Chemical fertility of forest ecosystems. Part 1: common soil chemical analyses were poor predictors of stand productivity across a wide range of acidic forest soils

Karna Hansson[1], Jean-Paul Laclau[2,3], Laurent St André[1], Louis Mareschal[2,3], Gregory van der Heijden[1], Claude Nys[1], Manuel Nicolas[4], Jacques Ranger[1], Arnaud Legout[1*]

[1] INRA, BEF, F-54280 Nancy, France
[2] CIRAD, UMR Eco&Sols, F-34060 Montpellier, France
[3] Eco&Sols, CIRAD, INRA, IRD, Montpellier, SupAgro, University of Montpellier, Montpellier, France
[4] ONF, Département RDI, F-77300 Fontainebleau, France

* Corresponding author. arnaud.legout@inra.fr Tel.: + 33(0)383394073

Abstract

Forest soil fertility can be defined as a combination of physical, chemical and biological factors characterising the biomass production capacity of the soil. However, numerous ecological variables affect tree growth and the aim of the present study was to investigate the specific influence of soil chemical properties on tree productivity at 49 acidic forest sites. A standardized tree productivity index based on tree height expressed as dominant height of the studied stand divided by maximum tree height observed at the same age for the same species in the same climatic region was firstly computed at each site. This index was independent of species, ages and climatic-regions. A soil database was also compiled with data on soil properties from 47 temperate (France) and two tropical (Congo, Brazil) sites. Data included seven tree species, varying in age from 1 to 175 years. Commonly used indicators such as C:N ratio, soil pH, as well as available and total pools of soil nutrients were compared to the standardized tree productivity index, to find the most reliable indicator(s). Nutrient pools at fixed mineral soil depths (down to 100 cm) were used, as well as (for 11 stands) the depth comprising 95% of fine roots.

Our results show that none of the common soil chemical parameters tested in this paper could individually explain stand productivity. Combinations of different parameters were also tested using PCA and they could better explain the variability of the data set but without being able to separate the sites according to their standardized tree productivity index. Moreover, random Forests performed on our dataset were unable to properly predict the standardized tree productivity index. Our results reinforce the idea that the influence of the soil chemical fertility on stand productivity is complex and the soil chemical parameters alone (individually or combined) are poor predictors of tree productivity as assessed by the H_0:H_{max} index. In this paper we focused on static soil chemical indicator and more dynamic indictors, such as nutrient fluxes involved in the biogeochemical cycles, could better explain stand productivity. A companion paper (Legout *et al.*, Submitted) focuses on the connection between productivity and different components of the biogeochemical cycle, using data from 11 of the stands presented in this paper.

Keywords: forest ecosystem; soil fertility; soil indicator; nutrient stocks; stand productivity

Abbreviations: EBC= Exchangeable Base Cations; TBC= Total Base Cations; R95%= soil depth including 95% of fine roots; H_0:H_{max} = standardized tree productivity index expressed as dominant height (H_0) of the studied stand divided by maximum tree height (H_{max}) observed at the same age for the same species in the same climatic region.

1 Introduction

Forest productivity is a major concern for forest management and research (Bontemps and Bouriaud, 2014), especially in the context of global changes. Indeed, forest ecosystems are subjected to numerous challenges (economic, environmental and social) and the current intention of forest policies to optimise the functions and services provided by forest ecosystems (wood production, carbon sequestration and climate change mitigation, water quality, etc.) may threatened their sustainability (Achat *et al.*, 2015; Thiffault *et al.*, 2015; Garcia *et al.*, 2018; Schmitz *et al.*, 2019). We need more than ever to better understand the role of environmental factors and other driving parameters on tree productivity on short to mid time scales.

Tree productivity relies on several key parameters (climate, topography, geology…), including the soil fertility which may increase or decrease the production within the timeframe of forest management (Schoenholtz *et al.*, 2000; Binkley and Fisher, 2012). The notion of soil fertility is commonly used in forest research (Augusto *et al.*, 2002a; Schroth and Sinclair, 2003; Fernández-Ondoño *et al.*, 2010; Kalliokoski *et al.*, 2010) and can be defined as "the sum of physical, chemical and biological factors characterising the biomass production capacity of the soil" (Ranger and Turpault, 1999; Augusto *et al.*, 2002b)(Fig. 1). Several attempts have been made to quantify soil fertility and to identify key soil indicators, both in agricultural (reviewed by Bastida *et al.*, 2008) and forest soils (reviewed by Schoenholtz *et al.*, 2000), using biological, physical or chemical soil properties. Soil fauna (Stork and Eggleton, 1992; Velasquez *et al.*, 2007; Rousseau *et al.*, 2013) and ratio between Gram-positive and Gram-negative bacteria (Gartzia-Bengoetxea *et al.*, 2009) are examples of biological indicators, while water content at field capacity (Gartzia-Bengoetxea *et al.*, 2009) and soil particle size distribution (Aertsen *et al.*, 2012) are examples of soil physical properties used as fertility indicators.

In this study, we choose to focus on the specific influence of soil chemical properties, such as pH, C:N ratio, or nutrient content on tree productivity. Soil chemical properties have been commonly used in the past as soil fertility indicators (Schoenholtz *et al.*, 2000), namely because they are easily comparable, using standardised analyses. Successful indicators should optimally be sensitive to a large range of disturbances, easily and quickly measured, cheap, and should include a sufficient number of samples to cover spatial and temporal variabilities, using standardised methods of analysis (Velasquez *et al.*, 2007). Many studies have been carried out at the scale of forest plots or small geographical regions, and local soil fertility indicators have been suggested. For example, Bautista-Cruz *et al.* (2012) found that the best soil properties to be used in tropical montane cloud forests in Mexico were soil organic carbon, soil pH, plant-available P, O horizon thickness and exchangeable Al^{3+}. Conversely, in *Eucalyptus* stands in Congo, CEC, clay and organic matter contents were the best predictors of stand productivity (Bikindou *et al.*, 2012). Studies dealing with the generalisation of local indicators at a larger scale are scarce and it may be difficult to find a simple soil chemical fertility indicator capable to predict biomass production for all forest ecosystem types. A combination of several parameters may be used to quantify forest soil chemical fertility on a large scale, but so far there is little consensus as to what those parameters ought to be and a standardisation of methods is lacking. We hypothesised that forests growing on soils with the lowest nutrient stocks would also have the lowest productivity relative to the maximum values measured for the same species in the same ecological region.

Our study aims to gain insight into the influence of soil chemical properties (commonly used as indicators of soil fertility) on stand productivity for a wide range of acidic forest ecosystems. We used data from 49 field studies, 47 temperate (France) and two tropical (Congo, Brazil) forests, all in acidic environments ($pH<6$ in top soil) without water-logging. A standardized tree productivity index expressed as dominant height (H_0) of the studied stand divided by maximum tree height (H_{max}) observed at the same age for the same species in the same climatic region was used, which allows to focus on the specific influence of soil on tree productivity, minimising the role of other parameters such as climate.

2 Materials and methods

2.1 Study sites

Our study was carried out in 49 sites, most belonging to the French forest research network SOERE-F-ORE-T (http://www.gip-ecofor.org/f-ore-t/). 38 sites among 102 in the Renecofor French Permanent Plot Network (http://www.onf.fr/renecofor/@@index.html) were selected. The temperate sites included both coniferous and broad-leaf species (Table 1): *Picea abies* (L.) Karst. (12 sites), *Fagus sylvatica* L. (15 sites), *Quercus petraea* (Matt.) Liebl. (10 sites), *Pseudotsuga menziesii* (Mirb.) Franco (7 sites), *Abies alba* Mill. (5 sites), *Abies nordmanniana* Spach (1 site) and *Pinus nigra* Arnold (3 sites). At the tropical sites, *Eucalyptus* (different species) was the only studied genus (Table 1). Sites with pH> 6 in the top soil were excluded, as well as water-logged sites. We chose to focus on acidic soils, as they are the most common in French forest ecosystems and tropical planted forests (our data set), and they are sensitive to disturbances, such as slash removal and whole tree harvesting (Wall, 2012; Achat *et al.*, 2015). A reliable characterisation of soil fertility is crucial for a sustainable management of such forest ecosystems.

In addition to the 38 Renecofor sites, 11 other sites (9 French and 2 tropical sites), with more data available at each site, were also included. Some of these sites include more than one tree species and/or stand age. Some basic properties of each site are listed in Table 1, with more details in Supplementary Material 1. Chronosequences were sometimes used as a proxy for covering the whole rotation length (Au1, Fou and Vau, Table 1). At sites with fertilization experiments, only control plots were included in the present study. At the tropical sites, all plots (also control treatments) received some baseline fertilization, as practised in the industrial management (Table 2). All sites have been forested for at least 60 years (often much longer), except the *Eucalyptus* stand in Congo (established in 1992 on soil that had been covered by an herbaceous savannah for 3000 years), and the Renecofor sites DOU23, EPC34 and EPC87 (established on old agricultural land in the 1960s). Stand age was approximated for some old growth stands (>100 years) when detailed data was missing. The adjacent sites Au1 and Au2 were separated because the bedrock differed (Fichter *et al.*, 1998).

2.2 Data collection and calculations

Average data (published and unpublished) for each site, tree species, age and soil depth was used. Data from the mineral soil and, when available, from forest floor layer (LFH) were included. At some sites (Abr, Ard, Au1, Au2, Bre, Fou, Gem, Kon), data covering 2 to 4 different sampling dates were available, whereas data from only one sampling date were available at most sites.

2.2.1 Soil depths

Sampling depth varied between studies. While fixed soil depths for all profiles were used at some sites, soil horizons were sampled at other sites. To compare results between sites, data from 0-10, 10-30, 30-70 and 70-100 cm, as well as from 70 cm to 95% rooting depth (R95%, soil depth including 95% of fine roots), were linearly interpolated from horizons above and below. To make the interpolation possible, data including at least 50% of soil depth/thickness had to be available. For sites where data was available down to 85 cm depth or deeper, this data was used for the 70-100 cm soil layer. For sites where data was not available below 80 cm depth, only the soil data down to 70 cm depth was used for the soil profile.

At some sites, detailed rooting data was available, with biomass or fine root densities throughout the soil profile (Abr, Fou, Ita); whereas for other sites we used rooting depth as noted in soil profile descriptions (Ard, Au1, Au2, Bon, Bre, Gem, Vau, Renecofor sites). At Kon (Congo, *Eucalyptus*), where detailed rooting data was available down to 5 m, but with no data for total rooting depth, we assumed the same total rooting depth as for Ita (Brazil, *Eucalyptus*) and also the same rooting pattern (the absence of physical and chemical barriers to root growth down to > 15 m depth was checked at both sites). At Fou, the only site where root data was available both from biomass sampling and profile descriptions, it could be verified that the noted rooting depth in profile descriptions was similar to the R95% from biomass samplings. The rooting depth defined in soil profile descriptions was therefore assumed to be 95% of total rooting depth for all sites without detailed root sampling. For the Renecofor sites, soil chemical data was available down to 100 cm depth, and it was only possible to calculate pools down to R95% at 19 of those sites, since the remaining sites had rooting depths deeper than 100 cm.

2.2.2 Soil and forest floor data

Fine earth mass was calculated from soil depth, bulk density and percentage fine earth. Coarse material (>2mm diameter) was not considered in this study. In absence of measured data for a given soil sample, bulk density and % fine earth in mineral soil were estimated using site specific regressions based on measured bulk density data and soil depth. Weight of the LFH layer was directly measured, but in two cases (Ard, Au1) average data available from publications were used for profiles with missing data and in one case (Bon) stocks in humus layers could not be calculated due to lack of LFH layer weight data. For some parameters, data from the LFH layer were insufficient for comparison between sites.

Chemical analysis methods (summarised in Table 3) were generally similar between sites, with some differences, assumed to have minor impact on the results. Data on available P_2O_5 included different methodologies (extraction with citric acid, extraction with sulphuric acid and sodium hydroxide, extraction with ammonium oxalate, anion exchange resin adsorption) depending on the study site. The Duchaufour method (Duchaufour and Bonneau, 1959) extracts more P than the Dyer method (Dyer, 1894), used at most of the Renecofor sites (Bonneau *et al.*, 2003). The resin method, used at the Ita site (Laclau *et al.*, 2010), has been shown to have a strong correlation with P uptake by plants in tropical soils (van Raij *et al.*, 1984; da Silva and van Raij, 1999). The Joret-Hébert method (Joret and Hébert, 1955), used for a few of the Renecofor samples, is suitable for soils with high calcium carbonate content (Mathieu and Pieltain, 2003).

Exchangeable elements were extracted with KCl, NH_4Cl or NH_4Ac, followed by titration (Al and H), or spectrophotometry determination (other elements), atomic absorption or ICP.

Three different electrolyte solutions (water, $CaCl_2$ and KCl) were used for measuring soil pH. In most cases pH was measured in both water and either KCl or $CaCl_2$, but sometimes data was only available for pH measured in KCl or $CaCl_2$. To compare pH measured in different solutions, we estimated pH(H_2O) based on linear equations for the relationship between pH(H_2O) and the other electrolyte solutions using measured data from the same sites.

Sum of exchangeable base cations (EBC) was calculated as the sum of Ca^{2+}, K^+, Mg^{2+} and (when available) Na^+ (expressed in kmol$_c$ ha^{-1} in each soil layer). Exchangeable acidity (Ac) was calculated as the sum of exchangeable H^+ and Al^{3+} (expressed in kmol$_c$ ha^{-1} in each soil layer). Effective cation exchange capacity (CEC_{eff}) was calculated as the sum of EBC and Ac. Base saturation (BS) was calculated as EBC divided by CEC_{eff}. Sum of total base cations (TBC) was calculated as the sum of total K_2O, Na_2O, CaO and MgO (kg ha^{-1}). Not all soil profiles contained data on all analysed variables. Data on total elements in mineral soil was not available for the Renecofor sites. When carbon (C) data was missing but organic matter (OM) data was available, carbon in mineral soil was estimated as OM*0.58; i.e. OM=C*1.72 (Baize 2000), whereas the ratio OM=C*2 was used for organic layers. For other elements, gaps were replaced with site-, depth- and species-specific average values, or left empty if such data was not available.

Nutrient concentrations were sometimes below the detection limit, especially at the poorest sites. For those samples we calculated a range in stocks based on a maximum (value=limit of detection) and minimum (value=0) level of the element. We chose to use the same limits for all sites, even though there were small variations due to methodological differences. The limits of detection used, and the sites with samples below those limits are listed in Supplementary Material 2. Original data below the defined limit of detection were replaced with detection limit and zero for maximum and minimum stock calculations, respectively. All presented results are based on the maximum stocks if not otherwise stated. With deep soil profiles, small differences in concentrations can give large differences in stocks. Nine of the sites (Abr, Au1, Au2, Bon, Bre, Gem, Ita, Kon, and Vau) had mean EBC based on data including one to several values below limit of detection (Supplementary Material 2).

Sensitivity of sampling methods is also important when comparing nutrient stocks. For most sites, the difference between "maximum" (Supplementary Material 2) and "minimum" (0) limits of detection was small (Supplementary Material 3), often representing a small proportion of the total number of samples. The site with lowest EBC, Ita, displayed the largest difference between maximum and minimum EBC stocks for all depths (Supplementary Material 3), confirming that low, reliable detection limits are important for very poor deep soils.

2.2.3 Maximum available water storage

Soil water availability, part of soil physical fertility, partly determines nutrient transport and uptake by plants and thus influences soil chemical fertility. Precipitation ranged from 700 to 1900 mm year^{-1} depending on the site (Supplementary Material 1). Time series of soil water contents were not measured for all sites. To give an estimate of the amount of plant available water, we calculated maximum available water storage (mm, MAWS). For each site and soil layer, MAWS was calculated as available water (g 100 g^{-1}) multiplied by bulk density, percentage fine earth and thickness of the soil layer. Available water was defined as water content at pF 2.5 minus water content at pF 4.2, estimated for each soil textural class using data from Jamagne *et al*. (1977), cited in Baize (2000). For the Renecofor sites, estimated bulk densities for each soil textural class were used for the calculations of MAWS (Baize, 2000).

2.2.4 Standardized tree productivity index

The productivity of forest ecosystems expressed for example as the net primary production, the production of wood cubic volume (m^3 ha^{-1} yr^{-1}) or biomass (tons ha^{-1} yr^{-1}) is assumed to vary as a function of climate, soil fertility, tree species, tree age and forest management practices (stand density, thinning frequencies, etc.) (Schoenholtz *et al.*, 2000; Binkley and Fisher, 2012). In order to study the relationship between soil fertility and tree productivity, we selected a new index based on forest stand dominant height, which is assumed to not be influenced by forest management practices. To limit the influence of climate, the study sites were each assigned to an ecological region (Cavaignac, 2009): for each region, a maximum dominant height (H_{max}) for each of the different studied tree species and tree ages (±3 years) was determined using data from the French National Forest Inventory. H_{max} is assumed to account for the limitation of forest growth by the climatic conditions. The database used contains data from more than 32000 plots in France, divided into 11 ecological regions (Cavaignac, 2009). After filtering the data depending on species, age and region, we used data from 8640 of those plots. Dominant height in the data base was defined as the average of the three highest trees per plot.

The standardized tree productivity index was then built from the ratio between dominant height (H_0) at time of sampling on each plot and the maximum tree height (H_{max}) for the same age and tree species and climatic region. H_0:H_{max} ratios were then used as a reference (with standardized productivity considered to be highest at sites with H_0:H_{max} =1) for comparison of different possible indicators of chemical soil fertility, both individual parameters and combinations. Sites were ranked depending on their H_0:H_{max} ratio: very low (VL, H_0:H_{max} =0-0.6), low (L, H_0:H_{max} =0.61-0.7), medium (M, H_0:H_{max} =0.71-0.8), high (H, H_0:H_{max} =0.81-0.9) and very high (VH, H_0:H_{max} =0.91-1) fertility.

Regional H_{max} data for *A. nordmanniana* was not available, so H_0:H_{max} for that stand at Breuil was calculated using H_{max} from *A. alba*. At Ard, dominant height could not be retrieved for the *Q. petrea* stand, as it was not even-aged; H_0:H_{max} was assumed to be the same as for the adjacent spruce stands. The tropical sites should be considered separately, as also the studied control plots received small amounts of nutrients with basic fertilization (Table 2), leading to a higher fertility than would be the case without fertilization. However, the amounts of nutrients added were small and soil chemical analyses a few months after fertilizer addition did not show significant differences in soil properties between control and fertilized plots (Almeida, 2009). H_{max} for tropical sites was based on stands receiving fertilizer doses optimised for non-limiting tree growth.

2.2.5 Statistical analyses

Relationships between exchangeable/available and total elements were expressed through linear regressions. Correlation between H_0:H_{max} and climatic parameters, as well as between H_0:H_{max} and chemical soil properties at different soil depths, were tested (Kendall correlation, with pairwise deletion of missing data; XLSTAT 2013.3.04).

Principal component analyses (PCA, XLSTAT 2013.3.04) were used to identify the main variables discriminating sites and species. Several PCA based on different combinations of possible indicators were tested, to find the combinations of soil parameters that best explained stand productivity, expressed as H0:Hmax.

Lastly, we performed Random Forests (Breiman, 2001) to explore the relationship between the standardized tree productivity index and soil parameters . We used the package ‘RandomForest’ version 4.6-14 (R).

3 Results

3.1 Vertical distributions of elements in soil profiles

EBC concentrations across all the forest sites tended to decrease from the topsoil to the 10-30cm depth, and then increase again in deep soil layers (Fig. 2). TBC contents tended to increase with depth except at Kondi, the only tropical site represented, where TBC remained constantly low at all depths (data not shown).

Mean EBC stocks and rooting depth are presented in Figure 3 for the 11 sites with the full data set (9 French and 2 tropical sites). The soil depth including 95% of the fine roots (R95%) ranged from 40 to 160 cm for the temperate sites and reached a depth of 400 cm for tropical sites (Fig. 3a). Kon (Congo) had the third largest EBC stock down to R95%, with EBC stocks increasing from 10.5 $kmol_c$ ha^{-1} (0-70 cm) to 63.5 $kmol_c$ ha^{-1} (0-R95%). In general, the deeper the rooting depth, the larger the increase when comparing EBC stocks 0-70 cm soil depth versus 0-R95%. At Fou however, the large increase in EBC stock (from 27.5 $kmol_c$ ha^{-1} for 0-70 cm to 180 $kmol_c$ ha^{-1} for 0-R95%),was also caused by high nutrient concentrations in deep soil layers, as a result of high Mg contents in the bedrock (Legout, 2008).

Rooting depths and EBC stocks for each of the six species at the Bre site (25-year-old stands, central France) were highly dependent on the tree species (Fig. 3b). R95% ranged from 80 cm (beech, Douglas fir) to 130 cm (Norway spruce). Oak stands tended to have the largest EBC stock in the 0-70 cm soil layer, whereas spruce stands tended to have the largest stock down to R95%.

3.2 Relationship between different soil layers

For most soil parameters, there was a strong positive correlation between the upper soil layer (0-10 cm) and deeper layers across the 49 forest soils (Table 4 and Fig. 4). There were no significant correlations between variables in LFH and in the 0-10 cm layer, except for pH and total P_2O_5 stocks. The relationship between the 0-10cm depth and other depths (10-30cm, 30-70cm, 70-100cm) was clear, which is also supported by the high and significant correlation coefficients (Table 4).

3.3 Relationships between soil parameters

Despite the diversity of forest ecosystems studied, most of the soil parameters commonly measured in soil analyses were strongly correlated (Supplementary Material 4). The C:N ratio was negatively correlated (Kendall) with most other soil parameters, except stocks of N, available P_2O_5, exchangeable K and Na and BS. N was positively correlated with all other elements except exchangeable Na. EBC was positively correlated to all other parameters, except pH, which was not significantly correlated, and C:N, which was negatively correlated with EBC. BS was significantly correlated with most other parameters, except C:N, and exchangeable Na and Mn.

Correlations between exchangeable elements (K, Na, Ca, and Mg) were always positive and significant, as well as correlations between available/exchangeable and total elements (Supplementary Material 4).

When stocks of elements from all 11 sites with available total elements data were plotted together, the relationship was weak (R^2=0.3-0.5), whereas the relationship tended to be stronger within each site. R^2 between exchangeable and total Ca ranged from 0.6 to 0.99 in individual sites, except for Bon and Au2, where the relationship was weak (Fig. 5, R^2=0.53 when comparing 11 sites). A strong relationship could also be found between available and total P, with R^2=0.42 when comparing all sites, while R^2 ranged from 0.72 to >0.99 when the sites were plotted separately (Fig. 5).

3.4 Relationship between H_0:H_{max} and soil chemical parameters

The soil fertility of the sites was first ranked based on H_0:H_{max}, and then compared with soil chemical fertility indicators such as C:N ratio, pH, stocks of EBC and P (Fig. 6). The H_0:H_{max} index ranged from 0.5 to 1.0 across the 49 study sites. Some of the tested soil chemical parameters were significantly correlated with H_0:H_{max} (Table 5), but the correlations were weak.

C:N ratios were not significantly correlated with H_0:H_{max} in any soil layer, although both C and N stocks down to 70 cm depth were negatively correlated with H_0:H_{max} (Table 5, Fig. 6). By contrast, H_0:H_{max} was positively correlated (R = 0.2 – 0.3) with soil pH and BS, whatever the layer in the mineral soil, across the 49 sites. Surprisingly, the correlation between H_0:H_{max} and Avail. P_2O_5 was negative.

Principal component analysis was used to identify the most relevant variables explaining the productivity differences (expressed as H_0:H_{max}). The PCA carried out with C, N, pH, exchangeable Ca, K and Mg and available P_2O_5 in the 0-10 cm mineral soil layer as input variables was the best fitted PCA: the first three axes of the PCA explained 85.2% of the variability. Fig. 7 (a) shows the position of the different sites in the space formed by PCA components 1 and 2. No single variable explained more than 20% of the variability on the first axis (data not shown), confirming that soil fertility was a result of many different components. With another PCA, including C:N, pH, EBC and available P_2O_5 in the 0-10 cm soil layer, the first two axes explained 64.79% of the variability (Fig. 7 b).

3.5 Relationship between H_0:H_{max} and other parameters

H_0:H_{max} was slightly correlated (Kendall, $p<0.05$) with elevation ($R=-0.18$) and temperature ($R=0.32$), and also precipitation($R=-0.19$) when only comparing temperate sites (Fig. 8). By contrast, H_0:H_{max} was not correlated with rooting depth, MAWS and stand age. Mean temperature and precipitation ranged respectively from 4.9 to 8.5 °C and from 703 to 1894 mm yr^{-1}. MAWS ranged from 32 to 484 mm, R95% from 40 to 400 cm depth, elevation ranged from 50 to 1400 m and stand age ranged from 1 to 400 years.

4 Discussion

4.1 Changes in chemical properties throughout soil profiles

4.1.1 Relationship between total and exchangeable/available elements

Total and exchangeable (or available) elements in the soil were generally significantly positively correlated. Despite the high variability, the sites with the highest content of total elements generally had the highest content of exchangeable (or available) elements, as reported by other authors (Mareschal *et al.*, 2015; Porder *et al.*, 2015; Wuenscher *et al.*, 2015). Several studies suggested that the main factors controlling the size of nutrient pools in a soil at a given time were the chemical composition of the parental material and the extent of weathering of primary minerals (e.g. Schlesinger, 1997; Giehl and von Wirén, 2014). Mineralogy is a key parameter and when minerals containing K, Ca, Mg or P are abundant in a layer, weathering may resupply the exchangeable/available pools. In the frame of our study, we concluded that we could either use total or exchangeable elements as indicators and both gave broadly similar results (especially using PCA).

4.1.2 Forest floor and topsoil as relevant proxies for the entire soil profile?

Forest floor properties are easier to measure than mineral soil properties, making them potentially interesting as indicators (Velasquez *et al.*, 2007, Ponge et al, 2014). However, the link between physico-chemical properties of the forest floor and site fertility (expressed as H_0:H_{max}) was not significant in our study and most of the carbon and nutrient stocks in the forest floor were not correlated with the pools in the mineral soil. Weak correlations between the mineral soil and the forest floor have sometimes been reported in the literature for pH, base saturation and nutrient contents between the mineral soil and the forest floor but the lack of common agreement among studies suggests complex relationships and feedbacks between these two contiguous compartments of the ecosystem (Legout *et al.*, 2008; Ponge, 2013), which our results appear to confirm. A distinction between forest floor layers, an integration of biological and morphological criterions to account for the dynamic behaviour of the forest floor, as well as a division of the topsoil in thinner layers might be useful to a clearer to find relationship with soil parameters.

In contrast, the relationships between the topsoil (0-10 cm depth) and deeper soil layers were generally significant. The relationships became weaker with increasing depth probably due to the vertical distribution of available nutrients in the upper meter of soil: accumulation in the topsoil and at some sites in deep soil layers. The constant interaction of biogeochemical processes, such as weathering, atmospheric deposition, nutrient leaching, and biological cycling, lead to the formation of vertical and horizontal nutrient gradients within the soil (Giehl and von Wirén, 2014). In our study, the accumulation observed in the topsoil may be mainly attributed to plant cycling (through litterfall, fine root turnover, OM accumulation in the topsoil increasing the CEC, etc...). Jobbagy and Jackson (2001) compared soil exchangeable/available nutrient distributions with depth on a global scale, and showed that topsoil concentrations of elements were higher in the poorest soils. Furthermore, nutrients strongly cycled by plants, such as K and P, were more concentrated in the topsoil than elements less taken up by plants, such as Na (Jobbágy and Jackson, 2001; Jobbágy and Jackson, 2004). This was not always the case in our study, where the ratios between stocks of exchangeable Ca, K and Mg in 0-10 cm and 30-70 cm soil layers were 0.59, 0.43 and 0.61, respectively, while the ratio was only 0.25 for available P. The large accumulation in the deep soil layers at some sites may be mainly attributed to the richness of the parent material (presence of minerals bearing nutrients and high weatherability). Our study suggests that topsoil properties could be used as a proxy of soil properties throughout the whole profile (at least down to 70cm), but a particular attention must be given to the soil depth explored by tree roots, especially when working with stocks of element.

4.2 Importance of soil depth

Our results show that the available nutrient pools in deep soils (>1m) can be several times larger than what is suggested by shallow soil sampling, in agreement with other studies (Bond, 2010; Wigley *et al.*, 2013). Even though most roots are in the upper part of the soil profile, sampling deep soil layers is necessary to estimate correctly nutrient stocks because deep roots, although less abundant than in the topsoil, can be very important for nutrient uptake, especially when water stress occurs in the upper soil layers (reviewed by Kautz *et al.*, 2013). In a study at 5 arid and semi-arid sites, McCulley *et al.* (2004) showed that total amounts and concentrations of nutrients in depth were frequently as high (or higher) than in the first meter of soil and suggested that deep soil layers can represent an important source of plant nutrients. In *Eucalyptus* stands in Ita, Brazil, 95 % of the roots were in the upper 5 m soil depth at the end of the silvicultural rotation, whereas the depth of the root front was 16 m (Christina *et al.*, 2011). A decrease in soil water content at 10 m depth with increased stand age (and rooting depth) indicated that deep roots may be important for water uptake, but less is known about nutrient uptake (Christina *et al.*, 2018). A recent study showed that a $^{15}N\text{-}NO_3^-$ tracer injected at a depth of 6 m was taken by dominant *Eucalyptus grandis* trees (but not by suppressed trees) the first year after planting in monoclonal stands (Pinheiro *et al.*, 2019).

The role of deep roots to supply plant nutrient requirements has been little studied and is difficult to demonstrate since root foraging in the deepest layers can be multi-causal (water supply, specific nutrient deficiency etc...). Several studies showed nutrient uptake by trees from deep soil layers: Göransson et al. (2008) for N and Cs (analogue to K) in *Quercus robur*, *Fagus sylvatica* and *Picea abies* trees, Drouet et al. (2015) for Sr (Ca analogue) in *F. sylvatica* trees in Belgium, Bedel et al. (2015) for Sr (Ca analogue) in mixed broadleaf forest in France or da Silva et al. (2011) for Rb and Sr (analogues of K and Ca, respectively) in *E. grandis* in Brazil. However, the quantitative contribution of these deep layers to plant nutrition and tree productivity is unknown and further studies need to be conducted. Similarly, the role of rhizospheric soil volume versus the entire soil volume (Gobran et al, 1998), as well as the role of coarse soil fraction commonly excluded from soil analysis (Smail et al, 2014) should be further refined.

4.3 Soil chemical parameters as relevant indicators of tree productivity?

4.3.1 Single indicators

All the static soil chemical parameters used in our study were chosen from Schoenholtz et al. (2000) because they are commonly used to evaluate fertility, most of the times at a local scale (i.e. plot, forest or small territory). Our results demonstrated that although a single indicator may be relevant at a local scale, that is not necessarily the case at a larger scale, where many other factors can have a strong influence on tree productivity. Indeed, insignificant or weak relationships were found between H_0:H_{max} and all the soil parameters and the variability observed at each fertility level was large.

The C:N ratio is an often suggested as a possible fertility indicator (Schoenholtz *et al.*, 2000). In our study, the correlations between the C:N ratio and other soil parameters were often significant while they were not significant with H_0:H_{max}. C:N ratios decrease during organic matter decomposition, and materials with an initially high C:N value ("low quality") may reach low C:N ratios in later stages of decomposition (e.g. Johnson, 2010). This evolution, coupled with different organic matter quality, may partly explain why this indicator is less accurate at a global scale, although it may be interesting, combined with other factors.

Exchangeable or available elements as well as soil pH are also often suggested as fertility indicators. EBC in the mineral soil was not significantly correlated with H_0:H_{max} and some sites with among the smallest EBC stocks had very high H_0:H_{max}, suggesting that other factors compensated for their low soil nutrient content. Using EBC in the mineral soil as a fertility indicator ranked the tropical sites as among the least fertile; conversely, when using pH as a fertility indicator, these highly weathered soils were by contrast ranked among the most fertile, having comparatively high pH values. However, the processes explaining the pH values are very different in tropical and temperate soils, making comparisons difficult, and soils with low pH can be productive. The positive correlation between pH and H_0:H_{max} is weak but still significant when removing the tropical sites. Correlations between H_0:H_{max} and BS or the Ca:Al ratio, also suggested as possible indicators of soil fertility (Cronan and Grigal, 1995), were also positive and significant. However, as for pH, the variability was high which makes all these indicators little relevant across the sites.

Available P_2O_5 and exchangeable K were significantly negatively correlated with H_0:H_{max}. Mineralogy of parental material may partly explain this trend and these elements were probably not the most limiting growth factors in many situations. However, caution is required because plant nutrient limitation may often be a problem of effective availability in the rhizosphere, rather than low nutrient stocks in the bulk soil, as reviewed by Giehl and von Wirén (2014).

4.3.2 Combination of soil chemical parameters

Although it was possible to split the entire population, fertility classes based on the H_0:H_{max} index (VL, L, M, H, VH) overlapped widely in the different planes of the PCA. Other combinations of soil parameters also resulted in similar PCA results (data not shown), confirming that many soil properties are closely related, also shown by the correlations between parameters. Few studies (e.g. Schoenholtz *et al.*, 2000; Bautista-Cruz *et al.*, 2012; Bikindou *et al.*, 2012) have used a combination of soil parameters to evaluate the specific role of chemical properties on tree productivity, as huge databases are needed at large scale, which is expensive and time consuming. Although this approach is cumbersome, our results on a large number of acidic soils demonstrate that tree productivity cannot be simply described using linear combinations of chemical properties of soils. Moreover, random Forests performed on our data set to predict H0:Hmax show that less than 15% of the variance was explained by the studied soil parameters (Supplementary Material 5).

4.4 Limits and potential role of other factors

Our results reinforce the idea that the influence of the soil chemical fertility on stand productivity is complex and the soil chemical parameters alone (individually or combined) were poor predictors of tree productivity as assessed by the H_0:H_{max} index. Many other factors listed below and partly covered in this study may explain part of the inter-site variability of tree productivity and could therefore partly mask or dilute the link between the soil parameters and tree productivity.

Firstly, the productivity is also a function of physical and biological components of soil fertility (Fig. 1). The physical component of the fertility has been integrated in our study through bulk density, MAWS and soil texture (silt, sand, clay) at different soil depths. However, the correlations between these soil physical parameters and H_0:H_{max} were not significant (except clay content at 0-10 cm soil depth) and the importance of these variables as measured by random Forests was low (Supplementary Material 5). Biological fertility properties were not included in our data set, so that component of soil fertility could not be tested.

Secondly, although the use of a standardized tree productivity index made it possible to focus on the influence of soil chemical parameters, there was still weak but significant correlations between H_0:H_{max} and temperature and elevation. Even though the data was divided into 11 ecological regions, there was still variability within each region. However, the size of our dataset does not enable to untangle the role of climate at a more detailed geographical scale. It may also be noted that the results of Random Forests show the limited effect of climate on H_0:H_{max} (Supplementary Material 5). High elevation (> 1000m) and low temperatures (Supplementary Material 1) may partly explain the low H_0:H_{max} ratios observed at some sites. The relationship between H_0:H_{max} and MAWS was not significant but low precipitation in combination with low MAWS (Fig. 8) may lead to water deficiency (and reduced nutrient availability), especially in warmer/drier climatic regions where evapotranspiration is high and drought periods are common. However, water deficiency cannot be the only explanation to the low observed H_0:H_{max} ratios (e.g. the tropical sites have a high H_0:H_{max} even though water deficiency may occur during the dry season).

Thirdly, tree requirements and resource-use strategies could also partly explain the discrepancies between soil chemical parameters and the standardized tree productivity index. H_0:H_{max} was not designed to completely account for possible differences in nutrient requirements between tree species or stand ages. For instance, the H_0:H_{max} response to decreasing nutrient availability in the soil may vary between tree species. However, even if nutrient contents in aerial biomass are usually higher for hardwood species than for coniferous species, the coniferous species produce more biomass and their rotation lengths are shorter than hardwood species (Binkley, 1995; Augusto *et al.*, 2002b). In other words, though biomass increment may be greater for coniferous species, the nutrient uptake flux may be similar between hardwood and coniferous species. It is thus not possible to rank the species in the order of nutritional requirements and studying each species separately was not an option, since the data sets would then be too small. The resource-use strategies could also be different between tree species due to their autecology, as well as within a tree species in response to environmental constraints (e.g. soil compaction, water deficit…). Depending on the distribution of roots in the soil, a variable fraction of nutrient uptake may originate from the deep soil layers (Turpault *et al.*, 2005; Mareschal *et al.*, 2013). During short dry periods, internal remobilization and uptake of more energetically fixed water with a different chemical composition than gravitational soil solutions may differ between tree species (Silla and Escudero, 2003). Nutrients released from the forest floor could also be taken up directly by trees, without replenishing the soil reservoir in the most extreme case (Laclau *et al.*, 2004). At tropical sites but also at some temperate sites, a large share of soil fertility can be contained in the forest floor. Indeed, N stocks in the humus layer accounted for 74 % of those in the 0-10 cm soil layer at Kon (294 vs. 400 kg ha^{-1}) compared to on average 40 % in the temperate soils. A rapid and efficient turnover of nutrient stocks may thus contribute to a mismatch between high biomass productions at these sites despite low nutrient stocks in the mineral soil. All these strategies and mechanisms are not considered when using static soil indicators, which could partly explain that they are poor predictors of tree productivity.

Lastly, past land use may also have a large impact on soil parameters (Dupouey *et al.*, 2002; Dambrine *et al.*, 2007) and tree productivity but too few data were available to investigate this effect. Seasonal variation of soil nutrient pools and fluxes is also an important aspect of soil heterogeneity (Farley and Fitter, 1999; Devi and Yadava, 2006), not taken into account in our study due to the lack of information on exact sampling date and spatial variation for most data.

5 Conclusions

We used a standardized tree productivity index (H0:Hmax) to investigate the specific influence of soil chemical properties on standardized tree productivity. Our results show that none of the common soil chemical parameters tested in this paper can alone predict stand productivity. Combinations of soil parameters could better explain the variability of the dataset (using PCA analysis) but were unable to separate the sites depending on the standardized tree productivity index. Different combinations of parameters gave similar results, suggesting that all soil chemical parameters are interdependent and that the relationship between soil parameters and productivity is complex. Other parameters (e.g. climate and elevation) may sometimes help understanding the productivity, but a large share of the variability observed is not understood, suggesting that other parameters, not included in this study, may also control the productivity.

In this paper we focused on static indicators, such as single measurements of soil chemical properties over a broad range of forest ecosystems, whereas more dynamic indictors, such as nutrient fluxes and cycling are probably needed to better explain and link static indicators with growth at sites differing in productivity. Contrary to our hypothesis, forests growing on soils with the lowest nutrient stocks did not always exhibit the lowest index of productivity (H_0:H_{max}). We suggest that the importance of different components of the biogeochemical cycles may vary in poor and rich soils: biological cycling can be a main source of nutrients in stands with low soil nutrient contents, whereas weathering and uptake from mineral soil can be predominant in stands with higher soil nutrient content. Considering this concept, static soil indicators, such as exchangeable or total element stocks, could well describe site fertility in ecosystems with high nutrient stocks, but could be misleading in ecosystems dominated by biological cycling. A companion paper (Legout *et al.*, Submitted) focuses on the connection between standardized tree productivity and different components of the biogeochemical cycle, using data from 11 sites presented in this paper.

6 Acknowledgements

We gratefully acknowledge the financial support received from the Office National des Forêts, the Région Lorraine, GIP ECOFOR, the FEDER and the LTER-ZAM (Zone Atelier Moselle). The BEF unit is supported by the French National Research Agency through the Laboratory of Excellence ARBRE (ANR-12-LABXARBRE-01). We thank all who contributed with data to this study: J. C. R. Almeida, E. Dambrine, A. El Gh'Mari, A. Ezzaïm, J. Fichter, J.L.M. Gonçalves, V. Maquere, R. Marques, D. Mohamed Ahamed, M.-P. Turpault, A. Versini and others. We also thank Alex Salaz Lopes for his initial work on the data base used in this study. Thanks to Institute National de l'Information Géographique et Forestière for making regional height data available for our study.

References

Achat, D.L., Deleuze, C., Landmann, G., Pousse, N., Ranger, J., Augusto, L., 2015. Quantifying consequences of removing harvesting residues on forest soils and tree growth – A meta-analysis. For. Ecol. Manage. 348, 124-141.

Aertsen, W., Kint, V., De Vos, B., Deckers, J., Van Orshoven, J., Muys, B., 2012. Predicting forest site productivity in temperate lowland from forest floor, soil and litterfall characteristics using boosted regression trees. Plant Soil 354, 157-172.

Almeida, J.C.R., 2009. Nutrição, crescimento, eficiência de uso de água e de nutrientes em povoamentos de Eucalyptus grandis fertilizados com potássio e sódio. In. University of Sao Paulo, Brazil, p. 112.

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002a. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59, 233-253.

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002b. Impact of several common tree species of European temperate forests on soil fertility. Annals of Forest Science 59, 233-253.

Baize, D., 2000. Guide des analyses en pédologie. INRA, Paris.

Bastida, F., Zsolnay, A., Hernández, T., García, C., 2008. Past, present and future of soil quality indices: A biological perspective. Geoderma 147, 159-171.

Bautista-Cruz, A., del Castillo, R.F., Etchevers-Barra, J.D., Gutiérrez-Castorena, M.d.C., Baez, A., 2012. Selection and interpretation of soil quality indicators for forest recovery after clearing of a tropical montane cloud forest in Mexico. For. Ecol. Manage. 277, 74-80.

Bedel, L., Poszwa, A., van der Heijden, G., Legout, A., Aquilina, L., Ranger, J., 2015. Unexpected calcium sources in deep soil layers in low-fertility forest soils identified by strontium isotopes (Lorraine plateau, eastern France).

Bikindou, F.D.A., Gomat, H.Y., Deleporte, P., Bouillet, J.-P., Moukini, R., Mbedi, Y., Ngouaka, E., Brunet, D., Sita, S., Diazenza, J.-B., Vouidibio, J., Mareschal, L., Ranger, J., Saint-André, L., 2012. Are NIR spectra useful for predicting site indices in sandy soils under Eucalyptus stands in Republic of Congo? For. Ecol. Manage. 266, 126-137.

Binkley, D., 1995. The influence of Tree Species on Forest Soils : Processes and Patterns. In: Mead, D.J., Cornforth, I.S. (Eds.), Proceedings of the Trees and Soil Workshop, Lincoln University 28 February - 2 March 1994. Lincoln University Press, Canterbury.

Binkley, D., Fisher, R.F., 2012. Ecology and Management of Forest Soils. Wiley, New York.

Bond, W., 2010. Do nutrient-poor soils inhibit development of forests? A nutrient stock analysis. Plant Soil 334, 47-60.

Bonneau, M., Levy, G., Montpied, P., 2003. Évaluation de la pertinence des deux méthodes d'analyse du phosphore dans les sols forestiers. Rev. for. fr. 55, 57-64.

Bontemps, J.D., Bouriaud, O., 2014. Predictive approaches to forest site productivity: recent trends, challenges and future perspectives. Forestry 87, 109-128.

Breiman, L., 2001. Random Forests. Machine Learning 45, 5-32.

Cavaignac, S., 2009. Les sylvoécorégions (SER) de France métropolitaine. Étude de définition. Inventaire Forestier National.

Christina, M., Laclau, J.P., Gonçalves, J., Jourdan, C., Nouvellon, Y., Bouillet, J.P., 2011. Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. Ecosphere 2.

Christina, M., le Maire, G., Nouvellon, Y., Vezy, R., Bordon, B., Battie-Laclau, P., Goncalves, J.L.M., Delgado-Rojas, J.S., Bouillet, J.P., Laclau, J.P., 2018. Simulating the effects of different potassium and water supply regimes on soil water content and water table depth over a rotation of a tropical Eucalyptus grandis plantation. Forest Ecology and Management 418, 4-14.

Cronan, C.S., Grigal, D.F., 1995. Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. Journal of Environmental Quality 24, 209-226.

da Silva, E.V., Bouillet, J.-P., de Moraes Gonçalves, J.L., Junior, C.H.A., Trivelin, P.C.O., Hinsinger, P., Jourdan, C., Nouvellon, Y., Stape, J.L., Laclau, J.-P., 2011. Functional specialization of Eucalyptus fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. Funct. Ecol. 25, 996-1006.

da Silva, F.C., van Raij, B., 1999. Phosphorus availability in soils, determined by different extracting procedures. Pesqui. Agropecu. Bras. 34, 267-288.

Dambrine, E., Dupouey, J.L., Laüt, L., Humbert, L., Thinon, M., Beaufils, T., Richard, H., 2007. Biodiversity patterns in present French forests related to former Roman agriculture. Ecology 88, 1430-1439.

Devi, N.B., Yadava, P.S., 2006. Seasonal dynamics in soil microbial biomass C, N and P in a mixed-oak forest ecosystem of Manipur, North-east India. Appl. Soil Ecol. 31, 220-227.

Drouet, T., Herbauts, J., Demaiffe, D., 2015. Influence of deep soil horizons on Ca nutrition of forest stands along a loessic soil sequence. Plant and Soil, 1-17.

Duchaufour, P., Bonneau, M., 1959. Une nouvelle méthode de dosage du phosphore assimilable dans les sols forestiers. Bull. Afes 4, 193-198.

Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83, 2978-2984.

Dyer, B., 1894. XV.-On the analytical determination of probably available "mineral" plant food in soils. J. Chem. Soc., Trans. 65, 115-167.

Farley, R.A., Fitter, A.H., 1999. Temporal and spatial variation in soil resources in a deciduous woodland. J. Ecol. 87, 688-696.

Fernández-Ondoño, E., Rojo Serrano, L., Jiménez, M., Navarro, F., Díez, M., Martín, F., Fernández, J., Martínez, F., Roca, A., Aguilar, J., 2010. Afforestation improves soil fertility in south-eastern Spain. Eur. J. For. Res. 129, 707-717.

Fichter, J., Turpault, M.-P., Dambrine, E., Jacques, R., 1998. Localization of base cations in particle size fractions of acid forest soils (Vosges Mountains, N-E France). Geoderma 82, 295-314.

Garcia, W.D., Amann, T., Hartmann, J., 2018. Increasing biomass demand enlarges negative forest nutrient budget areas in wood export regions. Scientific Reports 8, 7.

Gartzia-Bengoetxea, N., González-Arias, A., Kandeler, E., Arano, I., 2009. Potential indicators of soil quality in temperate forest ecosystems: a case study in the Basque Country. Ann. For. Sci. 66, 303-303.

Giehl, R.F., von Wirén, N., 2014. Root nutrient foraging. Plant Physiology 166, 509-517.

Göransson, H., Ingerslev, M., Wallander, H., 2008. The vertical distribution of N and K uptake in relation to root distribution and root uptake capacity in mature *Quercus robur*, *Fagus sylvatica* and *Picea abies* stands. Plant Soil 306, 129-137.

Jamagne, M., Bétrémieux, R., Bégon, J., Mori, A., 1977. Quelques données sur la variabilité dans le milieu naturel de la réserve en eau des sols. Bull. Tech. Inf 324-325, 627-641.

Jobbágy, E.G., Jackson, R.B., 2001. The distribution of soil nutrients with depth: Global patterns and the imprint of plants. Biogeochemistry 53, 51-77.

Jobbágy, E.G., Jackson, R.B., 2004. The uplift of soil nutrients by plants: biogeochemical consequences across scales. Ecology 85, 2380-2389.

Johnson, D.W., 2010. Soil quality: Some basic considerations and case studies. In: Page-Dumroese, D., Neary, D., Trettin, C. (Eds.), Scientific Background for Soil Monitoring on National Forests and Rangelands: workshop proceedings, Denver, pp. 1-12.

Joret, G., Hébert, J., 1955. Contribution à la détermination du besoin des sols en acide phosphorique. In, Ann. Agron., pp. 233-299.

Kalliokoski, T., Pennanen, T., Nygren, P., Sievänen, R., Helmisaari, H.S., 2010. Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. Plant Soil 330, 73-89.

Kautz, T., Amelung, W., Ewert, F., Gaiser, T., Horn, R., Jahn, R., Javaux, M., Kemna, A., Kuzyakov, Y., Munch, J.-C., Pätzold, S., Peth, S., Scherer, H., Schloter, M., Schneider, H., Vanderborght, J., Vetterlein, D., Walter, A., Wiesenberg, G.L.B., Köpke, U., 2013. Nutrient acquisition from arable subsoils in temperate climates: A review. Soil Biology and Biochemistry 57, 1003-1022.

Laclau, J.-P., Ranger, J., de Moraes Gonçalves, J.L., Maquère, V., Krusche, A.V., M'Bou, A.T., Nouvellon, Y., Saint-André, L., Bouillet, J.-P., de Cassia Piccolo, M., Deleporte, P., 2010. Biogeochemical cycles of nutrients in tropical *Eucalyptus* plantations: Main features shown by intensive monitoring in Congo and Brazil. For. Ecol. Manage. 259, 1771-1785.

Laclau, J.P., Toutain, F., M'Bou, A.T., Arnaud, M., Joffre, R., Ranger, J., 2004. The function of the superficial root mat in the biogeochemical cycles of nutrients in Congolese Eucalyptus plantations. Annals of Botany 93, 249-261.

Legout, A., 2008. Cycles biogéochimiques et bilans de fertilité minérale en hêtraies de plaine. In, Institute des Scineces et Industries du Vivant et de l'Environnement. AgroParisTech.

Legout, A., Hansson, K., van Der Heijden, G., Laclau, J.P., Mareschal, L., Nys, C., Nicolas, M., Saint Andre, L., Ranger, J., Submitted. Chemical fertility of forest ecosystems. Part 2: Towards redefining the concept by untangling the role of the different components of biogeochemical cycling. Forest Ecology and Management.

Legout, A., Walter, C., Nys, C., 2008. Spatial variability of nutrient stocks in the humus and soils of a forest massif (Fougères, France). Ann. For. Sci. 65, 108-108.

Mareschal, L., Laclau, J.P., Nzila, J.D.D., Versini, A., Koutika, L.S., Mazoumbou, J.C., Deleporte, P., Bouillet, J.P., Ranger, J., 2013. Nutrient leaching and deep drainage under Eucalyptus plantations managed in short rotations after afforestation of an African savanna: Two 7-year time series. For. Ecol. Manage. 307, 242-254.

Mareschal, L., Turpault, M., Ranger, J., 2015. Effect of granite crystal grain size on soil properties and pedogenic processes along a lithosequence. Geoderma 249, 12-20.

Mathieu, C., Pieltain, F., 2003. Analyse chimique des sols. Méthodes choisies.

McCulley, R., Jobbágy, E., Pockman, W., Jackson, R., 2004. Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. Oecologia 141, 620-628.

Pinheiro, R.C., Bouillet, J.P., Bordron, B., Alo, L.L., Costa, V.E., Alvares, C.A., Van den Meersche, K., Stape, J.L., Guerrini, I.A., Laclau, J.P., 2019. Distance from the trunk and depth of uptake of labelled nitrate for dominant and suppressed trees in Brazilian Eucalyptus plantations: Consequences for fertilization practices. Forest Ecology and Management 447, 95-104.

Ponge, J.-F., 2013. Plant–soil feedbacks mediated by humus forms: A review. Soil Biology and Biochemistry 57, 1048-1060.

Porder, S., Johnson, A.H., Xing, H.X., Brocard, G., Goldsmith, S., Pett-Ridge, J., 2015. Linking geomorphology, weathering and cation availability in the Luquillo Mountains of Puerto Rico. Geoderma 249, 100-110.

Ranger, J., Turpault, M.P., 1999. Input-output nutrient budgets as a diagnostic-tool for the sustainability of forest management. Forest Ecology and Management 122, 7-16.

Rousseau, L., Fonte, S.J., Téllez, O., van der Hoek, R., Lavelle, P., 2013. Soil macrofauna as indicators of soil quality and land use impacts in smallholder agroecosystems of western Nicaragua. Ecol. Indic. 27, 71-82.

Schmitz, A., Sanders, T.G.M., Bolte, A., Bussotti, F., Dirnbock, T., Johnson, J., Penuelas, J., Pollastrini, M., Prescher, A.K., Sardans, J., Verstraeten, A., de Vries, W., 2019. Responses of forest ecosystems in Europe to decreasing nitrogen deposition. Environmental Pollution 244, 980-994.

Schoenholtz, S.H., Miegroet, H.V., Burger, J.A., 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. For. Ecol. Manage. 138, 335-356.

Schroth, G., Sinclair, F.L., 2003. Trees, crops and soil fertility: concepts and research methods. CABI.

Silla, F., Escudero, A., 2003. Uptake, demand and internal cycling of nitrogen in saplings of Mediterranean *Quercus* species. Oecologia 136, 28-36.

Stork, N.E., Eggleton, P., 1992. Invertebrates as determinants and indicators of soil quality. Am. J. Altern. Agric. 7, 38-47.

Thiffault, E., Bechard, A., Pare, D., Allen, D., 2015. Recovery rate of harvest residues for bioenergy in boreal and temperate forests: A review. Wiley Interdiscip. Rev. Energy Environ. 4, 429-451.

Turpault, M.P., Utérano, C., Boudot, J.P., Ranger, J., 2005. Influence of mature Douglas fir roots on the solid soil phase of the rhizosphere and its solution chemistry. Plant Soil 275, 327-336.

van Raij, B., Feitosa, C.T., Silva, N.M.d., 1984. Comparison of four extractors of soil phosphorus. Bragantia 43, 17-29.

Velasquez, E., Lavelle, P., Andrade, M., 2007. GISQ, a multifunctional indicator of soil quality. Soil Biol. Biochem. 39, 3066-3080.

Wall, A., 2012. Risk analysis of effects of whole-tree harvesting on site productivity. For. Ecol. Manage. 282, 175-184.

Wigley, B.J., Coetsee, C., Hartshorn, A.S., Bond, W.J., 2013. What do ecologists miss by not digging deep enough? Insights and methodological guidelines for assessing soil fertility status in ecological studies. Acta Oecol. 51, 17-27.

Wuenscher, R., Unterfrauner, H., Peticza, R., Zeheneter, F., 2015. A comparison of 14 soil phosphorus extraction methods applied to 50 agricultural soils from Central Europe. Plant Soil Environ 61, 86-96.

Figure list

Figure 1. Schematic overview of soil fertility, defined by biological, chemical and physical properties.

Figure 2. Box plots of exchangeable base cation (EBC) content (cmol$_c$ kg^{-1}) across 49 forest sites. Outliers are in blue and the red crosses represent the mean values. For the 70-100 cm depth, the maximum value (11.3 cmol$_c$ kg^{-1}) is not shown.

Figure 3. Mean EBC stocks (kmol$_c$ ha^{-1}, left axis) and rooting depth (R95%, cm, right axis) at 11 sites (a) and at the Bre site (b), all species, 25-year-old stands.

Figure 4. Relationship between available P_2O_5 pools (kg ha^{-1}) at 0-10 cm depth and in soil layers 10-30 cm, 30-70 cm and 70-100 cm (a) and EBC stocks (kmol$_c$ ha^{-1}) at 0-10 cm depth and in soil layers 10-30 cm, 30-70 cm and 70-100 cm (b) across 49 forest sites.

Figure 5. Relationship between exchangeable and total Ca (a) and between available and total P_2O_5 (b). Mean values (kg ha^{-1}) for each soil layer in each site are used (11 sites are included).

Figure 6. Relationship between a site productivity index (H_0:H_{max}) and soil pH, soil C:N, C (kg ha^{-1}), N (kg ha^{-1}), exchangeable Ca (kg ha^{-1}), exchangeable Mg (kg ha^{-1}), exchangeable K (kg ha^{-1}) and available P_2O_5 (kg ha^{-1}) stocks for different soil layers (0-10 cm, 10-30 cm, 30-70 cm and 70-100 cm) across 49 forest sites.

Figure 7. Principal component analysis of soil pH, C, N, available P_2O_5, exchangeable Ca, K and Mg (a) and C:N, EBC, available P_2O_5, and soil pH (b) at 0-10 cm depth in the mineral soil. Soil data are represented with grey lines and fertility with black lines. The distribution of all samples is labeled depending on fertility (expressed as H0:Hmax, with VL=very low, L=low, M=medium, H=high, VH=very high fertility).

Figure 8. Relationship between site index (H_0:H_{max}) and temperature (left axis, °C) and precipitation (right axis, mm) (a), maximum available water storage (left axis, MAWS, mm) and rooting depth (right axis, R95%, cm) (b) or elevation (left axis, m.a.s.l) and stand age (right axis, year) (c) at the 47 temperate sites.

Table list

Table 1. Basic information about the studied sites. Sites in bold have more complete data sets and are included in the companion paper Legout et al (submitted). More details about the stands are shown in Table A.2.

Table 2. Amounts of fertilizers applied in the tropical stands, and year of treatment and soil sampling.

Table 3. Summary of the soil analysis methods used

Table 4. Correlation (Kendall, $p<0.0001$) between the 0-10 cm layer and other soil depths, n.s. = not significant, n.a. = no data available. Data from 49 sites were computed except for total elements (11 sites).

Table 5. Correlation (Kendall) between $H_0:H_{max}$ and soil chemical properties in soil layers 0-10 cm, 10-30 cm, 30-70 cm and 70-100 cm across 49 field sites. n.s. = not significant ($p>0.05$).

Figure 1.

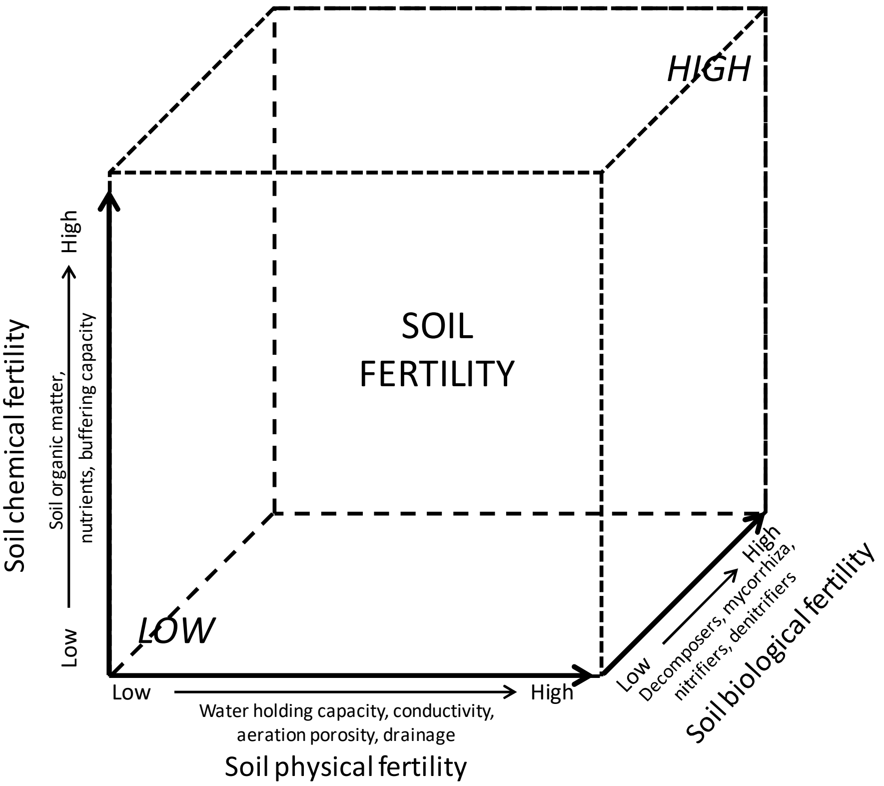
HIGH
SOIL
FERTILITY
LOW
Soil chemical fertility
Low
Soil organic matter,
nutrients, buffering capacity
High
Low
High
Water holding capacity, conductivity,
aeration porosity, drainage
Soil physical fertility
Low
Decomposers, mycorrhiza,
nitrifiers, denitrifiers
High
Soil biological fertility

Figure 2.

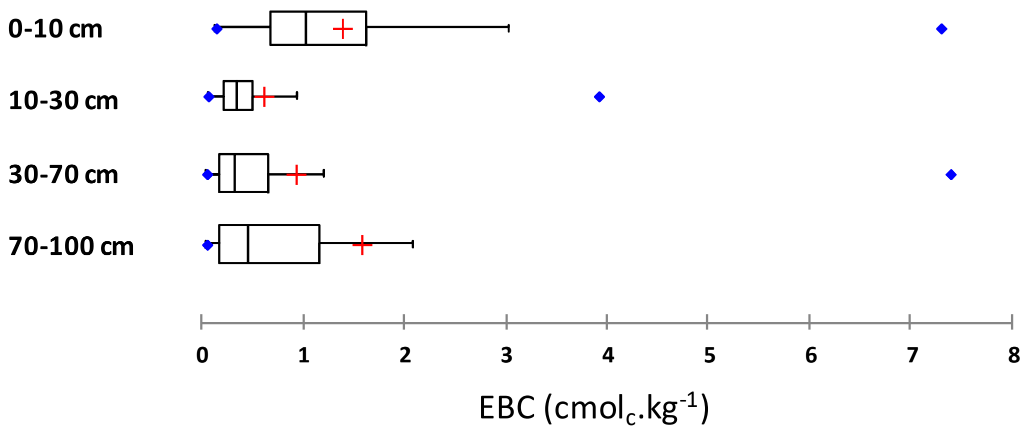

Figure 3.

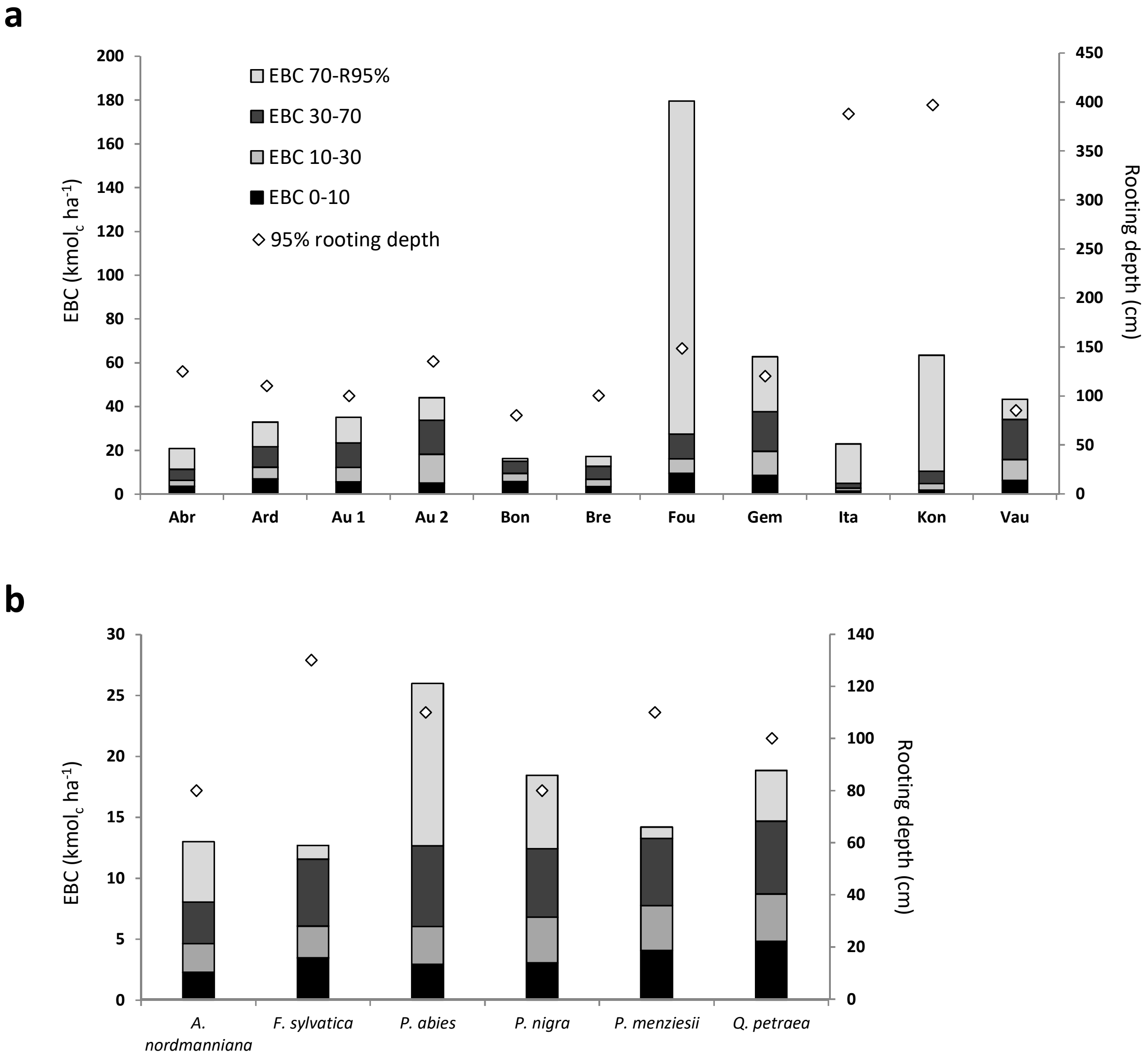
a
EBC (kmol$_c$ ha^{-1})
200
180
160
140
120
100
80
60
40
20
0
EBC 70-R95%
EBC 30-70
EBC 10-30
EBC 0-10
◇ 95% rooting depth
Rooting depth (cm)
450
400
350
300
250
200
150
100
50
0
Abr
Ard
Au 1
Au 2
Bon
Bre
Fou
Gem
Ita
Kon
Vau
b
EBC (kmol$_c$ ha^{-1})
30
25
20
15
10
5
0
Rooting depth (cm)
140
120
100
80
60
40
20
0
A. nordmanniana
F. sylvatica
P. abies
P. nigra
P. menziesii
Q. petraea

Figure 4.

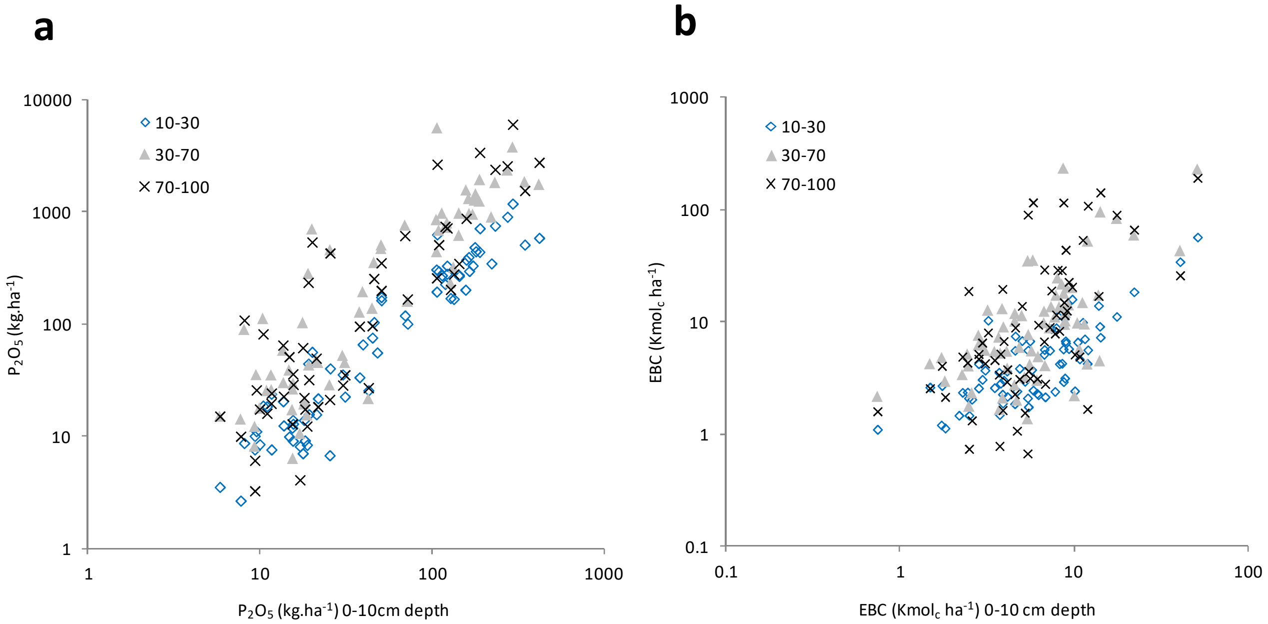
a
10000
1000
100
10
1
P$_2$O$_5$ (kg.ha^{-1})
1
10
100
1000
P$_2$O$_5$ (kg.ha^{-1}) 0-10cm depth
◇ 10-30
▲ 30-70
× 70-100
b
1000
100
10
1
0.1
EBC (Kmol$_c$ ha^{-1})
0.1
1
10
100
EBC (Kmol$_c$ ha^{-1}) 0-10 cm depth
◇ 10-30
▲ 30-70
× 70-100

Figure 5.

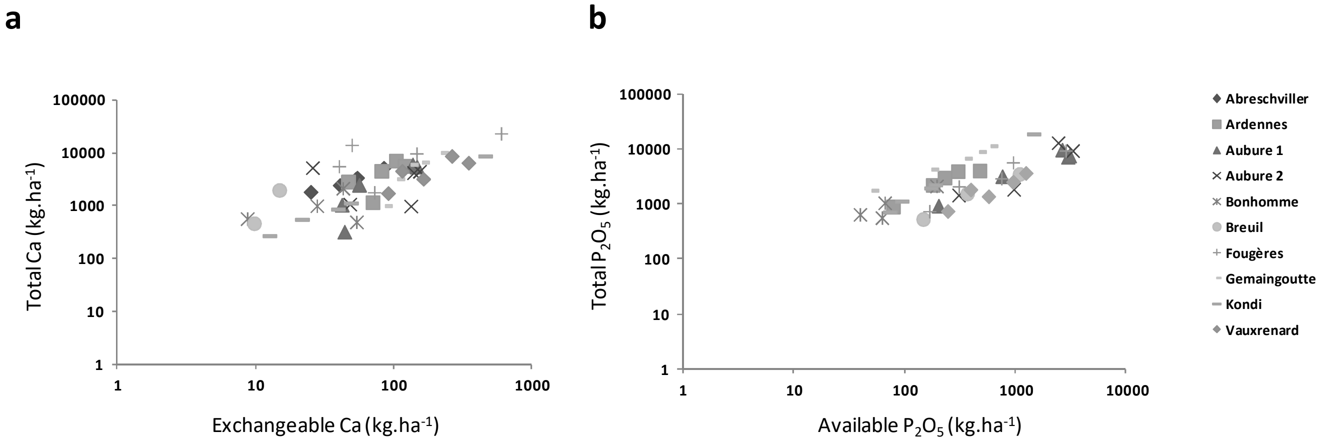
a
b
Total Ca (kg.ha-1)
Exchangeable Ca (kg.ha-1)
Total P2O5 (kg.ha-1)
Available P2O5 (kg.ha-1)
100000
10000
1000
100
10
1
1
10
100
1000
10000
Abreschviller
Ardennes
Aubure 1
Aubure 2
Bonhomme
Breuil
Fougères
Gemaingoutte
Kondi
Vauxrenard

Figure 6.

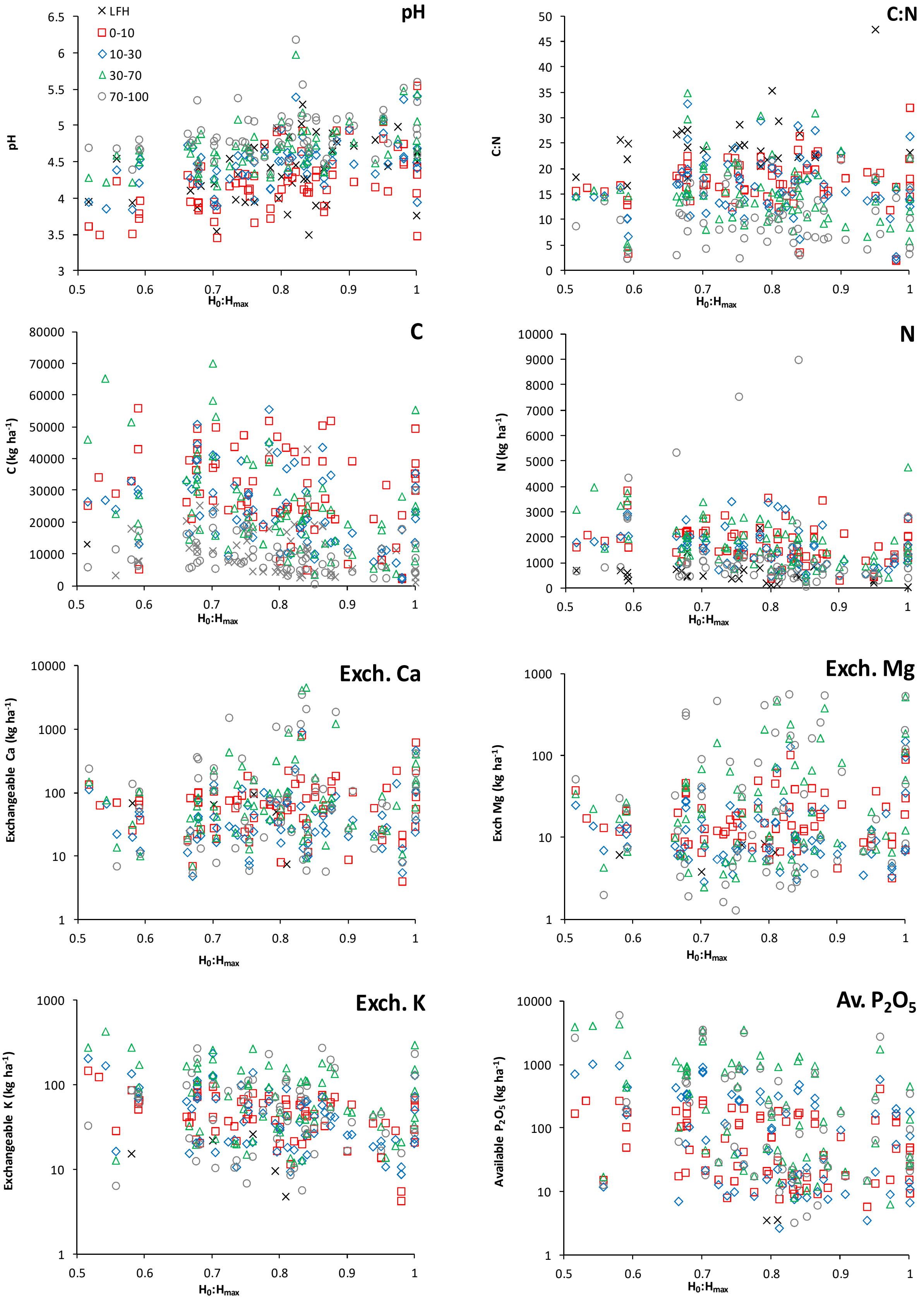
pH
× LFH
□ 0-10
◇ 10-30
△ 30-70
○ 70-100
pH
3
3.5
4
4.5
5
5.5
6
6.5
0.5
0.6
0.7
0.8
0.9
1
H_0:H_{max}
C:N
C:N
0
5
10
15
20
25
30
35
40
45
50
H_0:H_{max}
C
C (kg ha^{-1})
0
10000
20000
30000
40000
50000
60000
70000
80000
H_0:H_{max}
N
N (kg ha^{-1})
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
H_0:H_{max}
Exch. Ca
Exchangeable Ca (kg ha^{-1})
1
10
100
1000
10000
H_0:H_{max}
Exch. Mg
Exch Mg (kg ha^{-1})
1
10
100
1000
H_0:H_{max}
Exch. K
Exchangeable K (kg ha^{-1})
1
10
100
1000
H_0:H_{max}
Av. P_2O_5
Available P_2O_5 (kg ha^{-1})
1
10
100
1000
10000
H_0:H_{max}

Figure 7.

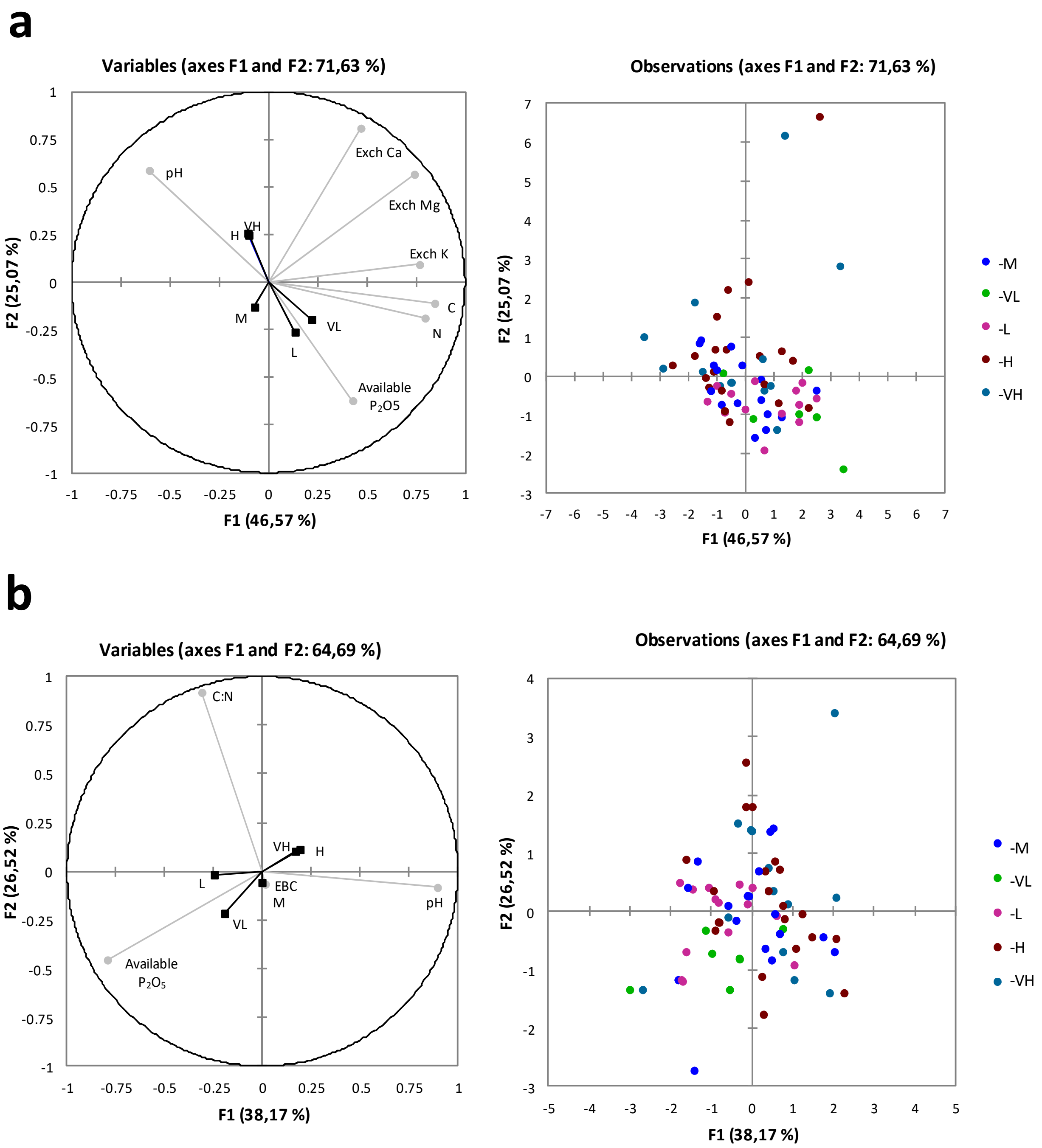
a
Variables (axes F1 and F2: 71,63 %)
F1 (46,57 %)
F2 (25,07 %)
pH
Exch Ca
Exch Mg
Exch K
C
N
Available P₂O5
VH
H
M
L
VL
Observations (axes F1 and F2: 71,63 %)
F1 (46,57 %)
F2 (25,07 %)
-M
-VL
-L
-H
-VH
b
Variables (axes F1 and F2: 64,69 %)
F1 (38,17 %)
F2 (26,52 %)
C:N
VH
H
L
EBC
M
VL
pH
Available P₂O₅
Observations (axes F1 and F2: 64,69 %)
F1 (38,17 %)
F2 (26,52 %)
-M
-VL
-L
-H
-VH

Figure 8.

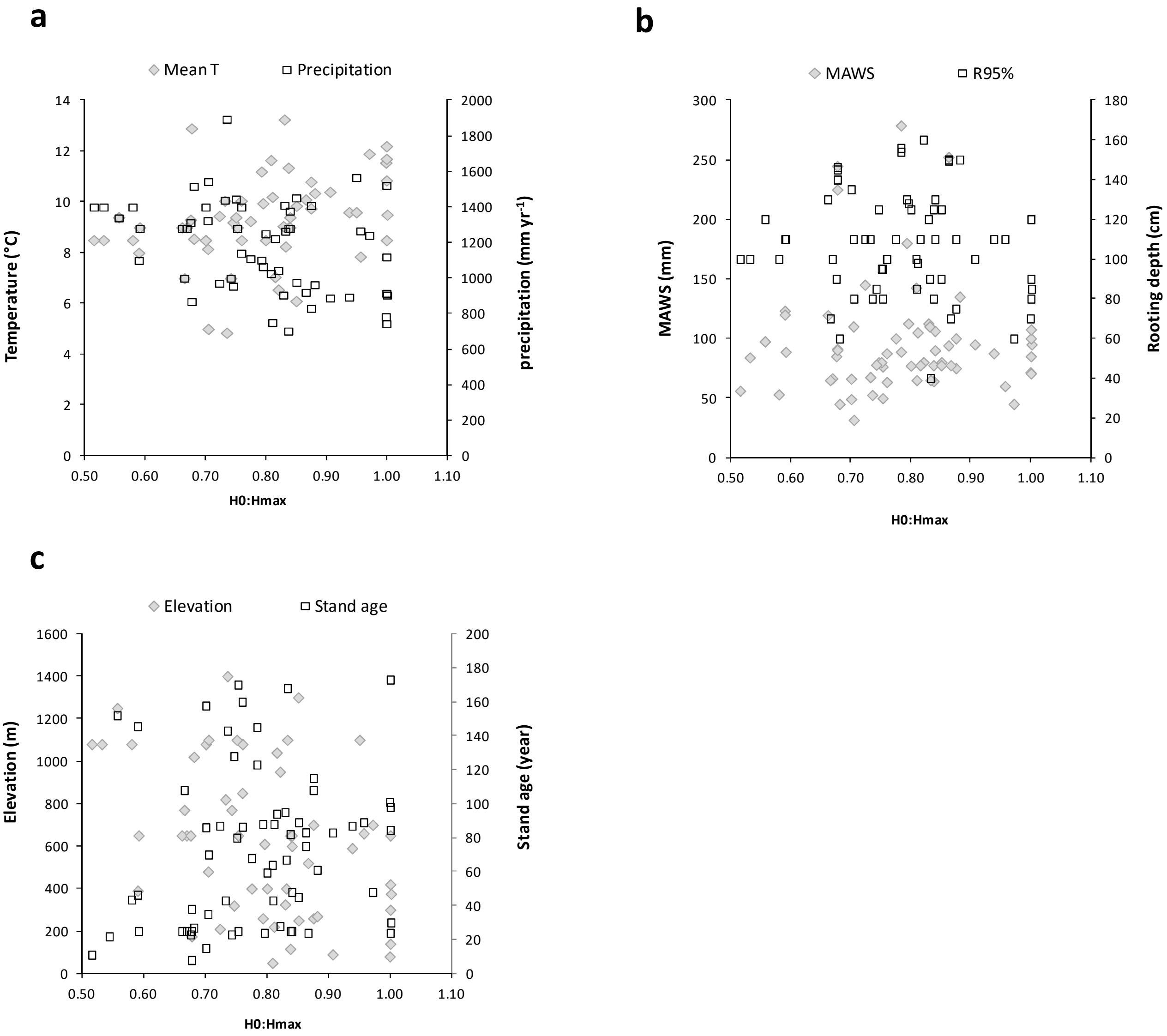
a
Mean T
Precipitation
Temperature (°C)
precipitation (mm yr-1)
0
2
4
6
8
10
12
14
0
200
400
600
800
1000
1200
1400
1600
1800
2000
0.50
0.60
0.70
0.80
0.90
1.00
1.10
H0:Hmax
b
MAWS
R95%
MAWS (mm)
Rooting depth (cm)
0
50
100
150
200
250
300
0
20
40
60
80
100
120
140
160
180
0.50
0.60
0.70
0.80
0.90
1.00
1.10
H0:Hmax
c
Elevation
Stand age
Elevation (m)
Stand age (year)
0
200
400
600
800
1000
1200
1400
1600
0
20
40
60
80
100
120
140
160
180
200
0.50
0.60
0.70
0.80
0.90
1.00
1.10
H0:Hmax

Table 1.

Site	Location	Tree species *	Stand age **	Soil type (WRB)	Main references
Abr	**Abreschviller, Vosges, France**	***Aa***	**M**	**Dystric cambisol**	**van der Heijden et al., 2011**
Ard	**Monthermé, Ardennes, France**	***Pa, Qp***	**M, VO**	**Dystric cambisol**	**Nys, 1987**
Au1	**Aubure, Vosges, France**	***Pa***	**VY, Y, M, O**	**Dystric cambisol**	**Fichter, 1997**
Au2	**Aubure, Vosges, France**	***Fs***	**VY, VO**	**Podzolic cambisol**	**Fichter, 1997**
Bon	**Bonhomme, Vosges, France**	***Pa***	**M**	**Podzolic cambisol**	**Mohamed Ahmed, 1992**
Bre	**Breuil, Morvan, France**	***An, Fs, Pa, Pm, Pn, Qp***	**Y, VO**	**Dystric cambisol**	**Mareschal 2008, van der Heijden et al., 2013**
CHS 01	Domaniale de Seillon, France	*Qp*	O	Dystric cambisol	Brêthes et al., 1997
CHS 03	Domaniale de Tronçais, France	*Qp*	VO	Dystric cambisol; dystric planosol	Brêthes et al., 1997
CHS 35	Domaniale de Rennes, France	*Qp*	VO	stagnic luvisol	Brêthes et al., 1997
CHS 57b	Domaniale de Mouterhouse, France	*Qp*	VO	haplic podzol	Brêthes et al., 1997
CHS 58	Domaniale de Vincence, France	*Qp*	M	stagnic luvisol	Brêthes et al., 1997
CHS 61	Domaniale de Réno Valdieu, France	*Qp*	O	haplic luvisol	Brêthes et al., 1997
CHS 81	Domaniale de Grésigne, France	*Qp*	O	haplic luvisol	Brêthes et al., 1997
CHS 86	Domaniale de Moulière, France	*Qp*	O	dystric cambisol	Brêthes et al., 1997
DOU 23	Sectionale du Maupuy, France	*Pm*	Y	humic cambisol	Brêthes et al., 1997
DOU 34	Domaniale des Avant-Monts, France	*Pm*	M	dystric cambisol; dystric leptosol	Brêthes et al., 1997
DOU 61	Domaniale d'Ecouves, France	*Pm*	Y	haplic luvisol; dystric cambisol	Brêthes et al., 1997
DOU 65	Communale de Lourdes, France	*Pm*	Y	dystric cambisol	Brêthes et al., 1997
DOU 69	Départementale de Brou, France	*Pm*	Y	dystric cambisol	Brêthes et al., 1997
EPC 08	Domaniale de la Croix-Scaille, France	*Pa*	Y	cambic podzol	Brêthes et al., 1997
EPC 34	Domaniale d'Espinouse, France	*Pa*	Y	cambic podzol	Brêthes et al., 1997
EPC 63	Sectionale de Manson, France	*Pa*	Y	mollic andosol	Brêthes et al., 1997
EPC 71	Domaniale de Glenne, France	*Pa*	M	cambic podzol	Brêthes et al., 1997
EPC 81	Domaniale de Nore, France	*Pa*	Y	cambic podzol	Brêthes et al., 1997
EPC 87	Sectionale de Monteil, France	*Pa*	Y	humic cambisol	Brêthes et al., 1997
EPC 88	Sectionale de Laveline, France	*Pa*	O	dystric cambisol	Brêthes et al., 1997
Fou	**Fougères, Bretagne, France**	**Br, Fs**	**VY, Y, O, VO**	**Dystric cambisol**	**Legout, 2008**
Gem	**Gemaingoutte, Vosges, France**	***Pa***	**O**	**Dystric cambisol**	**Mohamed Ahmed, 1992**
HET 03	Domaniale des Colettes, France	*Fs*	O	dystric cambisol	Brêthes et al., 1997
HET 09	Domaniale de Soulan, France	*Fs*	VO	cambic podzol	Brêthes et al., 1997
HET 14	Domaniale de Cerisy, France	*Fs*	O	dystric cambisol	Brêthes et al., 1997
HET 29	Domaniale de Carnoët, France	*Fs*	M	haplic luvisol	Brêthes et al., 1997
HET 30	Domaniale de l'Aigoual, France	*Fs*	VO	cambic podzol	Brêthes et al., 1997
HET 54a	Domaniale des Hauts Bois, France	*Fs*	O	dystric planosol	Brêthes et al., 1997
HET 55	Domaniale de Lachalade, France	*Fs*	O	haplic podzol	Brêthes et al., 1997
HET 64	Communale d'Ance, France	*Fs*	M	eutric cambisol	Brêthes et al., 1997
HET 65	Communale de Bize, France	*Fs*	VO	dystric cambisol	Brêthes et al., 1997
HET 76	Domaniale d'Eawy, France	*Fs*	O	haplic luvisol	Brêthes et al., 1997
HET 81	France	*Fs*	VO	cambic podzol	Brêthes et al., 1997
HET 88	Domaniale du Ban d'Harol, France	*Fs*	M	dystric cambisol	Brêthes et al., 1997
Ita	**Itatinga, São Paulo, Brazil**	***Eu***	**1, 3, 5**	**Ferralsol**	**Maquere, 2008; Almeida, 2009**
Kon	**Kondi, Pointe-Noire, Congo**	***Eu***	**1, 3, 6, 7, 8**	**Ferralic Arenosols**	**Laclau, 2001, Mareschal et al 2011**
PL 20	Territoriale d'Aitone, France	*Pn*	VO	humic cambisol	Brêthes et al., 1997
PL 41	Domaniale de Lamotte-Beuvron, France	*Pn*	M	haplic podzol; cambic podzol	Brêthes et al., 1997
SP 07	Domaniale de Lavillatte, France	*Aa*	O	cambic podzol	Brêthes et al., 1997
SP 09	Domaniale de Massat, France	*Aa*	VO	cambic podzol	Brêthes et al., 1997
SP 38	Domaniale de Saint-Hugon, France	*Aa*	O	dystric cambisol	Brêthes et al., 1997
SP 63	Domaniale du Livradois, France	*Aa*	VO	dystric cambisol	Brêthes et al., 1997

**Tree species Aa=Abies alba Mill., An=Abies nordmanniana Spach, Eu=Eucalyptus (E. grandis W. Hill ex Maiden at Ita, unknown hybrid at Kon), Fs=Fagus sylvatica L., Br=mixed broadleaves, Pa=Picea abies (L.) Karst. , Pn=Pinus nigra Arnold, Pm=Pseudotsuga menziesii (Mirb.) Franco, Qp=Quercus petraea (Matt.) Liebl.*

***Stand age VY=0-15 year, Y=16-40 year, M=41-70 year, O=71-100 year, VO>100 year. For tropical stands, stand age is indicated in years since planting.*

Table 2.

Site	Treatment	Fertilization	Year of stand establishment	Year of fertilization	Year of soil sampling*
Kon	Control	20 kg ha^{-1} N, 20 kg ha^{-1} P, 25 kg ha^{-1} K**	1992/1998/2005	At planting	1999, 2000, 2001, 2006
Ita	Control	32 kg ha^{-1} N,32 kg ha^{-1} P_2O_5, 2 tons ha^{-1} dolomitic lime***	2004	2004	2005, 2007

**litter layers sampled in 1998, 1999, 2000 and 2009 at Kon and annually from 2005 to 2010 at Ita.*

*** These amounts are very low in comparison with tree requirement throughout the rotation (Laclau et al., 2010).*

**** K was not added in this soil, and other plots in adjacent experiments show that K is the first factor limiting tree growth. Stand productivity was the same in the control plots sampled at Ita (despite the basic fertilization) as in other plots that did not receive any fertilizer addition.*

Table 3.

	Methods	**Reference**
Organic matter, carbon	Anne method, dry combustion	(Anne, 1945; Nelson and Sommers, 1996)
Organic and total N	Modified Kjeldahl method, dry combustion	(Kjeldahl, 1883; Bremner, 1996)
Soil pH	H_2O, KCl, CaCl	NF ISO 10390
Total elements	ICP following alkaline fusion	(Carignan et al 2001)
Available P_2O_5	Duchaufour method, resin extraction, Dyer (AFNOR NF X 31-160), Joret-Hébert method	(Dyer, 1894; Duchaufour and Bonneau, 1959; Amer et al 1955; Malavolta *et al.*, 1989; Joret and Hébert 1955)
Exchangeable Elements	Extraction with KCl, NH_4Cl or NH_4Ac followed by titration (H, Al), atomic absorption or ICP	NF X 31-130 2009: Espiau & Peyronel 1976

Table 4.

Correlation between depths	0-10 cm vs. LFH	0-10 cm vs. 10-30 cm	0-10 cm vs. 30-70 cm	0-10 cm vs. 70-100 cm
pH	0.45	0.66	0.58	0.5
C:N	*n.s*	0.7	0.4	*n.s*
C (kg ha^{-1})	*n.s*	0.38	0.19	*n.s*
N (kg ha^{-1})	*n.s*	0.41	0.36	0.23
Avail P_2O_5 (kg ha^{-1})	*n.a.*	0.77	0.72	0.64
Exch K(kg ha^{-1})	*n.a.*	0.64	0.58	0.5
Exch Na (kg ha^{-1})	*n.a.*	0.69	0.62	0.45
Exch Ca (kg ha^{-1})	*n.a.*	0.57	0.47	0.46
Exch Mg (kg ha^{-1})	*n.a.*	0.5	0.47	0.49
Exch Mn (kg ha^{-1})	*n.a.*	0.6	0.28	0.31
EBC (kmol$_c$.ha^{-1})	*n.a.*	0.51	0.47	0.45
BS (%)	*n.a.*	0.64	0.49	0.5
Total P_2O_5 (kg ha^{-1})	-0.64	0.49	0.64	*n.s*
Total K_2O (kg ha^{-1})	*n.s*	0.4	*n.s*	*n.s*
Total Na_2O (kg ha^{-1})	*n.a.*	0.74	0.82	0.55
Total CaO (kg ha^{-1})	*n.s*	0.59	0.59	*n.s*
Total MgO (kg ha^{-1})	*n.s*	0.75	0.67	0.76
Total MnO (kg ha^{-1})	*n.a.*	0.62	*n.s*	*n.s*
TBC (%)	*n.s*	0.36	0.33	0.43

Table 5.

	Mineral soil				Humus layer	
	0-10 cm depth	10-30 cm depth	30-70 cm depth	70-100 cm depth		LFH
pH	0.33	0.29	0.28	0.18	**pH**	*n.s*
C:N	*n.s*	*n.s*	*n.s*	*n.s*	**C:N**	*n.s*
C (kg ha^{-1})	-0.2	-0.28	-0.33		**C (Kg ha^{-1})**	-0.2
N (kg ha^{-1})	-0.25	-0.28	-0.35		**N (Kg ha^{-1})**	*n.s*
Avail P_2O_5 (kg ha^{-1})	-0.2	-0.26	-0.31	-0.26	**Total P (kg ha^{-1})**	*n.s*
Exch K(kg ha^{-1})	-0.25	-0.27	*n.s*	*n.s*	**Total Ca (kg ha^{-1})**	*n.s*
Exch Na (kg ha^{-1})	*n.s*	*n.s*	*n.s*	*n.s*	**Total Mg (kg ha^{-1})**	*n.s*
Exch Ca (kg ha^{-1})	*n.s*	*n.s*	*n.s*	*n.s*		
Exch Mg (kg ha^{-1})	*n.s*	*n.s*	*n.s*	*n.s*		
Exch Mn (kg ha^{-1})	*n.s*	*n.s*	*n.s*	*n.s*		
EBC (kg ha^{-1})	*n.s*	*n.s*	*n.s*	*n.s*		
BS	0.22	0.28	0.28	0.24		