Plant homeostasis, growth and development in natural and artificial soils

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Plant growth and development is dependent on factors internal and external to the plant. The effect of nutrient on root morphology has been widely studied in artificial soils or solution cultures. However, the effect of this experimental procedure has never been assessed by comparing plant response in artificial and natural soils. In a laboratory experiment, plants were submitted to three levels of nitrogen supply, in one artificial substratum made of pure sand and one natural soil. Deep differences in plant homeostasis, growth and development were observed between natural and artificial soils: (i) the chemical composition of plant tissues (%C and %N) was changing according to the nitrogen gradient in the artificial substratum, whereas it remained constant in the natural soil; (ii) the same amount of added nitrogen was responsible for a 17% increase in total plant production in the natural soil as compared with the artificial substratum; (iii) plant development differed deeply in the two substrata: in the artificial substratum, the shoot to root ratio was stable whereas the thick to fine roots ratio was increasing with increasing N supply, suggesting an exploration strategy to found an absent limiting nutrient. Conversely, in the natural soil, the thick to fine roots ratio was stable whereas the shoot to root ratio was decreasing with increasing N supply, suggesting an exploitation strategy dedicated to extract a limiting nutrient present in soil components. Even if mechanisms responsible for changes in homeostasis, growth and development were not elucidated, these results stress the importance to consider substrata with a minimal level of complexity if we expect to understand plant growth and development in natural conditions thanks to laboratory experiments.

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1. Introduction

The theory of homeostasis suggests that most living organisms are bound to maintain a given number of physical, chemical and biochemical parameters in a specific range of values (Kooijman, 1995). Plants are known to tolerate some deviations from strict homeostasis; nevertheless, the optimal functioning is reached within a narrow stoichiometric equilibrium range (Sterner and Elser, 2002). As a stable elementary composition in various conditions is considered optimal for plant growth and development, it is of prior importance to understand which factors have potential effect on homeostasis maintenance. However, these factors with potential effect on homeostasis maintenance are often neglected, especially in laboratory experiments, where plants are generally grown in simplified substrata such as solutions (hydropony), or inert solid substrata (such as sand, vermiculite . . .), without buffering capacity. Solution cultures or inert substrata, to which we will refer thereafter as artificial substrata, are ideal for a precise manipulation of environmental factors, with the insurance that observed effects are really due to the manipulated factor itself, and not to an interaction between this factor and some natural soil components. For example, when the manipulated factor is nutrient supply, the use of artificial substrata avoids the interactions between nutrient supply and organic matter, humus, clays or microorganisms. Because of this convenience, the use of artificial substrata largely dominated over the use of natural soil in studies about plant growth, morphogenesis and development (Drew and Goss, 1973; Misra et al., 1986; Wilson, 1988), as a testimony of the dominance of the reductionist paradigm. Nevertheless, given the fact that higher homeostasis is associated with higher growth and generally with higher fitness, interactions between plant resources and other soil components are likely to be integrated in plant developmental strategies, leading to differences in growth and fitness. These interactions between plant resources and other soil components are not possible in artificial substrata, due to the absence of organic matter, humus or clays. Plants could however interact with organisms colonizing the artificial substratum, but such rudimentary communities of bacteria, fungi and/or protozoa are far from the

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complex communities present in natural soils. Consequently, variations in the stoichiometry of plant tissues often observed in artificial substrata could be due to the simplification of the substratum.

To understand which factors control homeostasis is of tremendous importance, because several basic aspects of plant development and morphogenesis are linked with the composition of plant tissues in different elements. For example, many plant species are flowering only when the C/N ratio crosses a given threshold (e.g., Gobert et al., 2005); biomass allocation between shoots and roots (Shoot:Root ratio, S:R) is strongly dependent on the percentage of N in plant tissues (Thornley, 1972; Andrews et al., 1999, 2001); root system structure also depends on nutrient concentration in plant tissues (Zhang et al., 1999).

In this work, we thus tested the hypotheses that (i) nutrient homeostasis should be better maintained in a natural substratum than in an artificial one, due to the higher number of mechanisms helping to buffer environmental variations and maintain stability in the natural soil than in the artificial substratum. As a consequence, (ii) plant should have a higher primary production in the natural than artificial substratum. Moreover, (iii) plant traits under the control of plant internal status, such as the shoot:root ratio (S:R) and the thick root/fine root ratio (T:F), respond differently to a nitrogen gradient in both the substrata.

To test these three hypotheses, we conducted a laboratory experiment to compare the effect of a NH4+ gradient on plant tissue composition, production and biomass allocation in rice, in an artificial substratum made of pure sand and in a natural soil from a savannah from Ivory Coast with similar physical properties. To look for qualitative differences in plant behaviour between both substrata, we compare different simple models of S:R and T:F control to our data in a path analysis.

2. Materials and methods

2.1. Experimental design

There were two kinds of substratum (artificial and natural), three nitrogen levels per substratum (10, 100 and 1000 μmol l⁻¹) and four replicates per treatment in artificial and natural substratum. Plants were grown for three months in a climatic chamber.

2.2. Plants

Young rice seedlings (Oryza sativa L., cv Moroberekan) were grown for under artificial light (600 μmol photons m⁻² s⁻¹) with a 12 h photoperiod. Air moisture was kept at 75% ± 5% and temperature at 28 °C/day and 24 °C/night. Pots (10 cm in diameter and 16 cm high) were filled with 1 kg DW of substratum. About 100 seeds were sown, and a selection of a homogeneous pool of seedlings was made after one week. One seedling was planted in each pot.

2.3. Nutrient gradient

In both natural and artificial substrata, plants were supplied with fertilizer. Nitrogen was brought as NH₄SO₄ since NH₄⁺ is the preferred form of nitrogen taken up by rice (Fried et al., 1965; Sasakawa and Yamamoto, 1978). To avoid limitation of plant growth by another element than N, we used a 1/10 diluted modified Hoagland solution containing all macro and micro-nutrients at high and constant concentrations among treatments: K₂HPO₄: 2.939 mmol l⁻¹; CaCl₂: 2.495 mmol l⁻¹; MgSO₄: 3.950 mmol l⁻¹; Na₂SiO₃: 0.996 mmol l⁻¹; Fe-EDTA: 13% of Fe, 5 mg l⁻¹; Oligo-elements: H₂BO₃: 55 μmol l⁻¹; MnSO₄: 20 μmol l⁻¹; ZnSO₄: 0.6 μmol l⁻¹; Na₂MoO₄: 0.4 μmol l⁻¹; CuSO₄: 0.6 μmol l⁻¹. A nutrient flush was realised three times a week by adding a solution volume equal to the readily available water of each soil (400 ml), to eventually chase ions which could accumulate during the experiment.

2.4. Artificial and natural substrata

The artificial substratum consisted in a mixing of pure sand from Fontainebleau (France), used in glass industry, with a water retaining acrylamide polymer (Grain d’eau®), at the proportion 1 kg of sand for 1 g DW of polymer. The natural soil was a sandy ultisol from Lamto savannah (Ivory Coast). Soil characteristics were as follow (in weight proportion): sand = 78%; silt = 17%; clay = 5%; organic matter = 1–2%; total C = 0.91%; pH = 6.7; C/N = 17.3. Total nitrogen is particularly limiting in this soil: 500 mg kg⁻¹ (0.05%) (Abbadie and Lensi, 1990; Lensi et al., 1992), as well as its both mineral forms: 1.5–7.5 mg kg⁻¹ of NH₄⁺ and <1 mg kg⁻¹ of NO₃⁻ (Martin, 1990). Cation exchange capacity (CEC) is low: 3.4 cmol kg⁻¹ soil (Mordelet et al., 1993). Both kinds of soil presented the same modal granulometry and a close maximal readily available water (400 ± 40 ml per kg of dry soil). Before filling the pots, soil was sieved with a 2 mm mesh. Upland rice is commonly grown by farmers on this soil, close to the Lamto research station (personal observation).

2.5. Measured variables

Above and belowground biomass harvests were harvested after 3 months of growth. They were dried for 2 days at 45 °C and weighted to get dry biomasses.

Plant internal status in leaves (%C, %N) and roots (%C, %N) was measured with a CHN analyzer, and compiled by taking into account below and above ground biomasses to obtain a total plant internal status (%C, %N).

Concerning root system structure, root diameter has been said the characteristic that conveys the most information on root structural and functional properties (Lecompte et al., 2005). Root biomass distribution into diameter classes was obtained by applying a new method (Blouin et al., 2007) on the entire root systems. After three months of growth, shoots were cut, dried for 2 days at 50 °C in an oven and weighted. Roots were first separated from the bulk soil using a fine stream of water and then dried at 50 °C for two days. Dried roots were then cut at 2000 turns/min with the Polymix PX-MFC from Kinematica AG, with its 2 mm sieve. Root fragments were then passed on a column of sieves. Sieve meshes were corresponding to the AFNOR standard french norm: 800, 630, 500, 400, 315, 250, 200, 160, 125, 100 and 80 μm. The column of sieves was placed on an agitator as the Retsch AS 200 digit, during 22 min with a continuous agitation at the amplitude 60. Finally, the content of each sieve was weighted, and reported to the total root biomass. Biomass proportion in each diameter classes were pooled into the thick roots class (T) and the fine roots class (F), by putting together diameter classes whose the variation was the same along the N gradient (all classes with an increasing biomass proportion from 10 to 1000 μmol l⁻¹ together, and all classes with a decreasing biomass proportion together). Hence, the limit diameter between thick and fine roots was fixed at 315 μm in this study. The ratio between thick roots and fine roots (T:F) reflects the proportion of lateral roots, which is proportional to the energy investment of a plant in its exchange surface with the soil. This ratio is more adequate than the absolute number, length or biomass of fine roots, because total root biomass might change among N treatments. Note that T:F is decreasing when the proportion of fine lateral roots is increasing.

2.6. Statistical analysis

In order to compare the biomass production in natural and artificial substrata, we bootstrapped the difference of biomass
increase between the 10 (low) and 1000 (high) μmol l\(^{-1}\) treatment for each substratum. This was done by selecting random pairs of low and high N replicates for each soil type, then calculating the biomass increase (the difference of biomass between the replicate in high N and the one with low N), and finally by comparing them. At each simulation, four biomass gains were generated by soil type, which were used to perform a t-test. At the end of the simulations, we looked at the distribution of the t and P values to determine the significance of the differences between artificial and natural soil. ANCOVA were performed to determine the effect of the substratum, of the N-gradient and their interaction on S.R and T:F.

To understand the link between NH\(_4^+\) concentration in the nutritive solution, %N\(_i\) (percentage weight/weight of N in leaves) and T:F (percentage of thick root biomass/percentage of fine root biomass), a path analysis (Bollen, 1989) was fitted different models proposed in literature to the data of the two experiments in the aim to select the best in terms of its conformity and its parsimony (Burnham and Anderson, 2002). In the first model, coined the “nutritional” model, %N\(_i\) controls directly the LR emission, and thus the T/F. NH\(_4^+\) does not act directly on T/F, but rather on %N\(_i\), which therefore plays a role of mediator between NH\(_4^+\) and T/F (see also Section 3.4 and Fig. 4). Therefore, this model excludes the possibility that NH\(_4^+\) may act as a “signal molecule”, i.e. a molecule inducing a local response, without systemic effect. The second model was called the “non-nutritional” model. It is inspired from the dual-pathway model of Zhang et al. (1999): here NH\(_4^+\) and %N\(_i\) are two variables acting directly on the T/F ratio, with NH\(_4^+\) being a signal molecule inducing a stimulation of LR emission. In this model, NH\(_4^+\) does not influence %N\(_i\). The third model was called the “mixed” model. It corresponded to a double effect of NH\(_4^+\), which acts directly on the T/F ratio as a signal molecule, but also indirectly (via %N\(_i\)), because plant internal nutrient status is considered proportional to nutrient concentration in the environment.

Parameters of the models were estimated by the method of maximum likelihood. Because the three models were not hierarchical and had not the same number of parameters, chi2 statistics (and R\(^2\)) could not be used straightforwardly to compare them (Rex, 2004). Thus, we used the Bayesian Information Criterion, BIC (sometimes referred as “Schwarz criterion”, or SIC) to compare models (Burnham and Anderson, 2002): BIC = \(-2 \ln(L) + K \ln(n)\), with \(L\) the maximized value of the likelihood function for the estimated model, \(n\) the number of observations (the sample size), \(K\) the number of free parameters to be estimated. As a consequence, the BIC decreases with the likelihood of the model, and is penalised by free parameters. Therefore, model with the lowest BIC should be preferred. We used the library “sem” of the R language and environment for statistical computing (Team, 2008) for model fitting. We performed separately path analyses on data from the first experiment (artificial substratum) and from the second experiment (natural soil).

3. Results

3.1. Homeostasis

Plant stoichiometry (%C and %N) was varying in the artificial substratum but not in the natural soil (Fig. 1). The % of C was approximately the same in the artificial substratum at 100 μmol l\(^{-1}\) and in the natural substratum for all N levels. In the artificial substratum, a lower value of %C was observed in the roots of plants grown at 10 μmol l\(^{-1}\), and a higher value at 1000 μmol l\(^{-1}\) (Fig. 1a). Consequently, a significant correlation between %C\(_\text{tot}\) and the NH\(_4^+\) treatment was observed only in the artificial substratum, not in the natural one (Table 1).

The % of N was approximately the same in both substrata, except at 1000 μmol l\(^{-1}\) in the artificial substratum where it was higher, showing that the plant was not able to keep a constant %N when the N supplied in the environment was too high (Fig. 1b). Consequently, a significant correlation between %N\(_\text{tot}\) and the NH\(_4^+\) treatment was observed only in the artificial substratum, not in the natural one (Table 1).

3.2. Primary production

A significant progressive increase of total dry biomass was observed along the N-gradient in both substrata (Fig. 2a). The same pattern was observed for aboveground and belowground biomasses (Fig. 2b and c). At a given N-concentration, total biomass was always significantly higher in the natural than in the artificial substratum. The N-gradient effect on production (biomass at 1000 μmol l\(^{-1}\) minus biomass at 10 μmol l\(^{-1}\)) was stronger in the natural soil as compared with the artificial soil (+2.32 g DW, i.e. +17% for total biomass, +1.81 g, i.e. +47% for belowground biomass, +0.51 g, i.e. +5% for aboveground biomass). A bootstrap analysis showed that these differences between natural and artificial substrata were significant for total and belowground biomasses (P = 0.07 and P = 0.001 respectively), but not for aboveground biomass (P = 0.81). So, N-supply had a significantly stronger effect on biomass production in natural than in artificial substratum.

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Correlations between several parameters determined in linear models.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>Type of substratum</td>
</tr>
<tr>
<td>%C(_\text{tot}) ~ NH(_4^+)</td>
<td>Artificial</td>
</tr>
<tr>
<td>%N(_\text{tot}) ~ NH(_4^+)</td>
<td>Artificial</td>
</tr>
<tr>
<td>S:R ~ %N(_i)</td>
<td>Artificial</td>
</tr>
<tr>
<td>T:F ~ %N(_i)</td>
<td>Artificial</td>
</tr>
</tbody>
</table>

%C\(_\text{tot}\): Carbon percentage in plant tissues (shoot and root); %N\(_\text{tot}\): Nitrogen percentage in plant tissues (shoot and root); S:R: ratio of shoot to root biomasses; T:F: Ratio of thick to fine root biomass proportion; %N\(_i\): percentage of nitrogen in leaves.
The N-gradient and substratum had no significant impact on S:R but the interaction between these factors was significant (Table 2). This result reveals that the effect of the N-gradient on S:R can be understood only by taking into account the kind of substratum. In terms of mean comparison, there were no significant differences in S:R among NH₄⁺ treatments in the artificial substratum, but a significant decrease appeared between the 100 and 1000 μmol l⁻¹ treatments in the natural soil (Fig. 3a). S:R and N-gradient were significantly correlated only in the natural soil (P = 0.03).

Variations of T:F were opposite to those of S:R: there was no significant difference in T:F between N-treatments in the natural soil while a significant difference appeared between the 100 and 1000 μmol l⁻¹ treatments in the artificial one (Fig. 3b). In parallel, T:F was significantly affected by the N-gradient, by the substratum and by the interaction between these two factors (Table 2). So the T:F is affected by the N-gradient itself (and the substratum itself), but also by the interaction between the N-gradient and the substratum.

### 3.4. Path analysis

T:F was strongly correlated with the percentage of nitrogen in leaves (٪Nₗ) in the artificial substratum, but not in the natural soil (Table 1). This strong divergence in behaviour according to the kind of substratum led us to consider more deeply the control of T:F. To determine if there was a qualitative difference in the determinism of T:F among both the substrata, we performed a path analysis. More precisely, it was used to determine if, among the three models of T:F control described in Section 2.6, the same would be validated in the two kinds of substrata. In the artificial substratum, the nutritional model obtained the best results (BIC = −2); it showed a significant positive effect of the N-gradient on ٪Nₗ (c = +0.95) and of ٪Nₗ on T:F (b = +0.93); the worst model was the non-nutritional one (Fig. 4 and Table 3). In the natural soil, models’ performances were in the opposite order. The best one was the non-nutritional model (BIC = −2.5), with only a significant negative effect of the N-gradient on T:F (a = −0.58) and with no effect of ٪Nₗ. So, path analysis ranked the different models in opposite order according to the soil type (Fig. 4 and Table 3).

### Table 2

Results of the two-ways ANOVA for the shoot to root ratio (S:R) and the thick to fine root ratio (T:F) as a function of the dose of N applied (N-gradient) and the kind of soil (artificial or natural substratum).

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Factor</th>
<th>F value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>S:R</td>
<td>Substratum</td>
<td>2.70</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>N-gradient</td>
<td>0.30</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td>Substratum × N-gradient</td>
<td>7.79</td>
<td>0.01</td>
</tr>
<tr>
<td>T:F</td>
<td>Substratum</td>
<td>41.32</td>
<td>2.8 × 10⁻⁶</td>
</tr>
<tr>
<td></td>
<td>N-gradient</td>
<td>26.94</td>
<td>4.4 × 10⁻⁵</td>
</tr>
<tr>
<td></td>
<td>Substratum × N-gradient</td>
<td>6.39</td>
<td>0.02</td>
</tr>
</tbody>
</table>

### Table 3

Results of model selection by path analysis.

<table>
<thead>
<tr>
<th>Tested models</th>
<th>Parameters</th>
<th>Artificial soil</th>
<th>Natural soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>A Nutritional model</td>
<td>BIC = −2</td>
<td>2</td>
<td>−5.0 × 10⁻⁷</td>
</tr>
<tr>
<td></td>
<td>b = 0.93</td>
<td>0.95</td>
<td>0.02</td>
</tr>
<tr>
<td>B Non-nutritional model</td>
<td>BIC = 23</td>
<td>−2.5</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>a = −0.2</td>
<td>9.03</td>
<td>0.015</td>
</tr>
<tr>
<td>C Mixed model</td>
<td>BIC = 9.5 × 10⁻¹⁵</td>
<td>1.95 × 10⁻¹⁴</td>
<td></td>
</tr>
<tr>
<td></td>
<td>a = −0.24</td>
<td>1.16</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td>b = 1.16</td>
<td>0.95</td>
<td>0.002</td>
</tr>
</tbody>
</table>

Path analysis was applied on data from plants grown in an artificial substratum (pure sand from Fontainebleau, France) and in a natural soil (Lamto, Ivory Coast), to estimate the relevance of several simple models (described in Fig. 4); n = 4 per treatment. BIC: Bayesian Information Criterion. The lowest is the BIC value, the best is the model. Parameters were standardised to take into account the different units of variables.

* Parameters significantly different from 0.
conclusion, T:F control was qualitatively different in both the substrata.

4. Discussion

4.1. Interactions between N-supply and the kind of substratum

Among our results, four main findings corroborate our hypothesis about the importance of the interaction between soil properties and N-gradient on biomass allocation among plant organs: (i) biomass allocation among thick and fine roots (T:F) was significantly influenced by the N-gradient and the kind of substratum, but also by the interaction between N-gradient and substratum (Table 1) (ii) biomass allocation between shoots and roots (S:R) was only affected by the interaction between N-gradient and substratum, not by each single factor (Table 1) (iii) %N, which is considered as an important driver of plant development, was varying only in the artificial substratum (Table 2), whereas it stayed constant in the natural soil, probably due to complex ecological mechanisms linking plant and soil functioning. (iv) the kind of substratum was determinant in the performance of different statistical models to explain fine root development (Table 3). Taken together, these results indicated that the properties of the substratum have a great impact on plant development. Studies of plant development in substrata without a sufficient complexity level can lead to perturbations in plant metabolism, leading to erroneous conclusions on the development of plants in natural conditions. For example, in a study with Arabidopsis thaliana grown in heterogeneous agar gel, Zhang et al. (1999) observed that at 50 mM KNO₃ in the middle agar segment, plants were exhibiting a reduction in lateral root length, whereas an increase was observed from 0.05 to 10 mM; the “Dual pathways for regulation of root branching by nitrate” was deduced from these observations. This was probably due to the interaction between the poor/rich patches contrast and the overall nitrate concentration (Blouin and Puga-Freitas, 2011). But these results would probably not hold at the same nitrate doses in natural soils with a sufficient complexity level.

4.2. Homeostasis

One of our main results is the robustness of plant stoichiometry in the natural soil as compared with the artificial substratum (Fig. 1). In the artificial substratum, low values of %Ctot were observed at low N supply (10 μmol l⁻¹ of NH₄⁺) (Fig. 4a), especially in the roots as compared with the shoots (results not shown); we speculate that some stored or even structural carbon was respired to furnish the energy allowing to increase the assimilation of NH₄⁺. At high N-supply, both %C and %N were increasing, suggesting that plants were not able to evacuate the N in excess. In the natural soil, plants maintained their homeostasis along the N gradient. It was not due to the adsorption of the entire N supplied on the soil absorbing complex (clay, humus, organic matter) or to an immobilization by microorganisms, since the fertilizer flush was ensuring a quick saturation of these compartments. Moreover, the N-supply had a stronger positive effect on plant production in the natural soil than in the artificial substratum, showing that N was available to the plants. It is more likely that several other mechanisms were involved in the observed response. Soil porosity is greatly influencing water availability to the plant, and can thus have strong effects on S:R (Wilson, 1988); variation in soil pore size and soil pressure can lead to mechanical resistance, which is also affecting biomass allocation to the roots and inside the root system (Wiersum, 1957; Drew and Goss, 1973; Montagu et al., 2001). However, both substrata presented rather similar textures and readily available water. Another explanation could be that microorganisms can change the chemical form of the supplied nitrogen, for example by transforming some of the NH₄⁺ into NO₃⁻ through nitrification, leading to a situation where homeostasis maintenance is easier and plant growth higher. Finally, biochemical signal between organisms can have a great impact on biomass allocation between shoots and roots: even in similar spatial and nutritional conditions, a plant can strongly modify its S:R when it is detecting a neighbouring plant (Gersani et al., 2001); bacteria can also deeply modify root system structure through the emission of signal molecules such as hormone-like compounds (Ping and Boland, 2004; Ryu et al., 2003). These feedback mechanisms are potentially responsible for homeostasis maintenance by avoiding a strict correlation between what is in and out of the plant system.

4.3. Growth and development

When plant homeostasis was maintained, a given increase of N supply from 10 to 1000 μmol l⁻¹ of NH₄⁺ was associated with a 17% higher gain in plant production in the natural soil than in the artificial substratum (Fig. 2 and Section 3.2). This result corroborates the idea that even if plant stoichiometry is not as strict in plants as in animals (Sterner and Elser, 2002), a stable plant chemical composition is associated with a higher growth rate. This result question the practice of growing plants in solution cultures or in artificial substrata when the objective is to produce the highest marketable yield. In addition to this quantitative effect on plant growth, stability of plant chemical composition affected qualitatively plant development. In the artificial soil, T:F was increasing with the N-supply (Fig. 3b), i.e. fine root proportion decreased. Since S:R was not varying and T:F was increasing, plants were increasing their absolute proportion of thick roots. This increase in thick root proportion could be explained by a shift of plant morphogenesis towards an exploration strategy which could help to find a limiting
nutrient. Despite numerous reports of fine root proliferation in rich patches of heterogeneous environments and corollary increase in thick roots proportion in poor patches (Robinson, 1994), it is, to the best of our knowledge, the first time that an increase in thick root proportion without changes in S/R ratio is observed at the scale of the whole root system. Conversely, in the natural soil, plants exhibited a stable T:F ratio and a varying S:R ratio. As we found no study reporting simultaneously root parameters in homogeneous natural and artificial soils, comparisons between our results and those obtained by other authors is not easy. Nevertheless, it has been found that in a homogeneous sandy soil similar to our natural soil, five perennial grasses exhibited changes in the root weight ratio (Root weight divided by total – shoot + root – weight) with N supply, whereas root system structure (Specific Root Length, Specific Root Area, mean diameter and % of fine roots) did not change (Boot and Mensink, 1990). This was also observed with four annual species, three other perennial species (and another identical to the previous experiment) and two annual dicots: root mass fraction (also called root weight ratio) was decreasing with the addition of N in a natural soil, whereas root system structure (Specific Root Length) was stable whatever the N supplied (Hill et al., 2006). Conversely, when 4 grass species were grown in solution culture, i.e. artificial substratum, and submitted to a nitrogen gradient, root system structure (SRL) was plastic whereas the shoot:root ratio was not modified according to the N gradient (Robinson and Rosior, 1988). In a fine nutrient-poor white quartz-sand mixed with 8% limestone, which can be considered as a substratum with an intermediate level of complexity between artificial and natural soils, Brachypodium pinnatum had a decreasing root weight ratio with increasing N supply, whereas the SRL was almost not changing; however, Dactylis glomerata exhibited changes along the N gradient for both root weight ratio and SRL (Ryser and Lammers, 1995). These results are coherent with the idea that plants grown in artificial substratum are not responding to a N gradient in the same way than they do in natural soils.

5. Conclusion

The balkanisation of scientific disciplines has led to different and sometimes segregated perspectives on the same scientific object. Plant physiologists are aware of the complexity of interacting metabolic and signalling pathways inside the plant. When they are studying plant growth and development, they are trying to unravel these complex networks in the simplest environment. On the other hand, plant ecologists are particularly interested in the complex network of interactions between plant and its biotic and abiotic environment. Consequently, they emphasize this “outside complexity” as compared with the “inside complexity” of plant metabolism, and are generally setting their experiments in natural soils. In this study, we demonstrated that the control of plant growth and development by internal factors was dependant on external factors such as soil components. We think that interdisciplinary studies should be conducted to discover the internal proxies for environmental variables, in the aim to bridge the gap between plant physiology and ecology.

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