

1 **Chemical fertility of forest ecosystems. Part 2: Towards**
2 **redefining the concept by untangling the role of the different**
3 **components of biogeochemical cycling**

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13 **Abstract**

14 Many forest ecosystems are developed on acidic and nutrient-poor soils and it is not yet clearly
15 understood how forests sustain their growth with low nutrient resources. In forestry, the soil
16 chemical fertility is commonly defined, following concepts inherited from agronomy, as the pool
17 of plant-available nutrients in the soil at a given time compared to the nutritional requirement of
18 the tree species. In this two-part study, Part 1 (Hansson *et al.*, submitted) showed, through the
19 compiled dataset of 49 forest ecosystems in France, Brazil and Republic of Congo, the limits of
20 this definition of soil chemical fertility in forest ecosystem contexts. In this study (Part 2), we
21 investigated the nutrient pools and fluxes between the different ecosystem compartments at 11
22 of the 49 sites in order to better characterize the role of the biogeochemical cycling of nutrients
23 in the chemical fertility of forest ecosystems, and in particular the roles of the biological and
24 geochemical components of biogeochemical cycling.

25 The analysis of our dataset shows different types of biogeochemical functioning. When the
26 geochemical component (inputs through mineral weathering and/or atmospheric inputs,
27 capillary rise) is predominant, sufficient nutrients are provided to the plant-soil system to
28 ensure tree nutrition and growth. Conversely, when the geochemical component of the cycle
29 brings too few nutrients to the plant-soil system, the biological component (litterfall, plant
30 internal cycling) becomes predominant in tree nutrition and growth. In the latter case, forest
31 production may be high even when pools of nutrients in the soil reservoir are low because small
32 but active nutrient fluxes may continuously replenish the soil reservoir or may directly ensure
33 tree nutrition by bypassing the soil reservoir.

34 This study highlights the necessity to include biogeochemical cycling and recycling fluxes in the
35 definition and diagnosis methods of soil chemical fertility in forest ecosystems. We show that the
36 chemical fertility is not only supported by the soil in forest ecosystem but by the sum of all the
37 ecosystem's compartments and fluxes between these pools.

38 **Keywords:** chemical fertility, biological cycling, geochemical cycling, nutritional functioning

39 **1 Introduction**

40 The productivity of forest ecosystem remains a fundamental concern in forestry (Bontemps and
41 Bouriaud, 2014) and is considered as one of the principal soil-based ecosystem services
42 (Bunemann *et al.*, 2018). However, past and present silvicultural, nutritional and/or climatic
43 pressures endured by forest ecosystems, often referred to as ‘global changes’, may widely
44 impact the chemical fertility of forest soils and productivity. Acidic atmospheric depositions in
45 Europe reached a maximum during the 1970s for sulphur (S) and the 1980s for nitrogen (N)
46 which in numerous cases caused accelerated soil acidification (Schulze, 1989) and tree nutrition
47 (Jonard *et al.*, 2015) and growth disorders. Although S deposition has decreased widely since the
48 1980s (Vuorenmaa *et al.*, 2017), N deposition has remained high (Boxman *et al.*, 2008; Schmitz
49 *et al.*, 2019) and decreasing rates of nutrient cations deposition have been observed in Europe
50 (Likens *et al.*, 1998; Jonard *et al.*, 2012; Verstraeten *et al.*, 2017; Pierret *et al.*, 2019).
51 Furthermore, the increased demand for bio-sourced energy and “environmental friendly”
52 materials (Achat *et al.*, 2015; Pyttel *et al.*, 2015; Thiffault *et al.*, 2015) may cause additional
53 pressure on forest ecosystems through large nutrient exports with biomass removal (Garcia *et*
54 *al.*, 2018). In the framework of ‘Driver-Pressure-State-Impact-Response’ proposed for soils by
55 Bunemann *et al.* (2018), these ongoing changes may threaten the chemical fertility of forest
56 ecosystems on the mid to long term, leading to more or less large changes in all ecosystem
57 functions (e.g. biomass production, biodiversity, water purification). A relevant assessment of
58 forest chemical fertility, as well as the understanding of the nutritional functioning of forest
59 ecosystems (i.e. the origin and fate of nutrients) and the possible causes of ecosystem
60 dysfunctioning are major concerns to predict the sustainability of forests in the context of global
61 change. This growing concern is of paramount importance to help give forest managers and
62 policy makers the most accurate picture of the potential of forest ecosystems and associated
63 threats (Forest-Europe, 2011).

64 Forest productivity is complex and difficult to assess, because numerous environmental
65 parameters may at the same time widely influence tree growth. Several studies have

66 demonstrated the significant influence of climate, topography, geology, atmospheric deposition
67 and soil properties on forest productivity (Seynave *et al.*, 2005; Charru *et al.*, 2017), but about
68 half of the variation in tree growth remains often unexplained (Seynave *et al.*, 2005). Some
69 studies have demonstrated the influence of soil water and nutrient resources on tree
70 productivity (Seynave *et al.*, 2005; Calvaruso *et al.*, 2017) and some fertility reference levels for
71 forest ecosystems only rely on the reservoir of soil nutrients available to plants (Bonneau,
72 1995). However, the productivity may differ widely between sites within the same climatic
73 region although they have similar plant-available nutrient stocks in the soil. Also, sites with
74 extremely low plant-available nutrient pools in the soil may exhibit very high productivity
75 (Hansson *et al.*, submitted). This shows the limits of our understanding of the nutritional
76 functioning of these ecosystems and of which factors effectively control forest productivity.
77 Forest soils are generally poor in terms of nutrient content, sometimes very poor, and are
78 colonised by perennial plants adapted to this context through a set of processes described as the
79 biogeochemical cycling of nutrients (Ranger and Turpault, 1999). Biogeochemical cycling is
80 known to influence the pools and availability of nutrients in forest soils (Ranger and Turpault,
81 1999; Jobbagy and Jackson, 2001). However, few studies deal with the relationships between
82 nutrient cycling, nutritional functioning of the ecosystem and tree biomass production (Ranger
83 *et al.*, 2002; Laclau *et al.*, 2010; Legout *et al.*, 2014; Johnson and Turner, 2019). Moreover, to our
84 knowledge, no study has focused on these relationships considering at the same time several
85 forest sites characterized by contrasting environmental contexts.

86 The aim of this study was to better characterize the role of the biogeochemical cycling of
87 nutrients in the chemical fertility of forest ecosystems, and in particular the role of the biological
88 and geochemical components of biogeochemical cycling (Figure 1). For this, we worked on 11 of
89 the 49 sites studied by Hansson *et al.* (submitted) where measurements on biogeochemical
90 cycling were available on the mid to long term. Input fluxes (weathering, deposition), output
91 fluxes (drainage losses, immobilisation in tree biomass) and internal cycling (litterfall,

92 throughfall, stemflow) were added to the database compiled by Hansson et al (submitted) on
93 these sites.

94 We hypothesized that in ecosystems with a large stock of exchangeable base cation, the
95 geochemical component of the cycle is predominant with high inputs to the ecosystem through
96 weathering and/or atmospheric deposition; the geochemical component of the cycle is thus a
97 major contribution to chemical forest fertility. Conversely, we hypothesized that the biological
98 component of the biogeochemical cycle becomes a major contribution to forest chemical fertility
99 when inputs to the ecosystem (weathering and/or atmospheric deposition) and soil
100 exchangeable stocks of base cations are low.

101 **2 Materials and methods**

102 **2.1 Study sites**

103 The present study focuses on nine temperate (France) and two tropical (Congo, Brazil) field
104 sites. Main references with background descriptions related to each site are listed in Table 1.
105 The majority of data used in this study has been described by previous studies, mainly focusing
106 on effects of stand age, species or fertilisation (Marques, 1996; Marques and Ranger, 1997;
107 Fichter *et al.*, 1998a; Fichter *et al.*, 1998b; Ranger *et al.*, 2002; Laclau *et al.*, 2003a; Laclau *et al.*,
108 2003b; Laclau *et al.*, 2003c; Legout, 2008; Legout *et al.*, 2011; van der Heijden *et al.*, 2011;
109 Mareschal *et al.*, 2013; van der Heijden *et al.*, 2013). All sites have been forested for at least 60
110 years (often much longer), except the *Eucalyptus hybrid* stand in Congo, which was established
111 in 1992 in a 3000-year-old savannah soil. Though geographically very close to one another, the
112 sites Au1 and Au2 were separated because the bedrock differed between the two sites. Five
113 temperate and two tropical tree species were included in the study (Table 2). At the tropical
114 sites, all plots, including control plots, received basic fertilisation, as practised in the industrial
115 management. However, the amounts of nutrients added were small and soil chemical analyses a
116 few months after fertilizer addition did not show significant differences in soil properties

117 between control and fertilized plots (Almeida, 2009). Details on fertilisation are described in the
118 Part 1 paper of this study (Hansson *et al.*, submitted).

119 **2.2 Data collection and calculations**

120 **2.2.1 Standardized tree productivity index**

121
122 As an index of tree productivity, a ratio ($H_0:H_{max}$) between the dominant height (H_0) at the age of
123 sampling and the maximum regional tree height (H_{max}) observed for the same tree species and
124 the same age (± 3 years) was calculated for each site (Table 2). H_{max} was estimated using data
125 from the French National Forest Inventory: the database contains data from more than 32000
126 plots in France, divided into 11 ecological regions (Cavaignac, 2009). Dominant height in the
127 data base was defined as average of the three highest trees per plot. $H_0:H_{max}$ ratios were then
128 used as a reference, with productivity considered to be highest at sites with $H_0:H_{max} = 1$. This
129 standardized tree productivity index thus takes into account variations related to tree species,
130 stand age and regional climatic conditions, making it possible to compare tree growth for
131 different species in different climatic regions. More details on calculations are described in the
132 Part 1 paper of this study (Hansson *et al.*, submitted).

133 C, Ca, K, Mg, N and P pools in the different ecosystem compartments and the fluxes between
134 compartments were compiled per site, treatment, tree species and stand age. Both data
135 originating from publications (see Table 1 for main references) and previously unpublished data
136 were included.

137 The change in available nutrients pool within the soil profile was estimated by calculating
138 annually nutrient input-output budgets (mass balance budgets) considering atmospheric
139 deposition and mineral weathering as the inputs, and nutrient leaching below the rooting zone
140 and current annual increment in tree biomass as the outputs. Data collection and analysis
141 methods were generally similar between sites, with some exceptions (Table 3). We assumed that
142 the small differences in methods between sites were of minor importance and did not impair
143 site comparison.

144 **2.2.2 Pools in the forest floor, mineral soil profile and aboveground tree biomass**

145 The physical and chemical properties of the forest floor and soil at each site and the methods are
146 described briefly in Table 3 and in more details in the supplementary materials 1 and 2. Biomass
147 and mineral content of the aboveground compartments (stem, leaves, branches and roots) were
148 measured destructively for 3 to 23 trees per site (Madgwick, 1982). Allometric equations were
149 then fitted using the sampled tree data and applied to stand inventory to quantify the stand
150 biomass and nutrient content on a per hectare basis (Table 3). Belowground biomass and
151 related mineral mass data were missing at some sites and could not be included in this study.
152 Nutrient concentrations in leaves were measured at all sites: green leaves and needles were
153 sampled in the top third section of the canopy from the dominant trees of each plot (at
154 temperate sites, broadleaves species were sampled at the end of August and coniferous species
155 in November).

156 **2.2.3 Input fluxes**

157 Atmospheric deposition was estimated as the sum of wet, dry and occult deposition. In a few
158 cases, when dry and occult deposition could not be estimated, bulk deposition was used instead.
159 Wet deposition was calculated from bulk precipitation. Dry deposition was estimated by
160 comparing throughfall and bulk precipitation, in most cases calculated according to equations
161 from Ulrich (1983).

162 Mineral weathering was estimated using the geochemical model PROFILE (Sverdrup and
163 Warfvinge, 1988), as historical weathering (Sudom and St. Arnaud, 1971) or through weathering
164 rates estimated from literature (Bonneau *et al.*, 1991). The total input flux refers to the sum of
165 the atmospheric deposition and mineral weathering flux.

166 **2.2.4 Output fluxes**

167 Soil solutions were collected at one (Au1, Au2) or several depths at each site. For most of the
168 sites, the deepest lysimeter depth was close to the maximum rooting depth. At some sites,
169 however, the depth including 95 % of the roots (R95%, see the Part 1 paper of this study

170 (Hansson *et al.*, submitted)) was deeper than the installed lysimeters (Table 2). Water samples
171 were collected weekly to monthly, depending on the site, and analysed for major elements (Ca,
172 Mg, K, Al, P, S, NO₃, NH₄). Nutrient leaching was estimated by multiplying the measured
173 concentrations by the estimated water flux at the corresponding depth (Table 3). The leaching
174 flux used in the nutrient input-output budget was the flux at the deepest depth of soil solution
175 sampling. Losses by superficial runoff of dissolved nutrients were negligible at the study sites.
176 For sites where whole-tree biomass data were available (all sites except Au1, Au2 and Bon), the
177 current annual increments in biomass (whole-tree and stem) and nutrient contents were
178 calculated from the change in standing whole-tree and stem biomass and mineral contents over
179 a period of time (usually 1-5 years). For Au2 and Bon, where no such data was available, the
180 mean annual increment was calculated as biomass and nutrient content divided by the stand
181 age. The difference between current and mean annual increment for a 150-year-old beech stand
182 (such as Au2), as well as for a 70-year-old spruce stand (such as Bon) is below 1 m³. ha⁻¹.yr⁻¹ in
183 northeast France (Decourt, 1973). For Au1, current annual increment was calculated for stem
184 only.

185 **2.2.5 Internal cycling**

186 We compared internal cycling through litterfall, throughfall, stemflow and net canopy exchange
187 (difference between foliar absorption and foliar leaching) at the different sites (Table 3).
188 Litterfall was collected, weighed and analysed 2 to 12 times per year, depending on the site.
189 Throughfall was collected at all sites; stemflow was collected at all sites except Abr, Au1, Au2
190 and Vau.

191 **2.2.6 Index calculations**

192 A ratio ($Y_{net\ uptake}$ expressed in years) was calculated for N, P, Ca, Mg, K for each stand as an
193 index of nutrient availability in the 0-70cm soil layer (exchangeable pools for Ca, Mg, K; available
194 pool for P; total pool for N) standardised by the net uptake immobilised in the stem and
195 expressed in years (i.e. the number of years of net uptake available in the 0-70cm soil pools):

196
$$Y_{net\ uptake\ X} = \frac{Soil\ pool\ X}{Net\ uptake\ flux\ X}$$

197 where *Soil pool X* is pool of nutrient X (in kg.ha⁻¹) in the 0-70cm soil layer and
 198 *Net uptake flux X* is the annual net increment of nutrient X in the stem (in kg.ha⁻¹.yr⁻¹).

199

200 A foliar remobilisation rate during senescence (*FRR* in %) was also calculated for N, P, Ca, Mg, K
 201 in each stand. We used this rate as an indicator of biochemical cycling efficiency:

202
$$FRR\ X = \frac{([X]_{Foliar} - [X]_{Litterfall}) \times 100}{[X]_{Foliar}}$$

203 where $[X]_{Foliar}$ and $[X]_{Litterfall}$ are concentrations of nutrient X (in mg g⁻¹) in green foliage and
 204 in litterfall, respectively.

205 Lastly, a nutrient use efficiency index to produce woody biomass ($E_{biomass}$ in t.kg⁻¹) from
 206 nutrients was calculated for N, P, Ca, Mg, K for each stand:

207
$$E_{biomass} = \frac{Annual\ biomass\ increment}{Net\ uptake\ flux\ X}$$

208 where *Annual biomass increment* is the annual woody biomass increment in stem (in t.ha⁻¹.yr⁻¹).
 209 1).

210 **2.3 Typology of nutritional functioning: Bio, Geo and BioGeo sites**

211 Following our hypothesis (detailed in the introduction section), we grouped the different sites
 212 into three categories: 'Bio', 'BioGeo' and 'Geo'. The categorization was based on the exchangeable
 213 pools of base cations (BC) in the 0-70cm soil layer and the inputs of BC to the soil through
 214 weathering of soil minerals and atmospheric deposition (Figure 2, Table 1):

- 215 • The 'Bio' sites were identified as having low pools of exchangeable BC in soils (< 15
 216 kmol_c.ha⁻¹), with low inputs to the soil (<1.1 kmol_c.ha⁻¹.yr⁻¹). This category was then
 217 subdivided into two subcategories distinguishing temperate (Bio Temp) and tropical (Bio
 218 Trop) sites.
- 219 • The 'Geo' sites were identified as having medium to high pools of exchangeable BC in
 220 soils (> 15 kmol_c.ha⁻¹) and high inputs to the soil (>1.1 kmol_c.ha⁻¹.yr⁻¹).

221 • The 'BioGeo' sites were identified as having medium to high pools of exchangeable BC in
222 soils ($> 15 \text{ kmol}_c\text{.ha}^{-1}$) and low inputs to the soil ($<1.1 \text{ kmol}_c\text{.ha}^{-1}\text{.yr}^{-1}$).

223

224 **2.4 Statistical analyses**

225 Pearson correlation tests (R version 3.4.4) were used to test correlations between different
226 parameters ($p \text{ value}=0.05$). Differences between site categories (Bio, BioGeo, Geo) were tested
227 by ANOVA (R version 3.4.4) and Tukey HSD tests (Tukey Honest Significant Differences, R
228 version 3.4.4) were computed for multiple pairwise-comparison between the means of groups
229 (confidence interval of 95%). The normality and the homogeneity of variance were tested prior
230 to performing the ANOVA.

231 **3 Results**

232 **3.1 Available and total pools of nutrients in soils**

233 Exchangeable stocks of Ca, Mg and K in the 0-70cm soil were on average significantly larger in
234 the Geo ($24.3 \text{ kmol}_c\text{.ha}^{-1}$) and BioGeo ($31.5 \text{ kmol}_c\text{.ha}^{-1}$) groups than in the Bio group (7.7
235 $\text{ kmol}_c\text{.ha}^{-1}$) (Figure 3), since EBC stocks were used to define the Bio, BioGeo and Geo categories
236 (Figure 2). EBC stocks were not significantly different between BioGeo and Geo groups. Available
237 phosphorous stocks in the 0-70cm soil displayed a different pattern than exchangeable
238 elements, with significantly larger stocks in the BioGeo group ($2903.8 \text{ kg.ha}^{-1}$) than in Bio (482.0
239 kg.ha^{-1}) and Geo (999.2 kg.ha^{-1}) groups (Figure 3).

240 Total pools of Mg and K in the 0-70cm soil were significantly higher in the Geo and BioGeo
241 groups than in the Bio group, while total pools of Ca were significantly larger in the Geo group
242 compared to the others (Figure 3). Total N and C stocks in the 0-70cm soil were significantly
243 lower in the Bio group (3.8 t.ha^{-1} and 51.9 t.ha^{-1}) compared to the Geo (7.1 t.ha^{-1} and 104.4 t.ha^{-1})
244 and BioGeo (7.5 t.ha^{-1} and 103.8 t.ha^{-1}) groups (Figure 3).

245 **3.2 Soil as a reservoir for nutrient uptake**

246 The $Y_{\text{net uptake}}$ indexes (the stock of available nutrient in the 0-70cm soil pool standardised by the
247 net uptake immobilised in the stem and expressed in years), is presented in Figure 4. The Y_{net}
248 $_{\text{uptake}}$ was significantly lower for exchangeable Ca (23yr), K (16yr) and for the sum of
249 exchangeable base cations (18yr) in the Bio group compared to the BioGeo and Geo groups
250 (average values > 65 years, with no significant differences between the two groups) (Figure 4).
251 For exchangeable Mg and nitrogen, $Y_{\text{net uptake}}$ indexes were significantly lower in the Bio group
252 (24yr and 283yr, respectively) than in the Geo group (163yr and 3047yr respectively). Available
253 P displayed a different pattern with a significantly higher $Y_{\text{net uptake}}$ index in the BioGeo group
254 (5490yr) compared to the Bio group (350yr).

255 The trends were similar between the tropical sites and the temperate sites within the Bio group.

256 **3.3 Site productivity related to nutrient pools in the soil and nutrient** 257 **inputs**

258 On average, H0:Hmax was significantly higher in the Bio Group (0.91) than in the BioGeo (0.72)
259 and Geo (0.73) groups (Figure 5). However, the mean H0:Hmax value of the Bio Temp sites
260 (0.78) was close to that of the BioGeo and Geo groups. The highest H0:Hmax did not match with
261 the highest exchangeable base cation pools in the 0-70cm soil layer and base cation pools ranged
262 from 3 to 40 kmol+.ha⁻¹ for values of H0:Hmax greater than 0.7 (Figure 5a). Similarly, the highest
263 H0:Hmax values did not match with the highest base cation inputs to the soil through
264 atmospheric deposition and weathering. Base cation inputs ranged from 0.28 to 1.78 kmol+.ha⁻¹.y⁻¹
265 for H0:Hmax greater than 0.7 (Figure 5b).

266 **3.4 Input-output budgets**

267 **3.4.1 Inputs**

268 Sites sampled in the 1980s and 1990s had the highest N atmospheric deposition (Table 4),
269 consistent with a higher N deposition in Europe during that time period (Fowler *et al.*, 2007).

270 Total inputs of N (i.e. atmospheric deposition since biological fixation of N₂ was considered
271 negligible in the stands studied) were significantly lower in the Bio group (7.7 kg.ha⁻¹.yr⁻¹)
272 compared to the BioGeo (20.1 kg.ha⁻¹.yr⁻¹) and Geo (16.7 kg.ha⁻¹.yr⁻¹) groups (Table 5, Figure 6).
273 Total inputs of Ca, Mg, K and base cations (BC) (i.e. atmospheric deposition and mineral
274 weathering) were significantly higher in the Geo group (BC=1.5 kmol+.ha⁻¹.yr⁻¹) than in the Bio
275 (BC= 0.6 kmol+.ha⁻¹.yr⁻¹) and the BioGeo (BC= 0.7 kmol+.ha⁻¹.yr⁻¹) groups. Differences in mineral
276 weathering fluxes were large between the three categories, with mineral weathering close to
277 zero at the tropical sites and high at Geo-sites, especially for Mg (4.2 kg.ha⁻¹.yr⁻¹) and K (10.5
278 kg.ha⁻¹.yr⁻¹) (Table 5, Figure 6). Litterfall fluxes were significantly higher in the Geo group
279 compared to the Bio group for N, P and K while no significant difference was observed between
280 groups for Ca and total base cations (Table 5). The litterfall flux of Mg was significantly higher
281 for the Bio group. For all three types, the litterfall flux was generally as large (for K, Mg) or larger
282 (for Ca, P, N) than total inputs (Table 5, Figure 6). For base cations, the litterfall flux represent
283 378% of the total inputs for the Bio Trop group, 176% for the Bio Temp group, 161% for the
284 BioGeo group and only 94% for the Geo group. This estimated contribution of litterfall in the
285 potential replenishment of the soil reservoir was therefore in order of importance depending on
286 the groups of nutritional functioning: BioTrop > BioTemp-BioGeo > Geo.

287 **3.4.2 Outputs**

288 Net uptake (accumulation within stem biomass) was significantly higher in the Bio group than in
289 the BioGeo and Geo groups for Mg, P and N (Table 5), mainly due to the Bio Trop sites (Figure 6),
290 while no difference was observed between the three groups for Ca and K.

291 In the BioGeo and Geo groups, the leaching fluxes of N and base cations matched the largest
292 proportion of total outputs. The leaching fluxes of Ca, base cations and N were significantly
293 lower in the Bio group (1.4 kg.ha⁻¹.yr⁻¹, 0.1 kmol+.ha⁻¹.yr⁻¹, 2.6 kg.ha⁻¹.yr⁻¹ respectively) than in
294 the BioGeo and Geo groups (>7 kg.ha⁻¹.yr⁻¹, >1 kmol+.ha⁻¹.yr⁻¹, >15 kg.ha⁻¹.yr⁻¹ respectively)
295 (Table5, Figure 6). For Mg and P, the leaching flux was significantly lower in the Bio group than

296 in the Geo group while K leaching ($11.3 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) was significantly higher in the BioGeo group
297 compared to the Bio ($0.8 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and Geo ($4.1 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) groups (Table5, Figure 6).

298 The leaching flux of base cations was higher for sites with elevated N leaching, with the highest
299 values for BioGeo and Geo sites (Figure 7a). High N deposition rates were highly correlated ($r =$
300 0.77) with N leaching fluxes (Table 4, Figure 7b).

301 **3.4.3 Input-Output budgets**

302 Input-output budgets were most often negative at the studied sites whatever the elements
303 (Table4). In the Bio group, except for N at the Bio Trop sites ($-18.0 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), budgets were
304 positive or close to 0 and tended to be higher than in the other groups, especially when
305 considering the Bio Temp sites (Table 5, Figure 6). In the BioGeo group, the budgets were very
306 negative and significantly lower for Ca ($-9.5 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), K ($-9.9 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and base cations ($-$
307 $0.9 \text{ kmol}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) compared to the Bio group (Table 5, Figure 6). In the Geo group, the budgets
308 were negative for Mg ($-6.6 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and significantly lower than in the other groups, while
309 the K budgets were very positive ($7.3 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and significantly higher than in the other
310 groups.

311 **4 Discussion**

312 **4.1 Typology of nutritional functioning of forest ecosystems**

313 **4.1.1 Soil reservoir and supply of available nutrients**

314 The categorization of the sites included in this study according to their stocks of exchangeable
315 base cations, their atmospheric and weathering inputs lead to three distinct groups.

316 As expected, the Geo sites were characterized by larger stocks of exchangeable base cations in
317 the soil and higher inputs to the soil through atmospheric and/or weathering fluxes (Figure 2 &
318 3 & 6; Table 5) than the Bio sites. The differences in stocks of exchangeable base cations in the
319 soil can be mainly explained by the chemical composition of the soil parent material and the

320 mineral weathering flux. On the one hand, over the entire dataset, significant positive
321 relationships were observed between total and exchangeable/available elements in the soil
322 (significant Pearson correlation coefficients between exchangeable/available and total 0-70cm
323 soil pools for Ca, Mg, K and P, respectively 0.50, 0.82, 0.83 and 0.53), as shown in other forest
324 soils (Mareschal *et al.*, 2015; Porder *et al.*, 2015; Wuenscher *et al.*, 2015). On the other hand,
325 even though atmospheric deposition fluxes of K, Ca, Mg and P were slightly higher at the Geo
326 sites than at the Bio sites, no relationship was observed between available elements in the soil
327 and atmospheric deposition inputs. The parent material of a soil determines the original supply
328 of nutrients released by weathering (Anderson, 1988) and soil mineralogy is a key parameter
329 controlling nutrient pools (Schlesinger, 1997; Giehl and von Wiren, 2014). It has also been
330 shown that a large proportion of atmospheric deposition of nutrients is i) rapidly and strongly
331 retained in the organic layer and at the surface of the mineral soil and ii) very rapidly taken up
332 by the trees thus limiting the influence of these inputs on the exchangeable/available pools in
333 the soil (Drouet *et al.*, 2007; van der Heijden *et al.*, 2014; van der Heijden *et al.*, 2017). At the Geo
334 sites, Ca, Mg, K or P-bearing minerals were more abundant and/or more weatherable than at the
335 Bio sites (Fichter *et al.*, 1998a; Ezzaim *et al.*, 1999; Legout *et al.*, 2011; van der Heijden *et al.*,
336 2011; van der Heijden *et al.*, 2013; Mareschal *et al.*, 2015), resulting in higher weathering fluxes
337 that may continuously supply the pools of exchangeable/available nutrients and keep them
338 higher than at the Bio sites. At the Bio sites, the contribution of nutrient recycling to supply and
339 preserve the stocks of exchangeable base cations in soil is much more important (Figure 6) than
340 at the Geo sites.

341 The BioGeo sites were intermediate, resembling Geo sites when comparing the stocks of base
342 cations in the soil but also resembling Bio sites when comparing the inputs of base cations to the
343 soil (Figure 2 & 6; Table 5). Our dataset is insufficient to explain all the processes characterizing
344 this group but we may hypothesize that these ecosystems are in transition, changing from Geo to
345 Bio types, and/or that a significant proportion of their current chemical fertility was inherited.
346 Indeed, exchangeable K and available P stocks in soils were higher at the BioGeo sites than at the

347 Geo sites while inputs to the soil through atmospheric and mineral weathering were lower,
348 which could be explained by a past agricultural use of these ecosystems with addition of
349 fertilizers (Dupouey *et al.*, 2002; Ranger *et al.*, 2002). The BioGeo type could possibly be better
350 defined further if data from more sites were available but it is reasonable to assume that there is
351 no sharp line between Bio and Geo types and they should be looked at more as a
352 gradient/continuum, with the BioGeo sites spread out along the middle.

353 **4.1.2 Nutritional functioning and tree productivity**

354 Unsurprisingly, when standardizing available nutrient pools in the mineral soil by the annual
355 aboveground biomass immobilization flux, the number of years of available nutrients in the soil
356 to ensure plant nutrition was much lower at the Bio types compared to the Geo types (Figure 4).
357 This was particularly true at the Bio Trop sites for the base cations, where approximately 15
358 years or less of 'stem net uptake' were available on average in soil. However, the Bio sites show
359 remarkable tree growth/productivity ($H_0:H_{max}$, Figure 5) and as shown in the companion
360 paper (Hansson *et al.*, submitted), the pools of available nutrients in the soil were not sufficient
361 to explain the differences in chemical fertility and tree growth/productivity between the sites of
362 this study. In forest ecosystems, the pools of available nutrients in the soil represent only a
363 fraction of the available amounts of nutrients in the ecosystem and the circulation of nutrients
364 through biogeochemical cycling can compensate the low availability of nutrients in the soil
365 (Ranger *et al.*, 1997; Ranger and Turpault, 1999; Laclau *et al.*, 2003b), thus enabling a high
366 productivity despite low available nutrient pools in soils. As discussed above, over the range of
367 sites included in this study, there was no evidence that the low availability of nutrients in the Bio
368 type sites was compensated by elevated atmospheric inputs. It should however be noted that as
369 the mineral weathering inputs of base cations decreased, the relative contribution of
370 atmospheric inputs to total inputs increased (Figure 6). This underlines the high sensitivity of
371 Bio type sites to changes in atmospheric deposition regimes.

372 There was no clear relationship between foliar nutrient contents and tree growth/productivity
373 (negative or non-significant positive Pearson correlation, data not shown), but the Mg, K and P
374 foliar contents in green leaves were on average higher at the Geo sites compared to the Bio sites
375 (Supplementary material 3). This may be partly due to tree species effects (some tree species
376 were only present in one of the groups; e.g. *Eucalyptus* at Bio sites, *Pseudotsuga* at BioGeo sites,
377 *Quercus* at Geo sites) but it is more likely that foliar contents mirror the levels of available
378 nutrients in soils, as reported by several authors. Thus, caution should be taken in the use of this
379 indicator since it may be more related to nutrient availability in the soil than to tree
380 growth/productivity.

381 Furthermore, in each group (Bio, BioGeo and Geo), the variability of tree growth may be high,
382 with $H_0:H_{max}$ ranging from circa 0.5 to 1 in the Geo and BioGeo groups (Figure 5; Table 2). No
383 clear relationship was observed between tree productivity and available pools of nutrient in the
384 soil, nor the nutrient fluxes in the ecosystem. This suggests that other factors may exercise
385 control over tree growth/productivity (e.g. climate, elevation...) (Seynave *et al.*, 2005; Charru *et*
386 *al.*, 2017) resulting in large differences within each group. We did not have sufficient data to
387 assess precisely the role of each factor and their effects on nutrient cycling, but another way of
388 looking at this could be that ecosystems with 'optimal/good' and 'non-optimal/ dys-' functioning
389 exist within each group. For example, accumulation of organic matter in the forest floor due to
390 harsh climate, or even elevated nutrient leaching due to strong soil acidification may result in a
391 non-optimal functioning and reduced growth. Optimal functioning on the other hand would
392 allow a high rate of growth/productivity.

393 **4.1.3 Strategy to maintain and optimise nutrients through biogeochemical cycling**

394 We define the efficiency as the capacity to maintain and optimize nutrients in the soil-plant
395 system. Many strategies can be considered and we relate hereafter this efficiency to the
396 hypothesized typology of nutritional functioning of forest ecosystems.

397 Firstly, tree biomass production may be maintained whilst reducing the amount of nutrients
398 taken up annually from the mineral soil reservoir. This may be achieved through
399 biological/biochemical processes such as internal translocation within the tree or prior to
400 litterfall, as suggested by several authors (Attiwill and Adams, 1993; Tiessen *et al.*, 1994; Ranger
401 and Turpault, 1999; Laclau *et al.*, 2003b). The litterfall fluxes of nutrients were not higher at the
402 Bio sites compared to the Geo sites (but rather the opposite, except for Mg at the Bio Trop sites)
403 (Table 5) but the relative contribution of this flux to annually supply the soil reservoir is smaller
404 for the Geo types than for the Bio types. Indeed, the recycling of nutrients appears of crucial
405 importance for the Bio types, simply because inputs to the soil through the Geo cycle were
406 scarce (Figure 6). The capacity of plants to remobilize part of the nutrients contained in their
407 foliage prior to litterfall is also a key process to maintain nutrients within plants (Lambers *et al.*,
408 2008; Achat *et al.*, 2018). Achat *et al.* (2018) found from a dataset composed of 102 forest
409 ecosystems in France that the larger the soil nutrient pool was, the lower was the remobilization
410 rate in tree foliage for S, N, P, Ca and Mg. Our dataset was smaller but we found similar patterns
411 for Ca, K and N, with significant negative relationships between foliar remobilization rates and
412 soil nutrient pools (significant Pearson correlation coefficient of -0.62, -0.66 and -0.53,
413 respectively) (Supplementary material 4), resulting on average in higher foliar remobilization
414 rate at the Bio sites compared to the other types for these nutrients. Another way of optimizing
415 nutrients relies on tree autecology and its capacity to produce woody biomass with low net
416 nutrient uptake, but no clear trend was observed in our dataset to support this view.

417 Secondly, the efficiency of biogeochemical cycles is highly dependent on the extent of nutrient
418 leaching. In the Bio group, nutrient leaching fluxes were lower than in the Geo and BioGeo
419 groups and represented a much smaller share of the total output flux (Figure 6). In temperate
420 forest soils, anions other than phosphate and to a lesser extend sulphate do not interact much
421 with the soil solid phase and, if not taken up by plants or soil fauna, are rapidly leached with
422 percolating water (Legout *et al.*, 2016). The positive correlation (Pearson correlation
423 coefficient=0.67, Figure 7a) between drainage losses of N and base cations at the studied sites

424 suggests that nitrates act as a major driver for the leaching fluxes. Previous studies support this
425 view at these sites (Marques and Ranger, 1997; Ranger *et al.*, 1997; Legout *et al.*, 2011; van der
426 Heijden *et al.*, 2013), as well as in other temperate and boreal forests (Hogberg *et al.*, 2006;
427 Hynicka *et al.*, 2016). However, other anions such as chloride or sulphate can also prevail over
428 nitrate at some sites (van der Heijden *et al.*, 2011; Akselsson *et al.*, 2013) but the input-output
429 fluxes were not available for these elements for most of the sites included in this study. To be
430 exhaustive, large nutrient leaching fluxes may also occur in the Bio type sites but the Bio sites we
431 studied showed low nutrient leaching fluxes, which likely contributes to explaining the high
432 efficiency and productivity at these sites. One thing is certain, geochemical cycling has to be as
433 conservative as possible with low nutrient leaching to maintain an optimal functioning and a
434 high production, especially for the Bio types where weathering and atmospheric inputs to the
435 soil are low.

436 Lastly, this efficiency relies on the balance between inputs (weathering and atmospheric
437 deposition) and outputs (tree net uptake and drainage losses) to the soil (Ranger and Turpault,
438 1999). Our results show that even if the inputs were high at the Geo and BioGeo sites, the input-
439 output budgets were on average not greater at these sites compared to the Bio sites (Figure 6;
440 Table 5), because of the high leaching fluxes previously discussed (Figure 7a). Several factors
441 may induce high leaching fluxes in forest ecosystems, such as climate, silvicultural practices or
442 land use change (Marques and Ranger, 1997; Jussy *et al.*, 2000), as well as past and/or current
443 high S-N deposition (Vuorenmaa *et al.*, 2017). In our study, N atmospheric deposition plays a key
444 role in nutrient drainage losses and nutrient budgets, with strong relationships between N
445 inputs and N drainage losses (Figure 7b) (significant Pearson correlation coefficient, $r = 0.77$), as
446 also reported by de Vries *et al.* (2007). These N depositions, combined at the BioGeo sites with a
447 possible past agricultural use, may have even at some sites caused N saturation of the ecosystem
448 (Aber *et al.*, 1989; Aber *et al.*, 1998; Aber *et al.*, 2003; Oulehle *et al.*, 2012; Rennenberg and
449 Dannenmann, 2015; Schmitz *et al.*, 2019) with N losses approximating or exceeding the N inputs
450 (Figure 7b). Regardless of the origin and cause, important nitrate losses may cause strong soil

451 acidification and ecosystem dysfunctioning, leading to soil degradation, tree nutrition disorder,
452 reduction of tree growth/productivity and more generally to the progressive loss of some
453 ecosystem functions (Reuss and Johnson, 1986; Schulze, 1989; Dambrine *et al.*, 1998; Jonard *et*
454 *al.*, 2015). As a result, no relationship was observed between tree productivity (H0:Hmax) and
455 the input-output budgets (Supplementary material 5). It should also be noted that the negative
456 input-output budgets at the Bio Trop sites (especially for N and K) do not result from elevated
457 leaching fluxes but from net uptake by trees. At these sites, *Eucalyptus* plantations are managed
458 in short rotations to maximize biomass production. The stands are fertilized to compensate for
459 nutrient imbalances, but fertilization inputs were not included in the budget calculations thus
460 explaining the observed negative budgets (Figure 6).

461 **4.2 Redefining the concept of chemical fertility in forest ecosystems**

462 Our results show that the concept of chemical fertility inherited from agronomy and defined as
463 the pool of available nutrient in the soil is not sufficient to explain forest productivity. The basic
464 principles of a new concept adapted to forest ecosystems were proposed by (Legout *et al.*, 2014)
465 and we update here the general outlines in the light of our results.

466 Firstly, our results underline the importance to include biogeochemical cycling in the definition
467 to account for the dynamic aspect of chemical fertility in forests: permanent circulating pool of
468 nutrient within the soil- plant system. The knowledge of the preponderance of the biological or
469 geochemical component of cycling is of paramount importance, as well as the amounts of
470 nutrients making it possible to insure (through recycling) a suitable functioning of the soil-plant
471 system.

472 Secondly, the definition needs to encompass time scales by considering both current and long-
473 term appraisals. The current chemical fertility level is defined by the plant available pools in the
474 soil, the small but regular fluxes of nutrients (litterfall, atmospheric inputs, remobilisation
475 within the tree, possible liming or fertilizer inputs), as well as the capacity of soils to retain

476 nutrients (especially linked to organic matter and clay contents), which enables to prevent
477 losses of nutrients added to the soil reservoir from the geochemical cycle (Bedel *et al.*, 2018).
478 The long-term chemical fertility level can be assessed through the capacity of the soil to maintain
479 or even restore its properties (chemical, but also physical and biological) after punctual or
480 regular pressures through nutrient inputs allowing stock restoration over time.

481 Lastly, the conversion of a potential production to an actual production needs to be determined.
482 For this, additional components closely related to the chemical fertility have to be considered to
483 assess tree production: hydrological constraints (excess or deficit of water), nutrient
484 requirements specific to each tree species (depending on autecology, rate of development and
485 production), soil exploration by roots depending on physical constraints (compaction, hypoxia,
486 water saturation, etc.) and the resource use strategy of each species (uptake relative to the soil
487 water potential with an access to different water types characterized by different chemical
488 compositions, temporal changes in the vertical distribution of uptake in the soil profile, etc.).

489 **4.3 Implications for forest management**

490 Forest management practices directly impacts the biological cycle, particularly through tree
491 biomass exports. Given the current context of increased demand for energy-wood (Achat *et al.*,
492 2015; Pyttel *et al.*, 2015; Thiffault *et al.*, 2015; Garcia *et al.*, 2018), the typology of nutritional
493 functioning proposed in our study clearly underlines the importance of management policies
494 regarding harvest residues, particularly when the chemical fertility and stand nutrition relies
495 primarily on the biological component of nutrient cycles (Bio-type forest ecosystems). In such
496 cases, the biological component is a major pillar of tree nutrition and may allow, through an
497 efficient recycling of nutrients, high growth rates/productivities in soils containing very low
498 stocks of bioavailable nutrients. However, any disruption of the biological cycle in these
499 vulnerable ecosystems can rapidly reduce growth rates/productivity (Nzila *et al.*, 2002), which
500 may be i) all the more strong and fast if the soil is nutrient-poor (Legout *et al.*, 2014), and/or ii)
501 accompanied by an acceleration of soil acidification (Reuss and Johnson, 1986). Conversely, Geo

502 type forest ecosystems may support higher nutrient exports thanks to large available soil pools
503 and its ability to continuously and abundantly replenish the soil reservoir through weathering,
504 atmospheric deposition or even, in some cases, other inputs such as capillary rise from deep
505 groundwater.

506 **5 Conclusion**

507 A typology of nutritional functioning of forest ecosystems based on the relative importance of
508 the different components of the biogeochemical cycles (Bio and Geo) emerges from our study.
509 When the Geo component of the cycle is predominant (inputs through mineral weathering
510 and/or atmospheric inputs, capillary rise), sufficient nutrients are provided to the plant-soil
511 system to ensure tree growth and to fill the soil reservoir, thus, participates significantly to tree
512 nutrition. Conversely, when the Geo component of the cycle brings too few nutrients to the
513 plant-soil system, the role of the Bio component (litterfall, organic matter mineralization, plant
514 internal cycling) of the biogeochemical cycles becomes predominant to supply the nutrient
515 demand for tree growth.

516 Our findings also show that the concept of chemical fertility inherited from agronomy and
517 defined as the pools of available nutrients in soil is not adapted to forest ecosystems, especially
518 when the Bio component is predominant in the biogeochemical cycles, because small but active
519 nutrient fluxes may continuously replenish the soil reservoir or may directly ensure tree
520 nutrition by bypassing the soil reservoir. In this case, forest production can be high even though
521 the pools of nutrients in the soil reservoir are very low. In contrast, even if high nutrient inputs
522 through weathering and atmospheric deposition are expected to importantly replenishing
523 available pools in soils at some sites, high drainage losses and/or dysfunction (elevated
524 acidification, elevated exportation by harvesting, etc.) may counteract these effects, leading to
525 low forest productivity. Further studies are needed to validate our typology and to gain insight
526 into the relationships between biogeochemical cycling, chemical fertility and tree productivity in
527 forest ecosystems.

528 Forest fertility commonly assessed by the dominant height of the forest stand reached at a given
529 age is not indicative of the sensitivity of the ecosystem to nutrient exports. Relying on current
530 production to determine forest harvesting could be very harmful for the ecosystem, depending
531 on its type (Bio Vs. Geo). Considering an equivalent production between a Bio type ecosystem
532 and a Geo type ecosystem, the consequences of any disruption of the biological cycling (elevated
533 biomass exportation, shortening of rotation, intensive harvesting of residues, etc.) would differ
534 between the types, because the Geo type would be more capable to buffer the endured pressure.
535 Our typology of forest ecosystem can contribute to understanding the nutritional functioning of
536 forest ecosystems, to identifying the possible causes of their dysfunctioning and to better
537 evaluating potential threats in a context of global changes.

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761

762 **Figure captions**

763 **Figure 1.** Schematic description of the biogeochemical cycling in forest ecosystems where the
764 biological cycle is dominant (left) and in forest ecosystems where the geochemical cycle is dominant
765 (right).

766 **Figure 2.** a. Relationship between exchangeable base cations (EBC) pools in the 0-70cm soil layer and
767 the inputs of base cations to the soil (weathering plus atmospheric deposition fluxes: W+AD), related
768 to the type of ecosystem functioning (Bio, BioGeo and Geo). b. Relationship between exchangeable
769 base cations (EBC) pools in the 0-70cm soil layer and the base cation weathering flux (W), related to
770 the type of ecosystem functioning (Bio, BioGeo and Geo). Tropical (Bio-trop) and temperate (Bio-
771 temp) forest ecosystems dominated by the biological cycle are distinguished.

772 **Figure 3.** Exchangeable/available and total pools of C, N, P, K, Ca and Mg in the 0-70cm soil layer,
773 related to the type of ecosystem functioning (Bio, BioGeo and Geo). Different letters indicate
774 significant differences ($p < 0.05$) between Bio (Temp+Trop), BioGeo and Geo groups (Tukey HSD test
775 following ANOVA).

776 **Figure 4.** Average number of years of potential nutrient uptake in the 0-70cm soil layer, computed
777 dividing the total nutrient stock by the net uptake ($Y_{net\ uptake}$ see material and methods section) for
778 exchangeable Ca, K, Mg and exchangeable base cation (BC) (left), total N and available P (right).
779 Different letters indicate significant differences between Bio (Temp+Trop), BioGeo and Geo groups
780 for each nutrient (Tukey HSD test following ANOVA).

781 **Figure 5.** a. Relationship between H0:Hmax and exchangeable base cations (EBC) pools in the 0-70cm
782 soil layer, related to the type of ecosystem functioning (Bio, BioGeo and Geo). b. Relationship
783 between H0:Hmax and the inputs of base cation to the soil (sum of weathering plus atmospheric
784 deposition fluxes = W+AD), related to the type of ecosystem functioning (Bio, BioGeo and Geo).

785 **Figure 6.** Annual fluxes (litterfall, atmospheric deposition, weathering, net uptake, drainage losses)
786 and input-output budget (I-O Budget) for base cation (BC), Ca, Mg, K, N and P computed at the
787 studied sites, related to the type of ecosystem functioning (Bio, BioGeo and Geo). Input-Output were

788 computed without litterfall fluxes (internal cycling within the ecosystem) and considering net uptake
789 as the increment in nutrient content in stem biomass. P input-output budgets were not computed
790 due to incomplete dataset.

791 **Figure 7.** N drainage losses related to Base Cation (BC) drainage losses (a) and N drainage losses
792 related to N atmospheric deposition (b) at the studied sites, depending on the type of ecosystem
793 functioning (Bio, BioGeo and Geo).

794 **Table List**

795 **Table 1.** Basic information about the nine temperate and two tropical sites and main references.

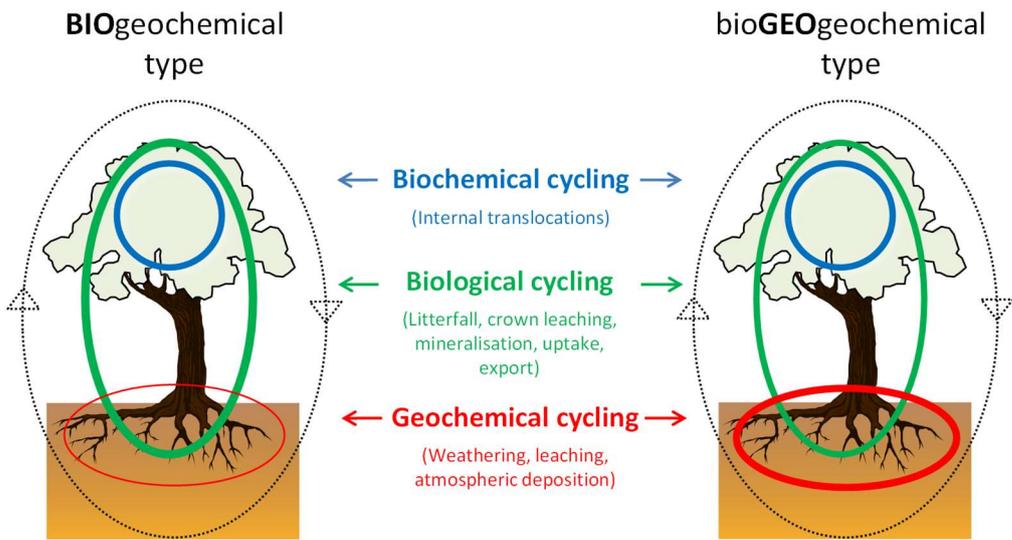
796 **Table 2.** Tree species, stand age, rooting depth (R95%), maximum measured drainage depth and
797 height index (see definition in the material and methods section) presented per site

798 **Table 3.** Methods used to quantify pools and fluxes of different elements

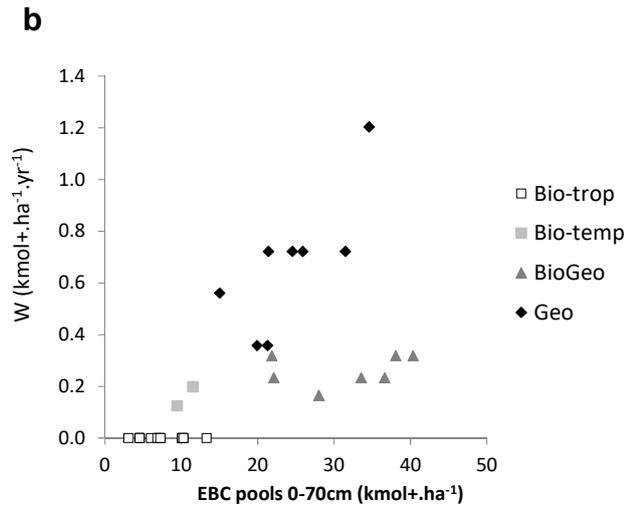
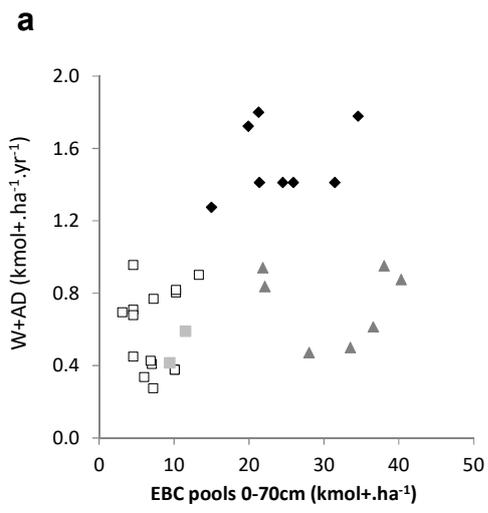
799 **Table 4.** Input-Output Budgets for Ca, K, Mg, N and P ($\text{kg ha}^{-1} \text{yr}^{-1}$) at the studied sites. Input-Output
800 Budget were computed considering net nutrient uptake as the increment in nutrient content in
801 above ground biomass.

802 **Table 5.** Mean values of litterfall, total inputs (weathering + deposition), net uptake (increment in
803 nutrient content in stem biomass), drainage losses and input-output budget for base cation (BC), Ca,
804 Mg, K, N and P, according to the type of ecosystem functioning (Bio, BioGeo and Geo). Input-Output
805 Budget were computed without litterfall fluxes and considering net uptake as the increment in
806 nutrient content in stem biomass. Different letters indicate significant differences between Bio
807 (Temp+Trop), BioGeo and Geo groups (Tukey HSD test following ANOVA).

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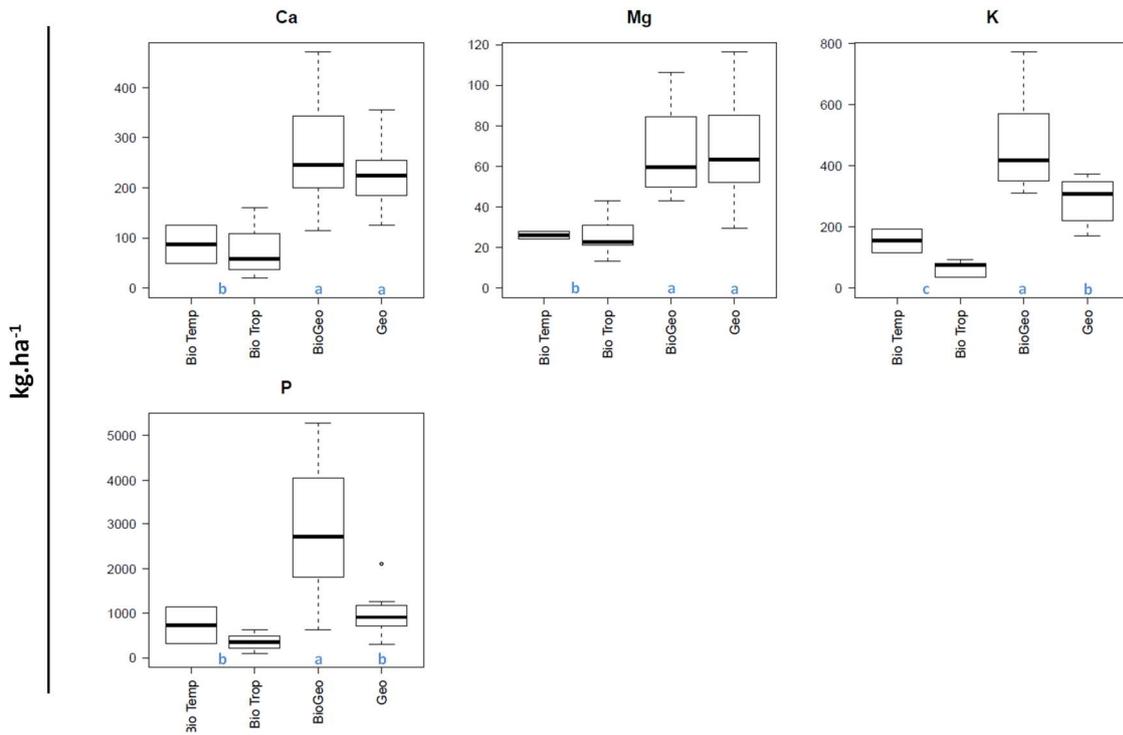


811 **Figure 2.**

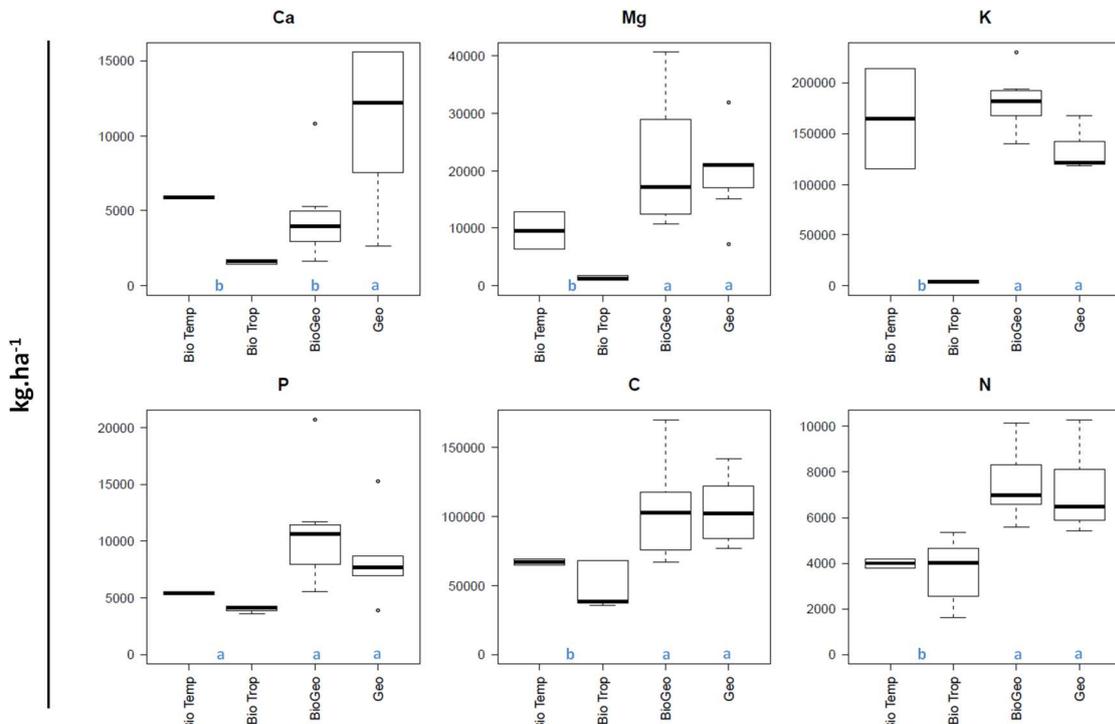


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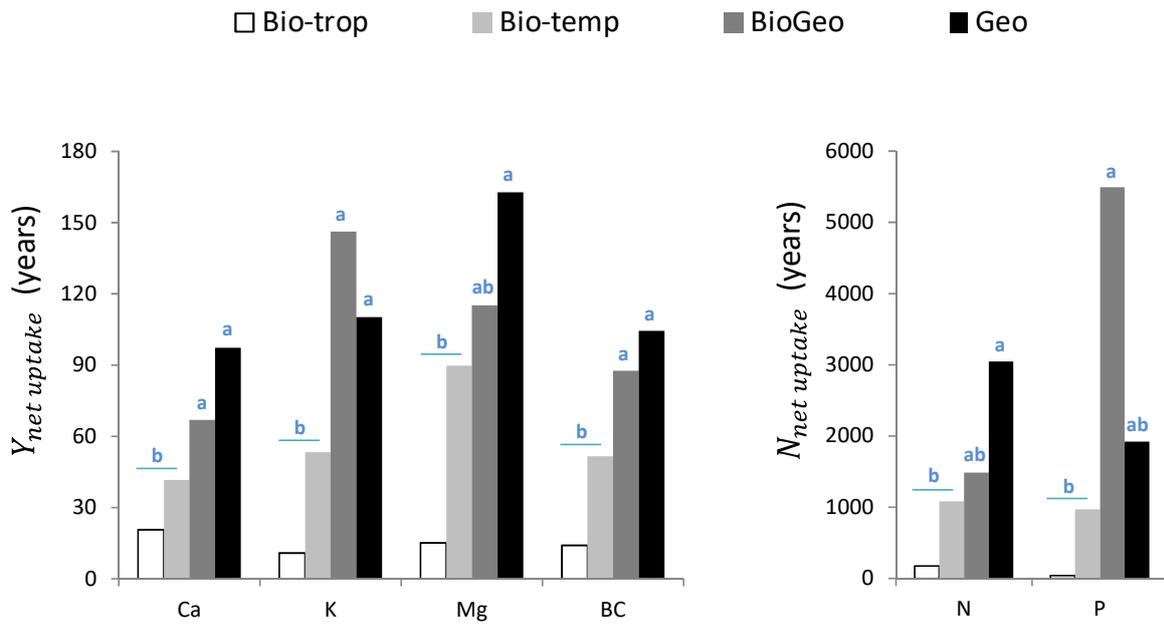
Exchangeable or available pools in the 0-70cm soil



Total pools in the 0-70cm soil

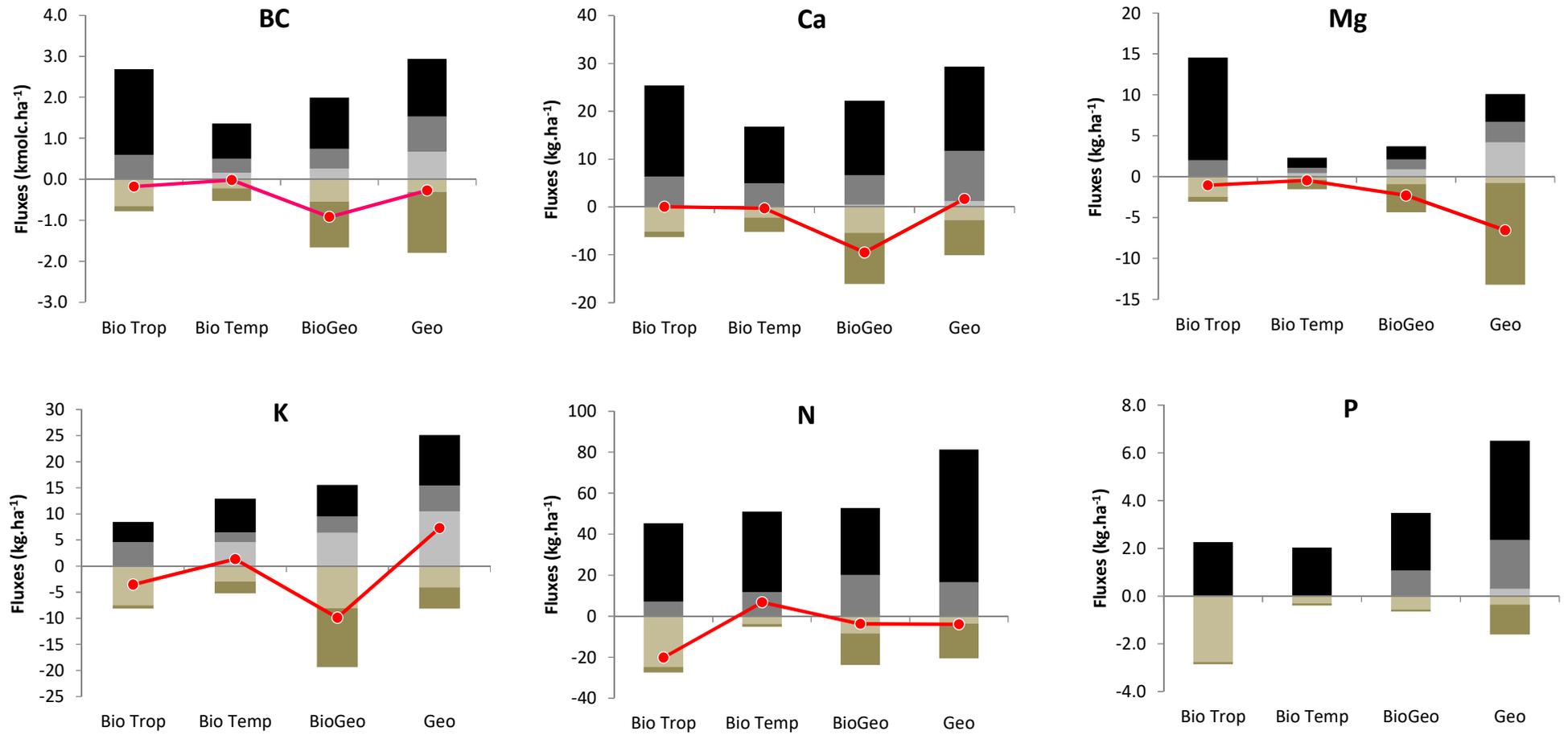


815 **Figure 4.**



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Litterfall
 Atmospheric Deposition
 Weathering
 Net uptake
 Drainage losses
 I-O Budget



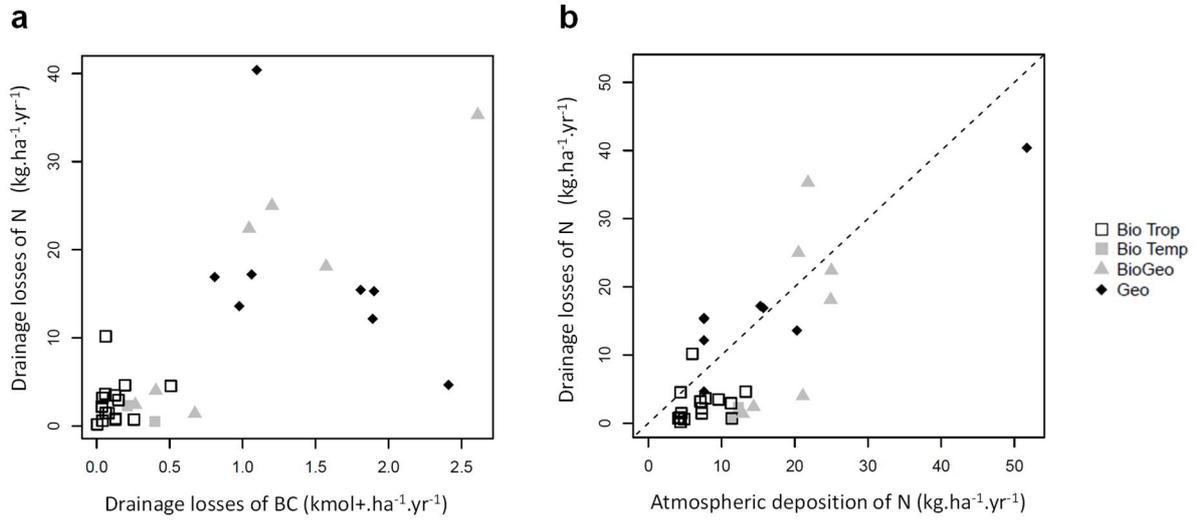


Table 1.

Site	Abbreviation	Location	Elevation (m)	Mean annual precipitation (mm year ⁻¹)	Mean Temp (C°)	Precipitation: temperature	Year of stand establishment*	Year of sampling	Bedrock	Soil type (WRB)	Main references	Type
Abreschviller, Vosges	Abr	48°38'N;7°05'E	400	1250	8,5°	147	1940	1994; 1998; 2007	Vosgian sandstone	Dystric cambisol	(van der Heijden et al., 2011)	Bio (Bio-temp)
Aubure, Vosges	Au1	48°12'N;7°11'E	1080	1400	8,5°	165	1900; 1958; 1978	1985; 1991; 1994; 1996	Brézouard granite, strong hydrothermal alteration	Dystric cambisol	(Fichter, 1997)	BioGeo
Aubure, Vosges	Au2	48°12'N;7°11'E	1080	1400	8,5°	165	1850	1985; 1991; 1994	Brézouard granite, weak hydrothermal alteration	Podzolic cambisol	(Fichter, 1997)	BioGeo
Bonhomme, Vosges	Bon	48°10'N;7°01'E	1100	1544	5°	309	1918	1988	Valtin leucocrate granite	Podzolic cambisol	(Mohamed Ahmed, 1992)	Geo
Breuil, Morvan	Bre	46°30'N;4°38'E	650	1280	9°	142	ca 1826; 1976	2001	Vire Type granite	Dystric cambisol	(Mareschal, 2008; van der Heijden, 2013)	Bio (Bio-temp)
Fougères, Bretagne	Fou	48°23'N;1°8'W	175	868	12,9°	67	1851; 1915; 1971; 1988	1996; 2001; 2003	Vire Type granite	Dystric cambisol	(Legout, 2008)	Geo
Gemaingoutte, Vosges	Gem	48°15'N;7°5'E	650	1120	8,5°	132	1904	1988; 1991	Varied lithology gneiss	Dystric cambisol	(Mohamed Ahmed, 1992)	Geo
Itatinga, São Paulo, Brazil	Ita	23°02'S;48°38'W	850	1370	19,2°	71	1998; 2004	2003; 2005, 2007	Detritic sands	Ferralsol	(Almeida, 2009; Maquere, 2008)	Bio (Bio-trop)
Kondi, Pointe-Noire, Congo	Kon	4°33'S;11°54'E	100	1200	25°	48	1992; 1998; 2005	1998, 2000, 2001; 2006	Continental sands	Ferralic Arenosols	(Laclau, 2001; Mareschal et al., 2011)	Bio (Bio-trop)
Monthermé, Ardennes	Ard	49°52'N;4°48'E	390	1100	8°	138	1831; 1931	1977; 1997	Blue-grey phyllites	Dystric cambisol	(Nys, 1987)	Geo
Vauxrenard, Beaujolais	Vau	46°10'N;4°38'E	770	1000	7°	143	1950; 1970	1993	Vosges Volcanic tuf	Dystric cambisol	(Marques, 1996)	BioGeo

Table 2.

Abreviation	Species	Stand age	R95% (cm)	Maximum measured drainage depth	$H_0:H_{max}$
AbrAa55	<i>Abies alba</i> Mill.	55	125	70	0.80
ArdPa50	<i>Picea abies</i> (L.) Karst.	50	110	60	0.59
ArdQp140	<i>Quercus petraea</i> (Matt.) Liebl.	140	110	60	0.59
Au1Pa15	<i>Picea abies</i> (L.) Karst.	15	100	60	0.52
Au1Pa35	<i>Picea abies</i> (L.) Karst.	35	100	60	0.58
Au1Pa85	<i>Picea abies</i> (L.) Karst.	85	100	60	0.76
Au2Fs150	<i>Fagus sylvatica</i> L.	150	135	60	0.70
BonPa70	<i>Picea abies</i> (L.) Karst.	70	80	60	0.70
BreFs30	<i>Fagus sylvatica</i> L.	30	80	60	0.75
FouFs13	<i>Fagus sylvatica</i> L.	8-13	140	120	0.68
FouFs150	<i>Fagus sylvatica</i> L.	145-150	155	120	0.68
FouFs30	<i>Fagus sylvatica</i> L.	25-30	145	120	0.86
FouFs86	<i>Fagus sylvatica</i> L.	80-86	150	120	0.78
GemPa84	<i>Picea abies</i> (L.) Karst.	84	120	60	1.00
ItaEu0-1	<i>Eucalyptus grandis</i> W. Hill ex Maiden	0-1	340	300	0.98
ItaEu1-2	<i>Eucalyptus grandis</i> W. Hill ex Maiden	1-2	340	300	0.98
ItaEu2-3	<i>Eucalyptus grandis</i> W. Hill ex Maiden	2-3	400	300	0.98
ItaEu3-4	<i>Eucalyptus grandis</i> W. Hill ex Maiden	3-4	400	300	0.98
ItaEu4-5	<i>Eucalyptus grandis</i> W. Hill ex Maiden	4-5	400	300	0.98
ItaEu5-6	<i>Eucalyptus grandis</i> W. Hill ex Maiden	5-6	400	300	0.98
KonEu0-1	<i>Eucalyptus hybrid (unknown)</i>	0-1	340	600	0.80
KonEu1-2	<i>Eucalyptus hybrid (unknown)</i>	1-2	400	600	0.80
KonEu2-3	<i>Eucalyptus hybrid (unknown)</i>	2-3	400	600	0.89
KonEu3-4	<i>Eucalyptus hybrid (unknown)</i>	3-4	400	600	0.90
KonEu4-5	<i>Eucalyptus hybrid (unknown)</i>	4-5	400	600	0.90
KonEu6-7	<i>Eucalyptus hybrid (unknown)</i>	6-7	400	600	0.95
KonEu7-8	<i>Eucalyptus hybrid (unknown)</i>	7-8	400	600	0.95
KonEu8-9	<i>Eucalyptus hybrid (unknown)</i>	8-9	400	600	0.95
VauPm20	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	20	85	60	0.74
VauPm40	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	40	85	120	0.81
VauPm60	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	60	85	120	0.93

Table 3.

		Method	Reference
Pools	Soil	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
		Total elements	ICP following alkaline fusion Carignan et al., 2001
		Available P ₂ O ₅	Duchaufour method, resin extraction, Dyer (AFNOR NFX 31-160) Dyer, 1894; Duchaufour and Bonneau, 1959; Amer et al 1955; Malavolta <i>et al.</i> , 1989
		Exchangeable Elements	Extraction with KCl, NH ₄ Cl or NH ₄ Ac followed by titration (H, Al), atomic abs or ICP NFX 31-130 2009: Espiau & Peyronel 1976
Pools	Forest floor	Dry matter, total elements	Collected per unit area, weighted and analysed (C, N, Ca, Mg, K, P). Coupling between dry matter and the corresponding measured concentrations
	Tree biomass & mineralmass	(i) stand inventories periodically, circumference at breast height (Circ1.30m) (ii) destructive sampling of trees distributed over the whole spectrum of inventoried Circ1.30 classes (iii) samples chemical analyses (C, N, Ca, Mg, K, P) (iv) fitting total above-ground biomass and mineralmass allometric equations (v) quantification of the stand biomass and nutrient content on a per hectare basis by applying the fitted equations to each stand inventory	Sattoo and Madgwick, 1982 applied in numerous studies (Alban et al., 1978; Ranger et al., 1995; Saint-André et al., 2005; Sicard et al., 2006)
Fluxes	Atmospheric deposition	Wet deposition calculated from bulk precipitation. Dry deposition was estimated from throughfall data, in most cases calculated according to equations from Ulrich (1983)	Ulrich 1983
	Weathering	Geochemical model PROFILE or historical weathering and, for the older sites Ard and Bon, weathering rates estimated from literature	Svedrup and Warfvinge 1988; Sudom and St Arnaud 1971; Bonneau et al 1991
	Uptake by trees	Current annual increment in aboveground biomass (and mineralmass) calculated as the difference in biomass (and mineralmass) between years, usually measured over 1-5 years.	Sattoo and Madgwick, 1982
	Leaching, throughfall, stemflow	Coupling between measured lysimeter concentrations and estimated water flux. Water fluxes estimated through water balance equation or model	Granier et al, 1999 ; van der Heijden et al, 2013; Legout et al, 2016
	Litterfall	Collected per unit area, weighted and analysed (C, N, Ca, Mg, K, P) 2-12 times per year, depending on sites. Coupling between dry matter and the corresponding measured concentrations for each period	

830 **Table 4.**

Site	Type	Atmospheric deposition					Weathering				Deep leaching					Net uptake (increment in aboveground biomass)					Budget				
		Ca	K	Mg	N	P	Ca	K	Mg	P	Ca	K	Mg	N	P	Ca	K	Mg	N	P	Ca	K	Mg	N	P
AbrAa55	Bio	5.7	2.3	0.6	11.4	0.0	0.3	6.2	0.3	0.0	4.7	1.9	1.4	0.5	-	3.8	3.4	0.3	6.5	0.4	-2.5	3.2	-0.8	4.4	
ArdPa50	Geo	20.6	5.6	3.3	51.7	0.3	1.5	8.5	0.8	-	14.0	6.9	2.7	40.4	0.1	6.7	5.2	1.1	8.5	0.8	1.4	2.0	0.3	2.8	
ArdQp140	Geo	18.7	6.6	3.2	20.3	0.3	1.5	8.5	0.8	-	11.8	3.6	3.6	13.6	0.1	5.1	4.1	0.5	9.0	0.7	3.3	7.4	-0.1	-2.3	
Au1Pa15	BioGeo	2.9	2.2	0.8	12.9	0.0	0.2	6.0	0.9	-	7.7	7.1	1.3	1.4	-	4.7	4.7	0.6	5.9	0.2	-9.3	-3.6	-0.3	5.6	
Au1Pa35	BioGeo	4.4	2.8	1.1	21.1	0.0	0.2	6.0	0.9	-	2.6	6.6	1.3	4.0	-	10.7	7.5	1.2	10.2	0.5	-8.7	-5.3	-0.6	6.9	
Au1Pa85	BioGeo	7.0	4.5	1.7	25.0	0.0	0.2	6.0	0.9	-	11.5	11.0	2.3	22.4	-	3.7	1.7	0.4	3.3	0.7	-8.0	-2.2	-0.2	-0.7	
Au2Fs150	BioGeo	3.8	1.7	0.9	14.4	0.0	0.2	4.0	0.7	-	2.4	3.1	0.8	2.4	-	3.2	2.3	0.4	2.8	0.2	-1.6	0.3	0.3	9.1	
BonPa70	Geo	9.6	4.4	1.5	15.7	2.5	1.0	18.7	0.4	-	7.9	7.2	2.8	16.9	1.1	3.2	3.2	0.8	4.9	0.6	-0.5	12.7	-1.7	-6.1	
BreFs30	Bio	3.7	1.6	0.8	12.3	0.0	0.2	2.9	0.5	0.0	1.4	2.6	0.9	2.3	0.1	5.6	8.9	1.2	14.3	1.3	-3.1	-7.0	-0.8	-4.3	-0.5
FouFs13	Geo	7.1	4.8	2.6	7.6	2.8	0.5	4.8	7.0	0.3	5.9	3.4	24.6	4.7	2.4	4.5	7.6	1.4	11.3	1.6	-2.8	-1.4	-16.4	-8.3	-0.1
FouFs150	Geo	7.1	4.8	2.6	7.6	2.8	0.5	4.8	7.0	0.3	2.7	3.4	20.4	15.3	1.7	7.5	21.3	2.9	33.9	4.2	-2.5	-14.4	-13.9	-38.5	1.2
FouFs30	Geo	7.1	4.8	2.6	7.6	2.8	0.5	4.8	7.0	0.3	2.6	2.7	20.6	12.2	2.5	8.6	15.9	2.8	9.1	1.0	-4.3	-9.1	-12.3	-17.0	-0.2
FouFs86	Geo	7.1	4.8	2.6	7.6	2.8	0.5	4.8	7.0	0.3	3.3	2.9	19.1	15.4	1.7	9.8	4.5	1.1	7.5	1.3	-4.9	1.7	-11.9	-15.2	1.0
GemPa84	Geo	6.9	4.2	1.5	15.3	2.0	3.8	28.7	3.4	-	10.2	2.3	6.0	17.2	0.4	14.1	6.6	2.1	30.4	2.5	-13.6	24.0	-3.2	-32.3	
ItaEu0-1	Bio	3.6	3.3	0.9	4.4	-	0.0	0.0	0.0	0.0	6.1	1.7	1.9	4.5	0.0	11.1	11.9	2.8	19.1	1.3	-13.6	-10.3	-3.9	-19.3	
ItaEu1-2	Bio	10.0	6.0	3.7	4.9	-	0.0	0.0	0.0	0.0	0.5	0.2	0.1	0.6	0.0	43.4	36.6	13.6	56.3	3.5	-33.9	-30.8	-10.0	-52.0	
ItaEu2-3	Bio	3.9	4.2	1.8	4.5	-	0.0	0.0	0.0	0.0	0.6	0.7	0.2	1.5	0.0	14.9	7.1	4.4	13.8	2.2	-11.6	-3.7	-2.8	-10.8	
ItaEu3-4	Bio	9.6	5.5	1.1	4.4	-	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.0	33.8	9.8	6.0	28.1	6.0	-24.3	-4.4	-4.9	-23.9	
ItaEu4-5	Bio	9.5	4.6	1.3	4.3	-	0.0	0.0	0.0	0.0	1.6	0.3	0.5	0.8	0.1	23.5	6.7	2.0	42.6	4.0	-15.7	-2.4	-1.2	-39.2	
ItaEu5-6	Bio	9.3	3.6	1.5	4.1	-	0.0	0.0	0.0	0.0	3.2	0.5	1.0	0.7	0.1	27.7	7.2	9.0	1.9	-0.3	-21.6	-4.1	-8.5	1.5	
KonEu0-1	Bio	2.8	2.1	1.0	6.0	-	0.0	0.0	0.0	0.0	0.4	0.8	0.3	10.2	0.1	10.2	13.6	8.8	12.9	3.1	-7.7	-12.3	-8.0	-17.0	
KonEu1-2	Bio	3.9	2.6	1.8	7.8	-	0.0	0.0	0.0	0.0	0.5	0.5	0.3	3.6	0.1	16.4	17.7	12.3	29.2	5.6	-13.0	-15.6	-10.7	-25.0	
KonEu2-3	Bio	4.8	3.2	1.3	7.1	-	0.0	0.0	0.0	0.0	0.3	0.4	0.2	3.2	0.1	15.2	15.0	10.6	29.8	5.4	-10.7	-12.2	-9.5	-25.9	
KonEu3-4	Bio	3.6	3.6	1.3	7.3	-	0.0	0.0	0.0	0.0	0.3	0.3	0.2	2.2	0.0	13.9	12.3	9.0	30.3	5.3	-10.6	-9.0	-7.9	-25.2	
KonEu4-5	Bio	3.6	3.6	1.3	7.3	-	0.0	0.0	0.0	0.0	0.7	0.5	0.4	1.4	0.1	12.0	9.6	7.4	32.7	5.8	-9.1	-6.5	-6.5	-26.8	
KonEu6-7	Bio	7.8	7.8	7.8	11.3	-	0.0	0.0	0.0	0.0	1.0	0.7	0.7	0.7	0.1	12.4	10.9	7.8	50.5	8.2	-5.3	-4.4	-4.7	-39.8	
KonEu7-8	Bio	7.8	7.8	7.8	11.3	-	0.0	0.0	0.0	0.0	0.7	0.8	0.8	3.5	0.2	9.3	8.2	5.9	37.5	6.1	-2.0	-2.9	-4.1	-31.4	
KonEu8-9	Bio	7.8	7.8	7.8	11.3	-	0.0	0.0	0.0	0.0	1.0	0.7	1.5	4.6	0.3	9.0	7.9	5.7	36.3	5.9	-2.8	-2.2	-3.8	-27.6	
VauPm20	BioGeo	7.5	3.3	1.2	21.8	0.9	0.9	7.5	1.0	-	25.0	25.0	8.8	35.3	0.2	17.0	35.9	3.6	33.2	2.9	-33.6	-50.1	-10.2	-46.7	
VauPm40	BioGeo	8.5	3.6	1.3	24.9	1.1	0.9	7.5	1.0	-	12.5	18.1	5.9	18.1	0.3	8.0	11.6	1.2	13.2	1.1	-11.1	-18.6	-4.8	-6.4	
VauPm60	BioGeo	8.7	3.6	1.3	20.5	1.2	0.9	7.5	1.0	-	13.5	8.1	3.9	25.0	0.2	2.6	1.8	0.3	4.0	0.3	-6.5	1.2	-1.9	-8.5	

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833 **Table 5.**

		Ca			Mg			K			BC			P			N		
		<i>(kg.ha⁻¹.yr⁻¹)</i>			<i>(kg.ha⁻¹.yr⁻¹)</i>			<i>(kg.ha⁻¹.yr⁻¹)</i>			<i>(kmol+.ha⁻¹.yr⁻¹)</i>			<i>(kg.ha⁻¹.yr⁻¹)</i>			<i>(kg.ha⁻¹.yr⁻¹)</i>		
		Bio	BioGeo	Geo	Bio	BioGeo	Geo	Bio	BioGeo	Geo	Bio	BioGeo	Geo	Bio	BioGeo	Geo	Bio	BioGeo	Geo
Litterfall	Mean	18.2	18.2	17.6	11.2	1.9	3.4	4.2	7.1	9.7	1.9	1.2	1.4	2.2	2.8	4.2	38.3	38.1	64.6
	Tukey HSD	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>b</i>	<i>ab</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>ab</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>
Total inputs	Mean	6.2	6.6	11.7	1.9	2.1	6.7	4.8	9.5	15.5	0.6	0.7	1.5	-	-	-	7.7	20.1	16.7
	Tukey HSD	<i>b</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	-	-	-	<i>b</i>	<i>a</i>	<i>a</i>
Net uptake	Mean	4.8	5.4	2.8	2.2	0.9	0.7	7.0	8.1	4.1	0.6	0.5	0.3	2.2	0.5	0.4	20.3	8.3	3.6
	Tukey HSD	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	<i>ab</i>	<i>b</i>
Drainage losses	Mean	1.4	10.7	7.3	0.7	3.5	12.5	0.8	11.3	4.1	0.1	1.1	1.5	0.1	0.2	1.3	2.6	15.5	17.0
	Tukey HSD	<i>b</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>a</i>	<i>a</i>
I-O Budgets	Mean	0.01	-9.5	1.7	-1.0	-2.3	-6.6	-3.0	-9.9	7.3	-0.2	-0.9	-0.3	-	-	-	-15.1	-3.7	-3.9
	Tukey HSD	<i>a</i>	<i>b</i>	<i>a</i>	<i>a</i>	<i>ab</i>	<i>b</i>	<i>ab</i>	<i>b</i>	<i>a</i>	<i>a</i>	<i>b</i>	<i>ab</i>	-	-	-	<i>a</i>	<i>a</i>	<i>a</i>

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