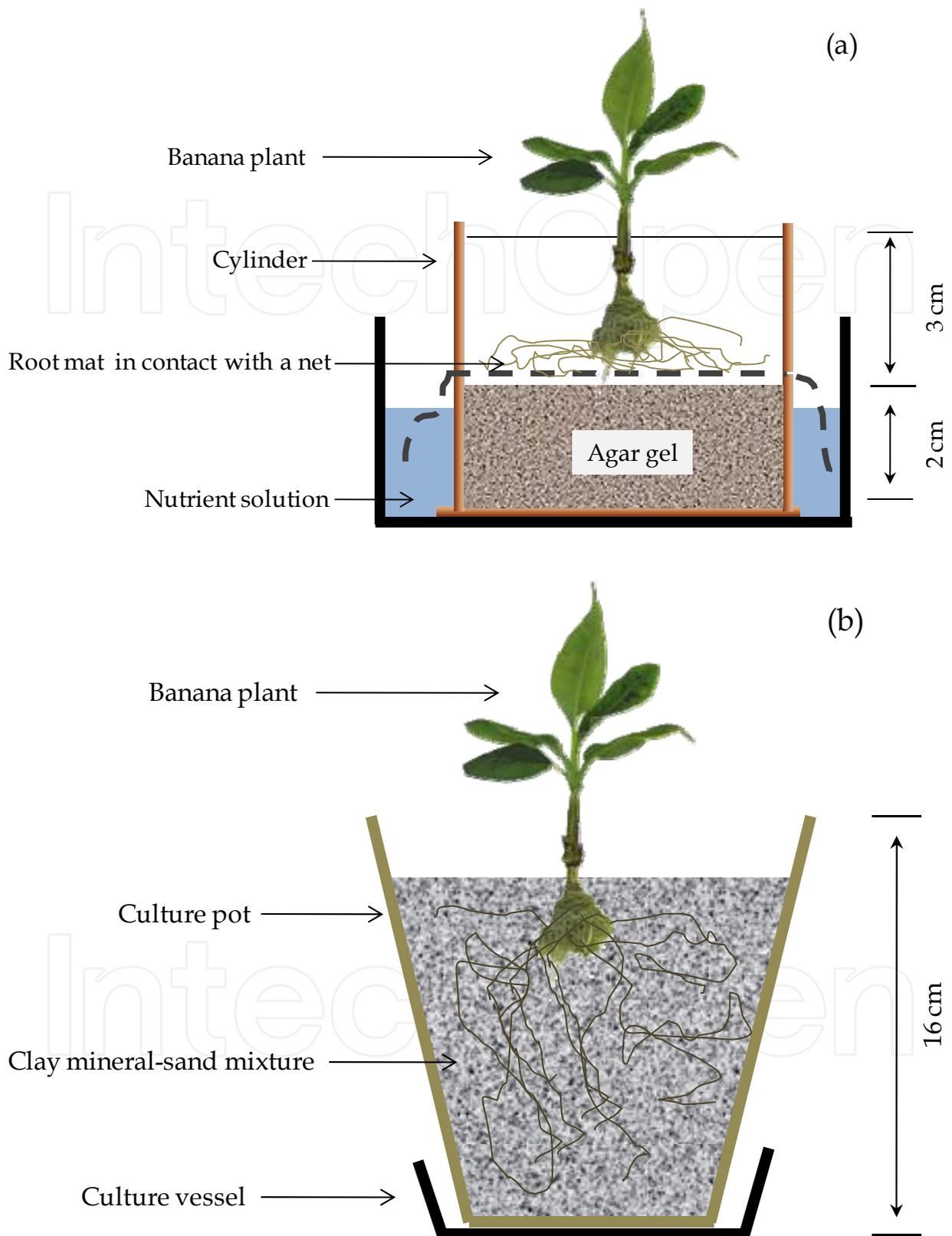


Fig. 2. (a) Culture device "agarose-clay substrate" and "agarose-soil mixture", adapted from Hinsinger et al. (1992) - (b) Culture device "quartz-clay substrate", adapted from Ruffyikiri et al. (2004)

tropics and that bananas have large nutrient requirements, little is known on the tolerance of bananas to soil acidity, Al toxicity and mineral deficiencies caused by Al stress. In this regard, hydroponic studies are very useful to understand the mineral nutrition of different banana cultivars.

Free Al is directly toxic to plant roots and, in most cases, is little absorbed or translocated to the aerial plant parts (Bernal & Clark, 1997; Rufyikiri et al., 2000b). Rufyikiri et al. (2000b, 2001) performed a hydroponic experiment using a continuous nutrient flow device (device 2) to study the effect of Al on young banana plants. Vitroplants were supplied by Vitropic (Montpellier, France) for Grande Naine. The other cultivars (Agbagba, Obino l'Ewai, Igitsiri and Kayinja) were produced in the *Musa* Germplasm Transit Centre (Heverlee, Belgium) of the International Network for Improvement of Banana and Plantain (INIBAP). They were weaned for 3 weeks in an aerated nutrient solution. Among 50 vitroplants per cultivar, the six tallest but homogeneous individuals were selected. The vitroplants were then transferred to 2.5 l pots (one plant per pot). Nutrient solution described above was supplied continuously by peristaltic pumps at a rate of 104 ml.h⁻¹ per pot. The mean residence time of solution in pots was 1 day. The experiments were conducted in growth chambers at 448 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photon flux density for 12h per day, 90% relative humidity, 28/25°C day/night temperature for the low altitude cultivars, and 24/20°C day/night temperature for the banana plants cultivated in the highlands (Igitsiri and Kayinja). Half of the plants were supplied with the same nutrient solution described above but with 78.5 μM Al (added as $\text{Al}_2(\text{SO}_4)_3\cdot 18\text{H}_2\text{O}$).

For most parameters (appearance of new leaves, total biomass, pseudostem height, leaf surface area, growth of lateral roots, number and diameter of root axes), the two plantains Agbagba and Obino l'Ewai appeared more Al-resistant and Kayinja more Al-sensitive than both Grande Naine and Igitsiri (Rufyikiri et al. 2000b). In all plants parts for all cultivars, Al reduced Ca and Mg contents, increased K and P contents, and did not change significantly N content. Since Mg content in plant parts was lower than the deficiency threshold concentrations reported in literature, leaf yellowing and marginal necrosis developing on Al-treated bananas is attributed to Mg deficiency (Rufyikiri et al., 2000b). The same hydroponic experiment was established to measure daily water and nutrient uptake (Rufyikiri et al., 2001). Water and nutrient absorption measurement were carried out twice a week during 40 days. Water uptake was assessed by weighing input and output solutions of each pot over 1 day. Aluminium reduced plant water and nutrient uptake and cumulative detrimental effects were observed. The water uptake was only 30-40% of the control and nutrient uptake rates were reduced by more than 50% relatively to the control. It is also demonstrated thanks to this hydroponic experiment that plantain bananas were more resistant to Al.

Aluminium ions are tightly fixed to root exchange sites (Dalghren et al., 1991; Tice et al., 1992), which originate from carboxylate groups of uronic acids of pectin and hemicelluloses in the root cell-walls (Horst et al., 1995). The subsequent changes in (i) physical properties which become less plastic and more resistant to elongation and (ii) in plasma-membrane properties and associated proteins and lipids are evoked, among others, in the literature to explain Al toxicity (Horst et al., 1995; Kochian, 1995). For instance, it has been demonstrated in hydroponic culture that bananas (*Musa* spp.), as many other crop species, accumulate aluminum (Al) in roots when grown in nutrient solution containing Al ions. Aluminum can

compete with calcium (Ca) and magnesium (Mg) on the root exchange sites, which has been reported as a possible cause for Al toxicity to the plant (Rufyikiri et al., 2003). The fixation and accumulation of Al in roots is accompanied by changes in the concentration of other cations, the most obvious effect being the noticeable decrease in Mg content. Competition between Al and other cations on the charged constituents in the apoplast can thus explain the detrimental effects of Al on plants (Horst, 1995; Keltjens, 1995). In non-acid soils, ionic Al activity in solution is low so that Ca, that has also high affinity for carboxylate groups, is dominating the exchange complex roots (Dufey et al., 2001). Despite this fact and thanks to hydroponic studies, Rufyikiri et al. (2002) suggest that the Al/Mg ratio on roots could be a better indicator of Al toxicity than the Al/Ca ratio. Indeed, among the Cu-extractable cations (Dufey & Braun, 1986), Ca was occupying about 50-60% of the exchange sites even when Al was present in the growth medium (78.5 μM), while adsorbed Mg was drastically reduced on root exchange sites (Rufyikiri et al., 2002).

The hydroponic systems are ideal devices to study the resistance of mycorrhizal plants to Al toxicity compared with nonmycorrhizal plants (Rufyikiri et al., 2005). In monoxenic cultivation, Rufyikiri et al. (2000a) show that arbuscular mycorrhizal (AM) fungi (*Glomus intraradices*) can be effective in alleviating the aluminium toxicity to banana plants. In that study, both banana plants and AM fungi grew very well in sand under continuous nutrient flow. During the 5 weeks preceding Al application, an average of one leaf was produced per week. The nutrient uptake rates by banana plants decreased with the increase of the addition of Al in the nutrient solution. The Mg uptake rate decreased by 4 to 18 times in the nutritive solution concentrated in Al (78 and 180 μM) for banana plants without arbuscular mycorrhizal fungi. A significant positive effect of arbuscular mycorrhizal fungi on plant growth was observed with aluminium treatment, and was most pronounced at the highest concentration. The benefits, compared with nonmycorrhizal plants, included: increase in shoot dry weight, uptake of water and of most nutrients (Ca, Mg, $\text{NH}_4\text{-N}$ and P), and in calcium, magnesium and phosphorus content, particularly in roots; decrease in aluminium content in root and shoot; and delay in the appearance of aluminium-induced leaf symptoms. The higher nutrient uptake rates in the mycorrhizal plants suggest that mycorrhizal roots were less affected than nonmycorrhizal roots by the presence of Al.

The banana plant is a model case study since this plant is very sensitive to Al stress (Rufyikiri 2000a, 2000b) and it exhibits very large K requirements and growth rate (Lahav, 1995), as well as selective root uptake of NH_4 (Rufyikiri et al., 2001). Thus banana plant has a high potential for acidifying its own rhizosphere, and thereby in solubilizing toxic forms of Al. The differences in symptoms observed between banana plants grown without and with Al is mainly related to Al toxicity, rather than to low pH caused by Al or by proton excretion by roots (excess of cations over anions absorbed). As explained above, banana plants (*Musa* spp.) are very sensitive to Al, which is mobilized in acid soil conditions. These plants may, however, contribute to their own intoxication because their roots can excrete protons in large quantities, implying nutrient mobilization from silicate minerals. A net proton excretion by roots can largely influence Al solubilization, and results from excess root uptake of cations relatively to anions (Marschner, 1995), particularly with NH_4^+ uptake. The protons flux generated by roots can be neutralized by the weathering of aluminosilicates (Hinsinger et al., 1992; Hinsinger, 1998), which release Si and plant nutrients (Hinsinger et

al., 2001), and can lead to an increase of soluble Al up to toxic levels for plants. As suggested by Rufyikiri et al. (2004), the rhizospheric weathering of aluminosilicates can thus be considered as a source not only for nutrient acquisition by plant roots (Hinsinger, 1998), but also for plant intoxication by trace metals (Lombi et al., 2001).

In this respect, the culture devices with substrate (device 3) allow to study the impact of the chemical environment of rhizosphere on the mobilization of elements from the solid phases in soil (Hinsinger et al., 1992; Delvaux et al., 2000; Rufyikiri et al., 2004). In the study of Rufyikiri (2004) (Fig. 2b), the sole source of Al is montmorillonite or kaolinite. The root-induced acidification and subsequent weathering of the minerals involved a preferential release of Al in the aqueous phase of the quartz:clay substrates, an increase of both ammonium-extractable Al from kaolinite and Mg from smectite. These respective root-induced mobilizations led to relatively large root uptake of Al in quartz:kaolinite and Mg in quartz:smectite. These results support that the mobilization of, respectively, Al and Mg are the limiting steps in the dissolution of the kaolinite and montmorillonite, just as demonstrated in previous chemical weathering studies (Nagy, 1995).

From a mica-agar substrate (Fig. 2a), Hinsinger et al. (1992) demonstrated that K is released and concomitantly the mica lattice expanded after 3 days of continuous exposure to the root mat, in response to K uptake by plants. The vermiculitization of mica (expansion of the mica lattice through replacement of K by more hydratable cations Ca and Mg) is detectable up to 1.5 mm from the root mat of ryegrass after 4 days. The trioctahedral micas such as phlogopite can thus contribute significantly to the supply of K around the most active parts of the roots.

3.2 Rice

The toxicity of Al present in the soil solution is also one of the major causes of the poor performance of rice grown on acid soils. The presence of Al is the unavoidable consequence of the spontaneous acidification of the soil either by the respiration of micro-organisms or the exchange hydrolysis of the cation adsorption sites of clay minerals (Eickman & Laudelout, 1961; Gilbert & Laudelout, 1965). Under certain environmental conditions, the normal acidification process may be greatly enhanced as in poorly buffered soils subject to acid precipitation or in acid sulphate soils where the oxidation of sulphur compounds involves the liberation of huge amounts of sulphuric acid. This is the case in the Mekong Delta in Vietnam where about 2 million ha are characterized by important environmental constraints. A study of the physiological response to Al toxicity of the rice plant in controlled hydroponic conditions is thus of great importance (Tang Van Hai et al., 1989).

A study of the effect of increasing aluminium concentration in a nutrient solution described above for rice (Table 1) has shown that Al exerts stimulation on dry matter production and nutrient uptake until a concentration threshold, which is influenced by nutrient solution composition and cultivar (Tang Van Hai et al., 1989). Nitrogen uptake either as NH_4^+ or NO_3^- was clearly influenced by aluminium concentration when its instantaneous value was measured by the technique of the continuously flowing culture solution. The NH_4^+ uptake rate of two cultivars was such that the more sensitive variety to aluminium took up less NH_4^+ and acidified less the culture solution flowing through the root system with a residence time of a few hours.

On the other hand, for plants like cereals, it is useful to identify criteria for early diagnosis of Al resistance with respect to grain yield before reaching maturity. Therefore, Tang Van Hai et al. (1993) evaluate whether the grain yield of 11 rice cultivars grown in nutrient solution with high Al concentration can be related to plant characteristics at the vegetative stage. Rice cultivars were supplied with a solution characterized by the composition described in Table 1. To test the toxicity of Al, a concentration of 150 and 400 μM Al was chosen since a concentration of Al between 15-45 μM stimulates the metabolic processes. In contrast to biomass production and mineral concentrations in shoots and roots, the tillering capacity (total number of tillers per plant) is a remarkable characteristic for early assessment of the effect of Al on grain production, as maximum tillering occurs 35-45 days after planting.

In waterlogged fields, the yield losses of rice in acid soils can be explained by the toxicity of aluminium and iron (Fageria et al., 1988; Genon et al 1994; Moore et al. 1990; Tang Van Hai et al., 1989, 1993). The increase of pH following reduction reactions can decrease the solubility of aluminium but induce the solubilization of ferrous ions well known for its toxicity (Ponnamperuma, 1972). Since the variations of pH and redox potential are interdependent in waterlogged soils, we are not able to fix a concentration of Al and Fe in aqueous phase of soil in field or pot experiments. The complex physicochemical behavior of Al and Fe in soils justifies therefore the interest of controlled hydroponic studies in nutritive solution in order to better constrain the consequences of Al and Fe excess on the rice growth. In hydroponic experiment using rice-solution described in Table 1, the increase of Al (from 74 to 370 μM) and Fe (from 18 to 357 μM) concentrations decrease the grain yield and biomass. The toxicity threshold of Fe (125-357 μM) is relatively low relative to the field threshold of 5000 μM (van Breemen & Moorman, 1978). The difference is certainly due to chemical speciation of Fe^{2+} in soil solution, influenced by the chemical equilibrium between solid and aqueous phases, and the complexing of organic anions (Quang et al., 1996). Moreover a high concentration of Fe^{2+} in soil solution does not necessarily coincide with a high concentration of Fe^{2+} in the aerated rhizosphere in which the formation of oxyhydroxides occur as a mechanism of protection against Fe toxicity (Becker & Ash, 2005).

Phosphate uptake rate did not affect plant biomass, but increase grain yield, i.e. it alleviated the yield losses due to increase of Al and Fe concentrations (Fig 3a). The increase of P uptake rate could result in the formation of Al-P complexes (AlHPO_4^+) that reduce the Al^{3+} concentration (Quang et al., 1996) (Fig. 3b). When P concentration exceed Al concentration, uncomplexed P is in the form of H_2PO_4^- . Conversely, the uncomplexed Al is mainly Al^{3+} and AlSO_4^+ (ratio of 3-4:1) (Quang et al., 1996). Iron is not involved in ionic associations and is mainly as Fe^{2+} . Thus Fe toxicity is not reduced through a physicochemical process with P. Some authors suggest that P could enhance oxidizing potential of the rhizosphere decreasing the availability of ferrous iron (van Breemen & Moorman, 1978). The effect of AlHPO_4^+ complexes and formation of Fe oxides on the surface of roots are described in Fig. 4.

Based on the statistical analysis performed by Quang et al. (1996), grain yield (Y) is related to the concentrations of the elements in nutritive solution (expressed in μM) by the following equation:

$$Y = 5.47 - 0.0079 \text{ Al} - 0.0058 \text{ Fe} + 0.0098 \text{ P} \quad (r^2=0.86)$$

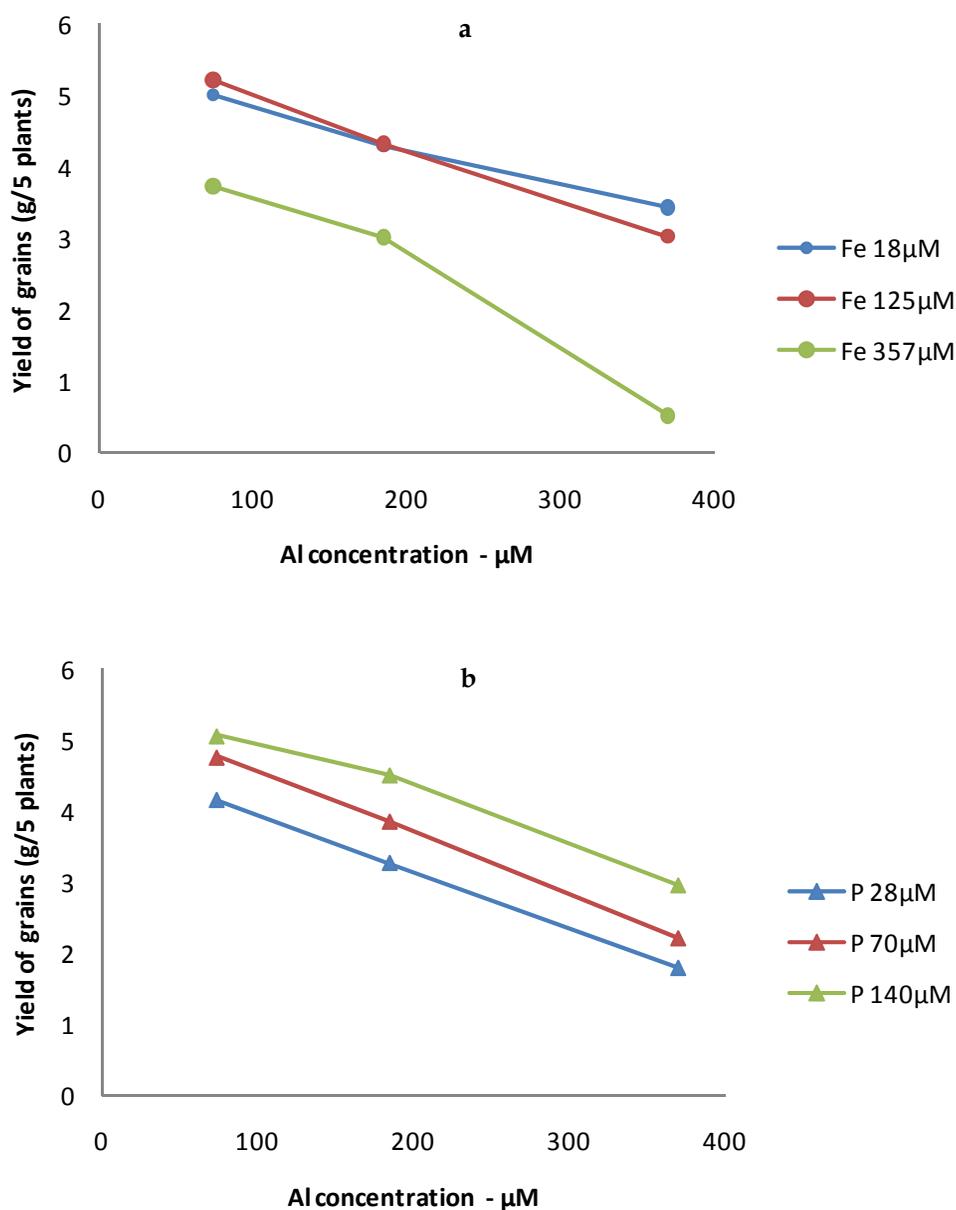


Fig. 3. Impact of the concentration of Al in nutritive solution on the grain yield: (a) for the three concentrations of Fe and (b) for the three concentrations of P (adapted from Quang et al., 1996)

These results cannot be directly extrapolated to the field because the soil solution can be re-alimented in Al and Fe through dissolution of solid phases, counteracting the positive effect of ionic complexation. However, controlled studies in hydroponics allow to understanding the mechanisms of mineral nutrition and can be extrapolated to the field by using equilibrium program between solid and aqueous phase, such as “Visual Minteq” and “PHREEQC”.

In another study, Quang et al. (1995) aimed to study the impact of temperature gradient on rice growth in acid sulphate soils thanks to a hydroponic experiment with rice-nutrient solution (Table 1). Two varieties of rice (IR64 and X2) were cultivated in controlled

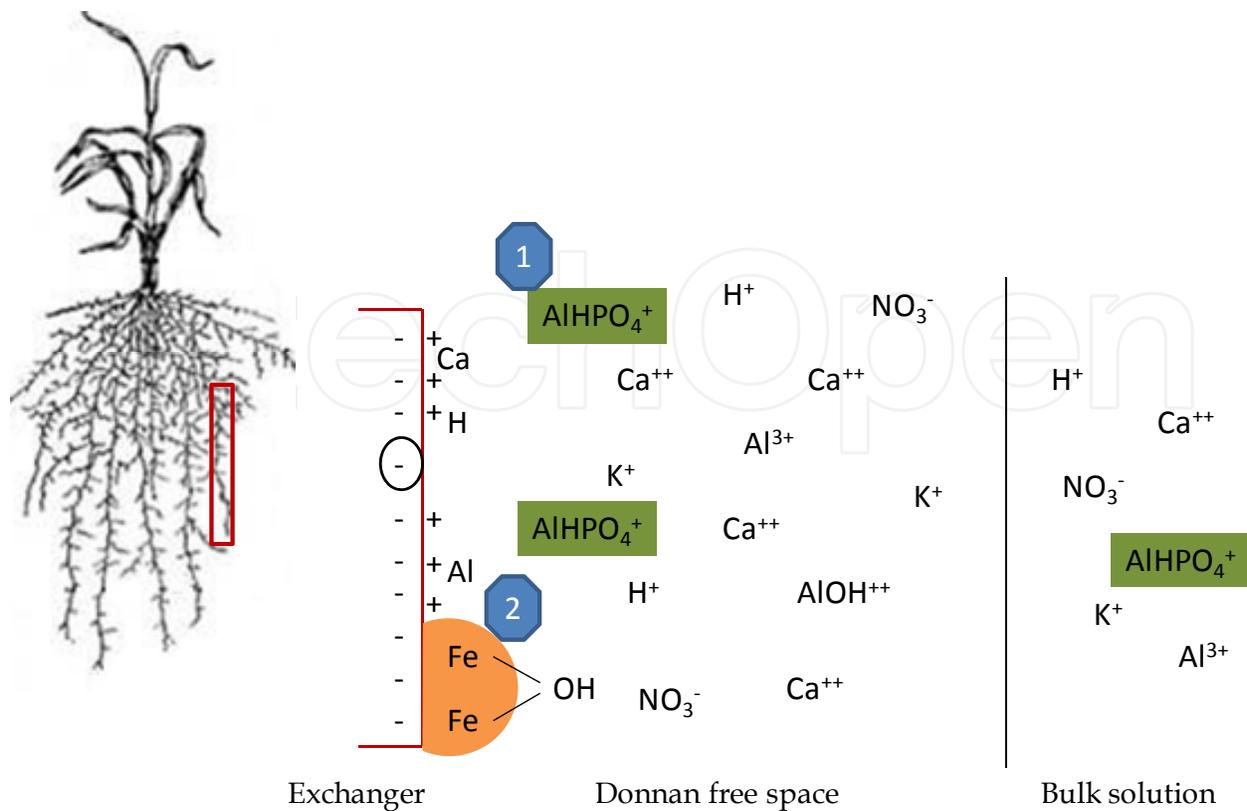


Fig. 4. Diagram of the ion exchange model adapted from Dufey et al. (2001). The two positive mechanisms of P to decrease the toxicity of Al and Fe are represented by (1) AlHPO_4^+ complex and (2) formation of oxyhydroxides layer on the surface of the roots

conditions in phytotrons at 19/21°C and 28/32°C (day/night) for 56 days. After 7 days, the young plants were transferred to a rice-nutrient solution. Two series of 60 plants per variety tightened with cotton on plastic disks were grown on 20L tanks, and the solutions were renewed every 2 days for 2 weeks. From those plants, eight series of 5 plants per variety were transferred on 450-ml vessels to which nutrient solution was continuously supplied by peristaltic pumps at a rate of about 100 ml.h⁻¹. The P concentration was increased up to 2 mg.l⁻¹ to ensure this element was not limiting for plant growth. Besides the tillering retardation at lower temperature (20°C), the hydroponic experiment demonstrated that the translocation of Fe from roots to shoots was stimulated upon rising temperature leading to plant death on the most acid soil at 30°C. Indeed severe reducing conditions were created at 30°C: redox potential (Eh) dropped rapidly down to about 0 V which is a value out of the range of $\text{Fe}^{3+}/\text{Fe}^{2+}$ buffering. Parallel to Eh drop, pH increased up to about 6-6.5 at 30°C, which prevented plants from Al toxicity commonly observed at pH below 4.5.

4. Uptake of polluting ¹³⁷Cs element by plants

Since the radioactive fallout from nuclear weapons tests and the Chernobyl (1986) and Fukushima (2011) nuclear accidents, radioactive air plumes contaminated large territories. The ¹³⁷Cs is one of the major radionuclides and implies considerable environmental issues because of its relatively long half-life (30.17 years). Soil acts as a major sink-source compartment in ¹³⁷Cs fluxes through plant and food chains (Delvaux et al., 2001).

The uptake of radiocesium by plants is proportional to its concentration in the solution around roots. However, root uptake of ^{137}Cs is largely influenced by K status of the solution. Above 1 mM K, varying K concentration has no significant effect on trace Cs uptake (Shaw et al., 1992). Nonetheless, some studies in hydroponic conditions showed that root uptake of ^{137}Cs is significantly increased with decreasing K concentration in solution, at K concentration below 1 mM (Cline & Hungate, 1960; Smolders et al., 1996). Smolders et al. (1996) have used ^{137}Cs spiked nutrient solution experiment to grow wheat at four concentrations of K added as KNO_3 (25, 50, 250 and 1000 μM). They have shown that ^{137}Cs activity concentrations in 18-day old plants drastically increased (123-fold in the shoot and 300-fold in the root) when K concentration decreased from 1000 μM to 25 μM . Such low K concentration around the roots are not abnormal in soil solution. So, amongst the different fertilizers, potassium fertilizers are generally most efficient in reducing ^{137}Cs transfer (Nisbet et al., 1993).

The behavior of ^{137}Cs in soils is largely affected by the rhizosphere solution composition. This latter differs from the bulk soil solution since many factors (pH, ionic strength, redox potential, presence of root exudates and specific rhizospheric microflora) affect the physicochemical processes controlling trace element mobility and availability, making the rhizosphere a unique environment where plant roots and soil minerals strongly interact (McLaughlin et al., 1998). In this regard, the bioavailability of radiocesium varies extensively between soils because of differences in (i) ^{137}Cs retention, affecting ^{137}Cs concentration in solution, and hence its supply to plant roots, and (ii) K availability, affecting the ^{137}Cs root uptake process. Based on these concepts, Absalom et al. (1999) developed a soil-plant ^{137}Cs transfer model in which the soil solution concentrations of ^{137}Cs and K were estimated from (i) the clay content and (ii) the exchangeable K content, and also from the total ^{137}Cs content in soil and the time after the contamination. More precisely, radiocesium is specifically retained on vermiculitic sites neighboring micaceous wedge zones (Delvaux et al. 2001; Maes et al., 1999). In acid soils, hydroxyl interlayered vermiculite weakly retain radiocesium. Organic matter can therefore influence the retention of trace Cs through Al complexation which deplete the concentration of Al in the soil solution and hence impedes Al-interlayering and maintains the interlayer sites accessible for Cs retention (Delvaux et al., 2001). Organic matter can also increase ^{137}Cs soil-to-plant transfer by a dilution effect of highly fixing sites born by mica-like minerals (illite, vermiculite, micaceous mixed-layered clays), particularly in upper soil horizons (Kruyts & Delvaux, 2002).

In addition, the rhizospheric mobilization of ^{137}Cs (Delvaux et al., 2000; Kruyts et al., 2000) has been characterized through experimental cropping device adapted from Hinsinger et al. (1992) (Fig. 2a). In this device, the soil samples were pre-treated to be homoionic with Ca^{2+} ions, whereas the plantlets of ryegrass previously germinated in a K-free nutrient medium. The soil artificially ^{137}Cs contaminated ($\sim 1000 \text{ Bq cm}^{-3}$) was mixed with a 10 g.l^{-1} agar gel prepared by using a solution free of potassium (Hinsinger et al. 1992). The nutrient concentrations of solution were in macroelements (mM): 3.5 $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, 1 MgSO_4 , 1 NaH_2PO_4 ; in microelements (μM), 10 H_3BO_3 , 100 FeEDTANa , 20 MnCl_2 , 0.2 ZnSO_4 , 0.2 CuSO_4 , 0.2 $\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$. The close contact between soil and root consists of a macroscopic rhizosphere intensifying the soil-root interaction. Using this device with a collection of 47 soil horizons from 17 pedons of widely varying soil properties from semi-natural environments (Delvaux et al., 2000), the ^{137}Cs soil-plant transfer factor varied almost

200-fold between soil materials and was strongly negatively correlated to soil vermiculite content. Kruyts et al (2000) investigated the relative contributions of the horizons of forest soil in the rhizospheric mobilization of radiocesium. Assuming negligible horizon to horizon transfer and equivalent root exploration in each soil horizon, the respective contributions of the soil horizons to the ^{137}Cs soil-to-plant transfer were 96.7% in Of (organic fragmented horizon), 0.13% in OAh (transitional organo-mineral horizon), 1.34% in Ah (organo-mineral horizon), and 1.84% in Bw (illuvial horizon). Such contributions are quite similar to those measured by Thiry et al. (2000) in the same forest soil, but using a pot experiment approach involving young spruce plants. This suggests that short experimental measurements are well designed to provide reproducible constrain on the ^{137}Cs mobilization, which provides a way to avoid time consuming pot experiments with longer procedures.

The soil-root interaction has been presented in terms of chemical processes occurring in the rhizosphere. The role of fungi, particularly the mycorrhizal fungal species in this interaction must be developed, from a mechanistic point of view. In this regard, monoxenic culture systems on a synthetic medium rapidly became a powerful system for studies of physiological and element transport processes in mycorrhizal symbioses (Rufyikiri et al., 2005). Among the microbial species, arbuscular mycorrhizal (AM) fungi are obligate symbionts that colonize the root cortex developing extraradical mycelia (ERM) that ramifies in the soil. It was shown that the ERM of an AM fungus can take up, possibly accumulate and unambiguously translocate ^{137}Cs to the roots (Declerck et al., 2003).

5. Silicon uptake and transport in plant

Silicon (Si) is the second most mass-abundant element (28.8%) of the Earth's crust (Wedepohl 1995) and it occurs in a large range of minerals at the Earth's surface, ranging from <0.5 wt% to ~47 wt% in the pedosphere (McKeague & Cline, 1963). As ultimate source, chemical weathering of silicate minerals liberates dissolved Si as monosilicic acid. The H_4SiO_4 contributes to soil formation through biogeochemical reactions such as neoformation of secondary minerals, adsorption onto Fe and Al (hydr)oxides and uptake by plants. The H_4SiO_4 concentration in the soil solution is controlled by biogeochemical processes and ranges from 0.01 to 1.99 mM (Karathanasis, 2002), with most common concentrations of about 0.1–0.6 mM (Faure, 1991).

In terrestrial ecosystems, Si is distributed between plant and soil before its land-to-rivers transfer since it is taken up as aqueous monosilicic acid (H_4SiO_4) and translocated to transpiration sites (where it polymerizes as amorphous biogenic opal called phytolith), which returns to the soil within organic residues (Smithson, 1956). By accumulating in terrestrial plants to a similar extent as some major macronutrients (0.1-10% Si dry weight), Si becomes largely mobile in the soil-plant system. Understanding the soil-plant Si cycle in surface environments and the dissolved Si export from soils into rivers is crucial (Cornelis et al., 2011) given that the marine primary bio-productivity depends on the availability of H_4SiO_4 for phytoplankton CO_2 -consumers that requires Si. In the terrestrial Si cycle, higher plants largely contribute to the global Si cycle since their annual Si production ranges from 1.7 to $5.6 \cdot 10^{12}$ kg Si yr⁻¹ (Conley, 2002), which rivals Si production of phytoplankton-diatoms in the oceans ($6.7 \cdot 10^{12}$ kg Si yr⁻¹) (Tréguer et al., 1995).

The biomineralization of amorphous silica seems to be restricted to some plant families (Epstein, 1999; Hodson et al., 2005) and appear in various shapes depending on the location of Si deposits and plant species (Carnelli et al., 2001, 2004). Based on active, passive or exclusive mechanisms of Si uptake, plant species are classified as high-, intermediate- or non-accumulator, respectively (Takahashi et al., 1990). A classification of the plant kingdom shows that the majority of Si high-accumulators (1–10 wt% Si in shoots) belong to the monocotyledons (e.g. banana, bamboo, sugar cane, soybean, rice, wheat, barley, sorghum and oat), while most dicotyledons absorb Si passively (0.5–1.0 wt% Si in shoots), and some dicots such as legumes have limited Si uptake (<0.5 wt% Si in shoots) (Liang et al., 2007; Ma et al., 2001; Ma & Takahashi, 2002).

5.1 Silicon nutrition in plants

The essentiality of Si for terrestrial plants is still extensively debated (Richmond & Sussman, 2003; Takahashi et al., 1990). So far, only two groups of plants are known to have an absolute and quantitatively major requirement for Si: the diatoms and other members of the yellow-brown or golden algae, the Chrysophyceae and the Equisitaceae (Epstein, 1999). Silicon is not considered as an essential element for higher plants, but its beneficial effects on growth have been reported in a wide variety of crops, including rice, wheat, barley, and cucumber (Korndörfer and Lepsch, 2001; Ma et al., 2001; Ma & Takahashi, 2002; Ma, 2004). There is a general consensus that Si improves the plant resistance to various biotic and abiotic stresses. Silica deposition in leaves is a resistant structural component (Raven, 1983), providing a more upright position, which favours light interception (Epstein, 1994; Marschner, 1995), and thus can play a role in the C cycle promoting photosynthesis. Moreover, biogenic silica in plant tissues creates a hard outer layer that serves as a defense against fungal and insect attacks (Bélanger et al., 2003; Kablan et al., 2011; Sangster et al., 2001; Vermeire et al., 2011). Finally, it is widely accepted that Si alleviates the toxicity of Al and other metal ions such as Mn in higher plants (Liang et al., 2007). Currently, there is no evidence of Si involved in plant metabolism (Ma et al., 2001) since no Si bearing organic compound has been identified in higher plants to date (Knight & Kinrade, 2001). The beneficial effects of Si remain reduced under optimum growth conditions, but are more obvious under stress conditions (Epstein, 1994; Bélanger et al., 1995). The Si accumulators wheat (*Triticum aestivum*) and rice (*Oryza sativa*), the premier crops for the nutrition of mankind, are susceptible to a variety of diseases if the Si supply is low (Epstein, 2001). Understanding the mechanisms that control Si uptakes by terrestrial plants (both for high and non-accumulator Si plants) in controlled hydroponics conditions is thus essential.

In **temperate forest ecosystems**, previous field studies show that the Si uptake varies considerably among tree species, ranging between 2 and 44 kg Si ha⁻¹ yr⁻¹ (Bartoli 1983; Gérard et al. 2008; Cornelis et al. 2010a). The different accumulation of Si in aerial parts may be due to the varying abilities of Si root uptake, soil mineralogical composition, transpiration rate and availability of silicic acid in the forest soil solution. Furthermore, such a difference of Si concentration in forest vegetation could affect tree seedling growth. The beneficial effect of Si supply on pine seedling growth has been demonstrated under water-stress conditions (Emadian & Newton, 1989), but remains poorly explored in optimal conditions.

With an hydroponic study, Cornelis et al. (2010b) aimed to understand the contrasting Si uptake between Douglas fir and Black pine and quantify the effect of Si on the growth of tree seedlings. For this purpose, *Pseudotsuga menziesii* and *Pinus nigra* seedlings were grown for 11 weeks in hydroponics (device 1) with a wide range of Si concentration in the nutrient solution (0.2-1.6 mM). The seeds were germinated for 15 days in the dark at day/night temperatures of 20/18°C. They were then weaned for 30 days in nutrient solution tanks before uniform seedlings were selected for the experiments. Batches of six seedlings were grown in separate cylindrical PVC pots containing 2.5 l of nutrient solution and placed on a perforated plate of expanded polystyrene which limits water loss by evaporation (Fig. 5). The experiment was conducted over 11 weeks in growth chambers at conditions described above (Table 1).

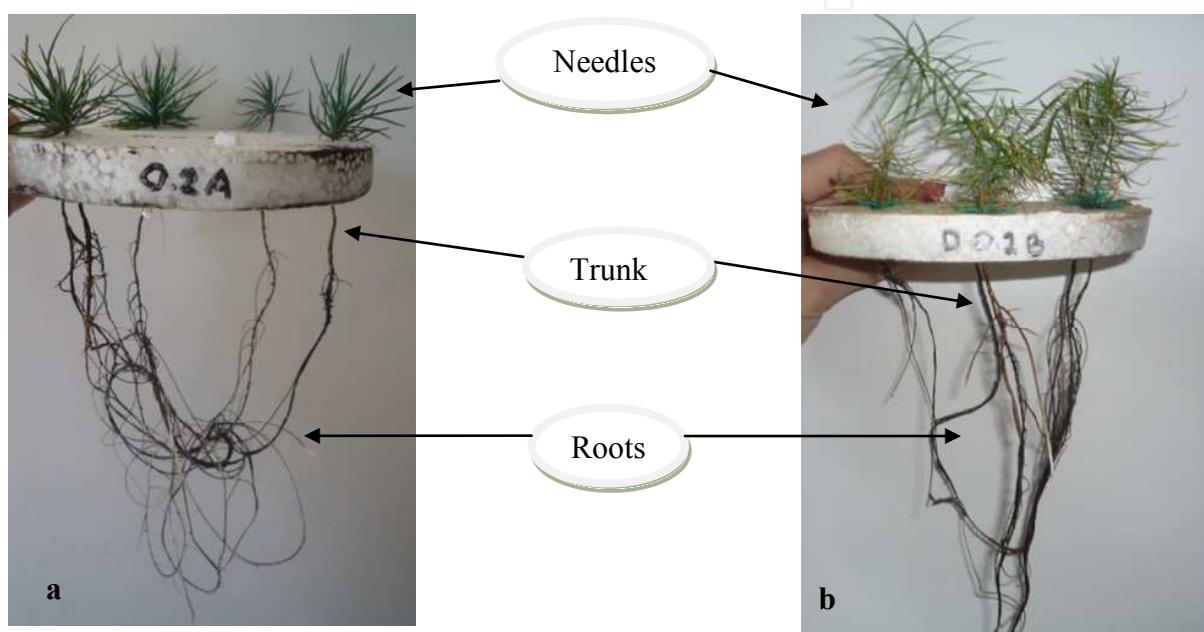


Fig. 5. Different parts of tree seedlings cultivated in hydroponics (from Cornelis et al. 2010b)

This experimental study using tree seedlings in hydroponic conditions confirms the in-situ observation of higher Si accumulation in Douglas fir leaves as compared with those of Black pine. Cornelis et al. (2010b) demonstrate that the mechanisms of Si uptake in hydroponics are identical between tree species: passive (mass-flow driven) uptake at realistic Si concentrations (0.2 mM) and rejective uptake at higher Si concentrations in nutrient solution. The contrasting Si accumulation in the leaves of coniferous tree seedlings could be attributed to the significant difference in the transpiration rates. The higher Si concentrations in nutrient solutions (0.8 and 1.6 mM) do not affect the growth of tree seedlings, probably because they are not subjected to stress conditions. This finding helps us to understand the mechanisms controlling the different Si uptakes by forest vegetations in order to better predict Si pathways in soil-tree systems.

In **banana plantations**, there are some evidences that fungic resistance is associated with Vertisols characterized by high concentration of Si in soil solution, whereas pathogens incidence seems to be high on largely desilicated ferrallitic soil (reviewed by Delvaux,

1995). Banana roots are able to induce silicate dissolution thereby increasing silicon availability in the rhizosphere (Hinsinger et al., 2001; Rufyikiri et al., 2004). In this respect, a study was conducted in hydroponic by Henriët et al. (2006) (device 2) to investigate the effect of Si supply on banana growth, water uptake and nutrient uptake under optimal and sub- or non-optimal conditions (Fig. 6). An experimental hydroponic device was designed to maintain the plants in optimal nutritional conditions and to allow the measurement of the daily water and nutrient uptake. The experiment was conducted in a growth chamber at conditions defined above (Table 1). Banana plants were grown in cylindrical PVC pots containing 2.5 l of nutrient solution which was continuously renewed at a rate of 104 ml h⁻¹ pot⁻¹, corresponding to an expected residence time of the solution in the pot close to 24 h. The composition of the nutrient solution is described in Table 1. Four treatments were applied in addition to a control, defined by concentrations of silicon in the nutrient solution

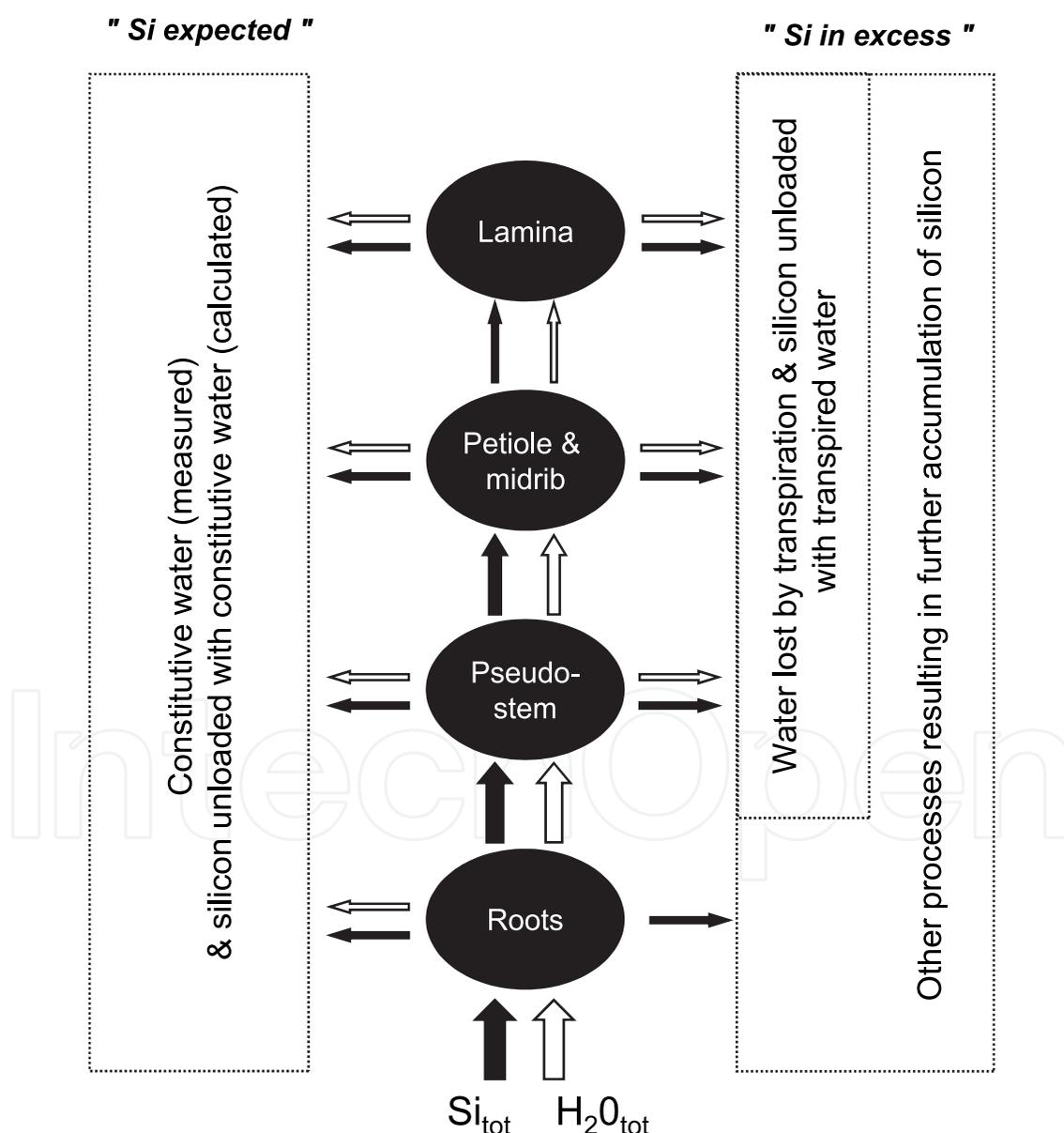


Fig. 6. Quantitative model of water and silicon movement and distribution in the plant (from Henriët et al., 2006)

of 0.0 (control), 0.08, 0.42, 0.83 and 1.66 mM, and to cover as much as possible the range of Si concentration that can be found in soil solutions (0.01-1.99mM). As described by Henriët et al. (2006), Si was supplied as H_4SiO_4 obtained by dissolving sodium metasilicate in demineralized water, followed by leaching on a protonated cation-exchange resin (Amberlite® IR-120). Neither Si precipitation nor H_4SiO_4 deprotonation was expected because Si concentration was below the solubility limit (<1.79 mM Si) and pH ranged between 5 and 6.5 (Stumm & Morgan 1996).

Henriët et al. (2006) demonstrate that the level of Si supply did not affect plant growth, nor the rate of water and nutrient uptake. The rate of Si uptake and the Si concentration in plant tissues increased markedly with the Si supply. The field studies confirm these results, since the leaf Si concentration is positively correlated with plant-available Si content ($CaCl_2$ -extractable), soil Si content and total reserve in weatherable minerals (Henriët et al. 2008a). Furthermore, soil weathering stage directly impacts the soil-to-plant transfer of silicon, and thereby the stock of biogenic Si in a soil-plant system involving a Si-accumulating plant (Henriët et al., 2008b). At the highest Si concentrations (1.66 mM), silicon absorption was essentially driven by mass flow of water (passive transport). However, at lower Si concentrations (0.02–0.83 mM), it was higher than its uptake by mass flow and caused the depletion of silicon in the nutrient solution, suggesting the existence of active processes of silicon transport in banana plant.

Recent studies demonstrate the existence of active Si transporters in rice roots (*Lsi1* and *Lsi2*) and shoots (*Lsi6*), responsible for the high Si uptake capacity of rice (Ma et al. 2006, 2007; Yamaji et al. 2008). *Lsi1* is an influx transporter of silicic acid, while *Lsi2* is an active efflux transporter of the same chemical compound. These findings imply that the active transport process operates in some places along the Si trajectory from the root to xylem loading sites. For banana plants, the increasing Si content in shoot organs (pseudostem < petiole and midrib < young lamina < old leaf) supports the major role of transpiration in silicon accumulation and was not dependent on silicon supply (Fig. 6).

5.2 Geochemical tracing of silicon uptake

An additional approach to better understand Si uptake in plant is to use geochemical tracers such as **stable silicon isotopes** or **Ge/Si ratios**.

Silicon has three stable isotopes of atomic mass units ^{28}Si (27.976927), ^{29}Si (28.976495), and ^{30}Si (29.973770) with respective abundance 92.23%, 4.67%, 3.10% (Faure & Mensing, 2005). Those isotopes can be discriminated by chemical, physical or biological processes, inducing an isotope fractionation between two compartments. Phytoliths were shown to display large Si isotope variations (Douthitt, 1982) supporting an impact of plant biological uptake on Si isotopes. Therefore, studying silicon stable isotope fractionation within plants is promising to better understand plant physiological mechanism. Banana plants represent an ideal case study to quantify plant-induced Si isotopic fractionation since banana is accumulating silicon in the sheath cells of vascular bundles in leaves and pseudostem. Through hydroponic experiment in controlled conditions, Opfergelt et al. (2006a, 2006b) aimed to quantify the Si isotope fractionation between dissolved Si source to banana plant, and between plant parts. The banana plants were cultivated in the same conditions than for the study of Henriët et al. (2006) (device 2). The Si isotope compositions of the plant parts and of

the nutrient solution were determined using a multicollector plasma source mass spectrometer (MC-ICP-MS). The results are expressed as $\delta^{29}\text{Si}$ relative to the NBS28 standard, with an average precision of $\pm 0.08\%$, with $\delta^{29}\text{Si} = [(^{29}\text{Si}/^{28}\text{Si}_{\text{sample}})/(^{29}\text{Si}/^{28}\text{Si}_{\text{NBS28}}) - 1] \times 1000$. A positive $\delta^{29}\text{Si}$ value stands for a heavy Si isotope composition relative to the standard, i.e. relatively enriched in heavy Si isotopes, whereas a negative $\delta^{29}\text{Si}$ value represents enrichment in light Si isotopes. The results of this study performed in hydroponics confirmed that plants fractionate Si isotopes by depleting the source solution in light Si isotopes ($\delta^{29}\text{Si} = +0.06\%$ in nutrient solution and -0.34% in root cortex) (Fig. 7) with a plant-source fractionation factor ($^{29}\epsilon$) of $-0.4 \pm 0.11\%$.

More specifically, Si isotope compositions of the various plant parts indicate that a similar mechanism of heavy isotopes discrimination should occur at three levels in the plant: at the root epidermis, for xylem loading and for xylem unloading. At each step, a preferential passage of light Si isotopes contributes to a progressive isotopic fractionation of the solution moving from the uptake sites in roots to the transpiration termini in lamina, and results in reproducible Si isotope compositions of the plant organs consistent with their position along the trajectory of the solution. On mature banana (*Musa acuminata* Colla, cv Grande Naine) from Cameroon, $\delta^{29}\text{Si}$ values range from -0.11% in the pseudostem to $+0.51\%$ in the lamina, with a net increase towards heavier isotopic composition in the upper parts of the plant (Opfergelt et al. 2006b, 2008). This strongly accords with results obtained in vitro on banana plantlets cultivated in hydroponics, where the Si isotope composition was increasingly heavier from pseudostems to lamina (Fig. 7).

Another useful tracer to understand Si uptake in plant is the **Ge/Si ratio**. Germanium (Ge) is a trace element which behaves as a chemical analog to Si, but is fractionated relative to Si in plants. Therefore, the Ge/Si ratio is a promising tool to trace the plant impact on surface processes (Kurtz et al., 2002; Derry et al., 2005). A study was conducted in hydroponic by Delvigne et al. (2009) on banana plant to better understand the Ge/Si fractionation in plants. The growth chamber conditions and the nutrient solution are described in Table 1. Initial nutrient solutions were doped both in Si (13.5 mg/l) and Ge (0.32 mg/l), and no additional Si or Ge was provided during the experiment (closed system for Si and Ge; as in device 1). In contrast with the finite pool kept for Si and Ge, the nutrient requirements were adapted to plant need and continuously supplied as dilute nutrient solutions with peristaltic pumps at a rate of $104 \text{ ml h}^{-1} \text{ pot}^{-1}$ (device 2). Ge was provided as Germanic acid $\text{Ge}(\text{OH})_4$ from GeCl_4 reaction with NaOH (Azam, 1974). Ge concentrations were higher than those observed in natural waters (1–20 ng/l Ge; Mortlock & Froelich, 1996), but toxic evidence in barley appears at much higher Ge content in solution ($>1.44 \text{ mg/l}$; Halperin et al., 1995).

Delvigne et al. (2009) demonstrate that Ge uptake by plants is similar to the Si uptake, and no discrimination against Ge appears to occur at the uptake step. This is in agreement with what is reported for rice roots (Takahashi et al., 1976; Ma et al., 2001). This contrasts with the Si isotopic observations (Opfergelt et al., 2006a) that demonstrate a preferential incorporation of the light Si isotopes at the root interface. The Si transporters likely responsible for the isotope fractionation may not differentiate between Ge and Si. This might explain why Si-rich plants like rice show also a tendency to accumulate more Ge. There is a large Ge/Si fractionation between roots and shoots, with Ge being trapped in roots as a probable response to the toxicity of this element for the plant. This selective Ge entrapment in roots is likely controlled by the relative higher affinity of Ge to form organic

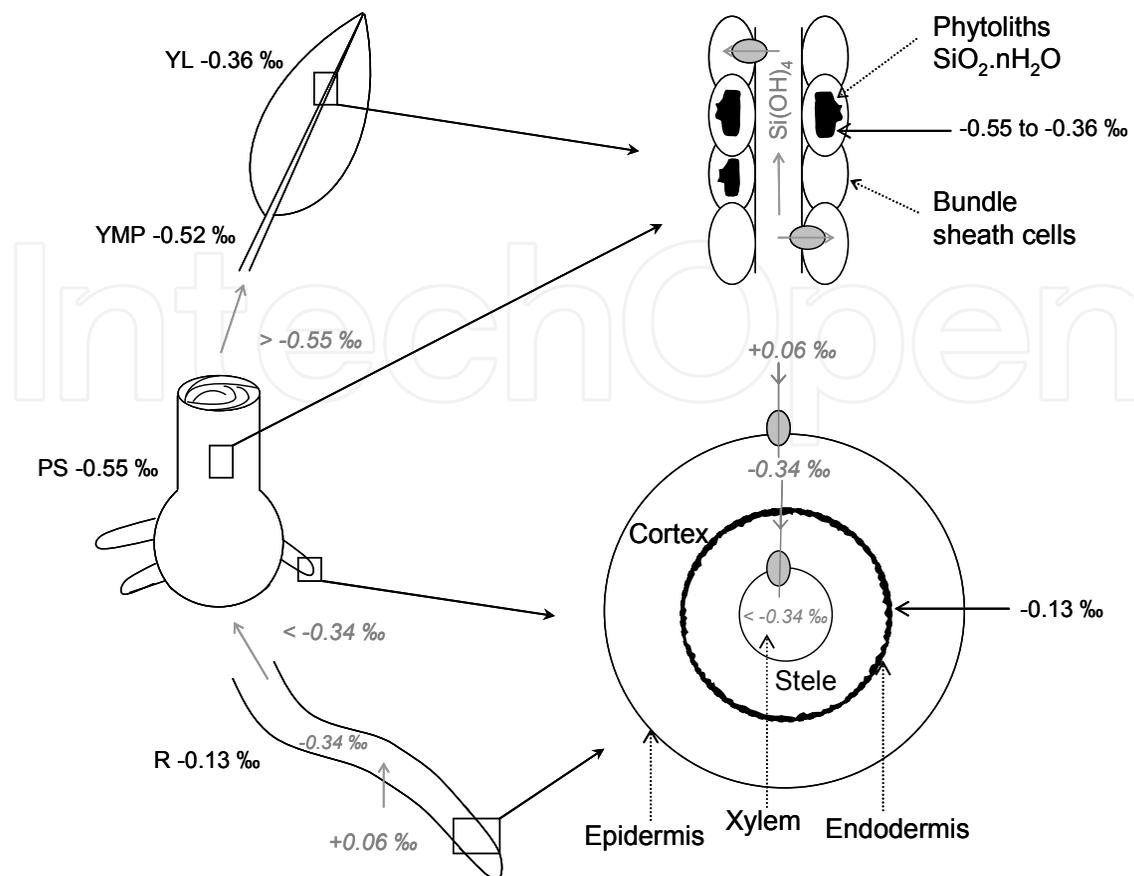


Fig. 7. Proposed schematic model of global Si isotope fractionation in banana plant. Black = Si isotope composition ($\delta^{29}\text{Si}$) of solid precipitated silica (phytoliths); grey and italic = Si isotope composition ($\delta^{29}\text{Si}$) of aqueous H_4SiO_4 . R = roots, PS = pseudostem, YMP = young midribs and petioles, YL = young lamina (from Opfergelt et al., 2006a).

complexes than Si. Owing to Ge trapping in roots, the xylem sap entering the shoots is depleted in Ge explaining the low Ge/Si reported in phytoliths (Derry et al., 2005; Blecker et al., 2007). In shoots Ge closely follows Si throughout the transpiration pathway with no evidence of any discrimination whereas Si isotopes are significantly fractionated along the transpiration pathway (Opfergelt et al., 2006a, 2006b, 2008).

This supports that combining hydroponic studies on stable Si isotopes and Ge/Si ratio in plants relative to a nutrient solution is useful to investigate Si uptake, transport and deposition in plant, and can provide new insights on Si and Ge mobility through plants.

6. Conclusions and perspectives

In field experiments, it is difficult to isolate factors affecting the nutrition of plants and mechanisms of element uptake. Indeed, the dynamic of nutrient (Ca, Mg, Na, K) beneficial (Si), toxic (Al) and polluting (^{137}Cs) elements largely depends on the physico-chemistry of the bulk soil solution and more particularly of the rhizospheric solution. We have illustrated in this Chapter that hydroponic culture was a suitable device to better constrain each of the external factors influencing the transfer of elements in the soil-plant system (pH, redox potential, activity of elements, dissolution/neof ormation of minerals ...). Moreover,

hydroponic devices allow to simulate environmental changes and their impact on the plant growth and nutritional status (humidity, temperature, luminosity ...).

An accurate knowledge of the dynamic of nutrient, toxic and polluting elements in soil-plant systems is vital to preserve the Earth's critical zone defined as "the external terrestrial layer extending from the outer limits of vegetation to the lower boundary of groundwater, inclusive of all liquid, gas, mineral and biotic components" (Brantley et al., 2007). This terrestrial system is permanently subject to environmental constraints which disrupt the homeostasis of the biogeochemical cycle of elements since the extent of human activities. The agronomic and environmental management of the soil-plant system is crucial to mitigate global change processes, while ensuring biomass production, which is related to the future needs of humanity.

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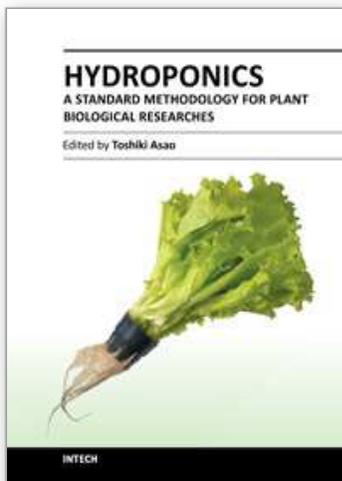
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Hydroponics-A standard methodology for plant biological researches provides useful information on the requirements and techniques needs to be considered in order to grow crops successfully in hydroponics. The main focuses of this book are preparation of hydroponic nutrient solution, use of this technique for studying biological aspects and environmental controls, and production of vegetables and ornamentals hydroponically. The first chapter of this book takes a general description of nutrient solution used for hydroponics followed by an outline of in vitro hydroponic culture system for vegetables. Detailed descriptions on use of hydroponics in the context of scientific research into plants responses and tolerance to abiotic stresses and on the problems associated with the reuse of culture solution and means to overcome it are included. Some chapters provides information on the role of hydroponic technique in studying plant-microbe-environment interaction and in various aspects of plant biological research, and also understanding of root uptake of nutrients and thereof role of hydroponics in environmental clean-up of toxic and polluting agents. The last two chapters outlined the hydroponic production of cactus and fruit tree seedlings. Leading research works from around the world are brought together in this book to produce a valuable source of reference for teachers, researcher, and advanced students of biological science and crop production.

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