Effects of decomposing beech (*Fagus sylvatica*) logs on the chemistry of acidified sand and loam soils in two forest reserves in Flanders (northern Belgium)

Els Dhiedt\(^a\), Luc De Keersmaeker\(^a\), Kris Vandekerkhove\(^b\), Kris Verheyen\(^a\)

**Affiliation of all authors:**

\(^a\) Forest & Nature Lab, Department of Environment, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle, Belgium

\(^b\) Research Institute for Nature and Forest, Gaverstraat 4, 9500 Geraardsbergen, Belgium

**E-mail addresses for all authors in order:**

els.dhiedt@ugent.be
luc.dekeersmaeker@inbo.be
kris.vandekerkhove@inbo.be
kris.verheyen@ugent.be

**Corresponding author:**

Els Dhiedt
els.dhiedt@ugent.be
Abstract

We studied the effect of coarse woody debris (CWD) on the soil nutrient status in two beech (*Fagus sylvatica*) dominated forest reserves in Flanders, Belgium: Wijnendale Forest, on a sandy soil and Kersselaerspleyn in Sonian Forest, on a loamy soil. More specifically, we looked at the chemical composition of beech logs of different stages of decay. In addition, we examined the chemical composition of the organic and the mineral soil at five distances from the decomposing logs. We considered the concentrations of the following elements: C, N, P, S, Ca, K, Mg, Mn, Fe, and Al.

The results indicate a difference in wood and soil chemical composition between the two forest sites. The soil and the aboveground biomass of Wijnendale had the highest total N concentration and the lowest concentrations of P and base elements (Ca, K, Mg, and Mn). There is an increase in element concentrations in CWD of both forests during the decomposition, except for K and C. The higher N concentration in Wijnendale, explained by high atmospheric nitrogen deposition in this forest, persisted during decomposition. By contrast, the concentrations of P, Ca, K, and Mg in dead wood of both forests became similar when decomposition proceeded. The effect of CWD was more pronounced in the organic soil layer than in the mineral soil. The organic soil in the proximity of CWD had a higher pH and higher concentrations of C, N, P, Ca, Mg, and Mn (in Sonian forest) and a lower Al concentration (in Wijnendale forest) and this is highly significant for Ca, a limiting nutrient in moderate to highly acidic forests. The percentage of the soil surface impacted by the logs is 0.92% and 0.36% for Sonian and Wijnendale respectively, which is expected to increase with time, considering the fact that both reserves are only recently left unmanaged. The results of this study highlight the contribution of CWD in sustaining the nutrient status and buffering capacity of forest sites, in particular on soils sensitive to acidification and exposed to high nitrogen deposition.
1. **Introduction**

Coarse woody debris (CWD) is an important component of forest ecosystems (Harmon et al., 1986). Nevertheless, there are only small volumes to be found in managed forests throughout Europe (Hahn & Christensen, 2004) and also in Flanders, northern Belgium (ANB, 2017). Intensive logging and short rotations prevent trees from dying a natural death. In addition, death or dying trees are often removed for sanitary and safety reasons.

CWD can play an important role in the nutrient cycle in forests. When CWD decomposes, nutrients stored in the wood and bark during its life are released gradually. Previous studies indicate predominantly an increase in the wood concentration of most essential elements during decay, except for C and K (Alban & Pastor, 1993; Arthur & Fahey, 1990; Brown et al., 1996; Busse, 1994; Ganjegunte et al., 2004; Johnson et al., 2014; Krankina et al., 1999; Rinne et al., 2016). This increase can be ascribed to retention of these nutrients, due to high C:nutrient ratios (Stark, 1972), exploration of cord-forming fungi (Bebber et al., 2011; Wells & Boddy, 1990), recycling of fruiting bodies (Hoppe et al., 2014), atmospheric deposition, plant litter and animal inputs, precipitation and throughfall (Holub et al., 2001).

The contribution of CWD to the nutrient cycle is small in comparison to other forest compartments, e.g. leaf and root litter production (Laiho & Prescott, 2004). Nevertheless, there is an increase in nutrients in the soil underneath CWD, which causes spatial heterogeneity (Hafner & Groffman, 2005). This is due to several processes. CWD can have a direct impact on the soil composition due to leaching (Hafner et al., 2005), but it can also have a structural effect by creating a more favourable microclimate for microorganisms and consequently a higher mineralisation rate (Pettit & Naiman, 2005) and by accumulating litter (Orndorff & Lang, 1981). In addition, nutrients are released at a slower rate than from fine litter, reducing the losses due to leaching and volatilisation (Harmon & Chen, 1991).

Despite generally decreasing atmospheric deposition, concerns remain regarding the related soil acidification in Flanders (De Schrijver et al., 2006; Verstraeten et al., 2012) and other parts of Europe (e.g. Ahokas, 1997; Van der Salm & De Vries, 2000). The impact of CWD on the acidification is not clear. On the one hand, CWD retains base cations and thus reduces leaching (Harmon & Chen, 1991; Kuehne et al., 2008). On the other hand it may enlarge the N pool (Brown et al., 1996) as nitrogen is retained in (Stark, 1972) and even actively...
transferred to the CWD (Bebber et al., 2011) by decomposer organisms. Also, depending on the type of decay, the leachate can have an acidifying effect on the soil (Spears & Lajtha, 2004).

There have been many studies reporting the changes of the nutrient composition during the decay. However, less is known how this differs among sites. Understanding the impact on the nutrients in the soil is less straightforward and studies report contrasting results (e.g. Kappes et al., 2007; Krzyszowska-Waitkus et al., 2006; Spears & Lajtha, 2004), possibly due to different decomposing tree species and site conditions.

Therefore, we examined patterns in the chemical composition of CWD and the surrounding soil at different stages of decay in two forest reserves with a different soil texture and nutrient status. In this way our study serves as an important addition to previous studies that examine processes (e.g. Kuehne et al., 2008), since we aim at comparing two forest sites. Although this is only a small part of the forest soil, we focused on the topsoil, not only because there we can expect the largest impacts, but also since many important ecological processes take place in the first few centimetres of the soil, like rooting of the understory vegetation, tree regeneration, and housing a large part of the soil fauna and microbiota. We hypothesised that (1) except for C and K, the nutrient concentrations in CWD increase with increasing decay class, with lower concentration in the heart wood than in the sap wood; (2) there is an increase in C, macronutrients (N, P, and S), base elements (K, Ca, Mg, and Mn), a rise of the pH and a decrease of Al and Fe concentration close to CWD; (3) the impact of CWD on the soil increases with the decay stage; and (4) CWD with a larger nutrient stock has a greater impact on the soil.
2. Materials and methods

2.1. Sites

The study was conducted in two unmanaged forest reserves, in Wijnendale Forest and in Sonian Forest. The reserves have been left unmanaged approximately since 1985 and were formally designated in 1996 and 1995, respectively (Baeté et al., 2002, 2004). A description of the site characteristics is given in Table 1.

Table 1: Site characteristics of the two study sites (Baeté et al., 2002, 2004; De Keersmaeker et al., 2009; DOV, n.d.; KMI, n.d.-a, n.d.-b; Vandekerkhove et al., 2018; Verstraeten, 2018; http://www.lter-belgium.be/).

<table>
<thead>
<tr>
<th>Area (ha)</th>
<th>Sonian Forest</th>
<th>Wijnendale Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unmanaged forest reserve</td>
<td>4400</td>
<td>280</td>
</tr>
<tr>
<td>Altitude asl. (m)</td>
<td>102.5-122.5</td>
<td>20-45</td>
</tr>
<tr>
<td>Coordinates</td>
<td>50°44'48&quot;N, 4°25'07&quot;E</td>
<td>51°04'12&quot;N, 3°02'35&quot;E</td>
</tr>
<tr>
<td>Mean annual temperature (°C)</td>
<td>10.2</td>
<td>10.5</td>
</tr>
<tr>
<td>Mean annual precipitation (mm)</td>
<td>909</td>
<td>846</td>
</tr>
<tr>
<td>Soil texture (WRB classification)</td>
<td>Loam (Retisol)</td>
<td>Sandy loam (Umbrisol)</td>
</tr>
<tr>
<td>Humus type</td>
<td>Moder</td>
<td>Mor</td>
</tr>
<tr>
<td>Dominant tree species in reserve</td>
<td>Beech</td>
<td>Beech and Oak (Quercus robur)</td>
</tr>
<tr>
<td>Volume living stand &gt; 30 cm DBH in reserve (m³ ha⁻¹)</td>
<td>708</td>
<td>429</td>
</tr>
<tr>
<td>Volume CWD &gt;30 cm DBH in reserve (m³ ha⁻¹)</td>
<td>110 (45)⁴</td>
<td>44</td>
</tr>
<tr>
<td>Natura2000 habitat type</td>
<td>9120</td>
<td>9120</td>
</tr>
<tr>
<td>LTER site</td>
<td>LTER_EU_BE_02</td>
<td>LTER-EU-BE-05</td>
</tr>
</tbody>
</table>

⁴110 m³ ha⁻¹ in the core area (15 ha) where most trees were sampled, 45 m³ ha⁻¹ in the whole area that was sampled (Vandekerkhove et al., 2012).

Wijnendale forest is located in the western part of Flanders. The forest is surrounded by agricultural land, mainly arable fields. The topsoil is an acid sandy loam soil, classified as an Umbrisol (IUSS Working Group WRB, 2015). There is a clay substrate below a depth of 90 cm that impairs water percolation and creates a shallow groundwater table. The reserve of Sonian forest is located in a larger forest complex covering 4400 ha and is mostly surrounded by residential and urban areas at the south-eastern border of the city of Brussels. The acid loamy soil, with moderately low base saturation and a deep groundwater table, is classified as a Retisol (IUSS Working Group WRB, 2015).
Both forests are Long-Term Ecosystem Research Network (LTER) sites that contain an ICP-Forests Level-II intensive monitoring configuration (icp-forests.net), adjacent to the studied unmanaged forest reserves (http://www.lter-belgium.be/sites). Nitrogen deposition and soil water chemistry have been monitored at both sites since 1994. At the beginning of the monitoring, inorganic N deposition amounted to approximately 25 and 40 kg ha\(^{-1}\) yr\(^{-1}\) in Sonian forest and Wijnendale forest, respectively (Verstraeten, 2018), whereas the critical loads for broadleaved deciduous forests are considered to be between 10 and 20 kg ha\(^{-1}\) yr\(^{-1}\). After 1994, inorganic nitrogen deposition gradually decreased to approximately 19 kg N ha\(^{-1}\) year\(^{-1}\) in Wijnendale and 11 kg N ha\(^{-1}\) year\(^{-1}\) in Sonian forest in 2014 (Verstraeten, 2018). However, Wijnendale is still classified as an N-saturated forest that is still further acidifying due to atmospheric deposition of N. In Sonian forest soil water chemistry in 2014 indicated an early recovery from N saturation, and a positive value of the acid neutralizing capacity in the topsoil, indicating a slight recovery from acidification (Verstraeten, 2018).

### 2.2. Selection of the logs

In the summer of 2017 a total of 148 logs (79 in Sonian Forest and 69 in Wijnendale Forest) of beech were selected for this study. Only logs with an original diameter at 1m from the base of 40 cm and more were examined. The selection additionally aimed to cover all decay stages (see below).

To test for the effect on the soil, a subset of 45 logs (30 in Sonian Forest and 15 in Wijnendale Forest) were selected. Additional selection criteria for these logs were established: they are in contact with the soil, they are not situated in a zone with noticeable anthropogenic soil disturbance or on slopes in the direction perpendicular to the log, and they are isolated from other logs to prevent ‘interference’.

### 2.3. Measurements and calculations of explanatory variables

Diameter of all logs was measured at 1 m from the base of the log with a tree calliper. The diameters of the logs in Sonian Forest show a larger range compared to the ones in Wijnendale (Vandekerkhove et al., 2018). An average decay class was determined for all 148 logs. For this purpose, the logs were subdivided in sections of 2 m starting from the base of the log. For the crown part of the tree, the main branch was considered, if multiple branches were present. The decay class of the middle of each section was determined on a 6 class scale (Table 2). The first class (0) incorporates trees that have died that same year and has the same characteristics as class one, except for the presence of leaves on the branches. The other decay classes
include: no decay visible (1), superficial decay (2), moderate decay (3), advanced decay (4), and residues in
the litter layer (5) (De Keersmaeker et al., 2005). The decay class of the log was calculated as the average of
the different sections.

<table>
<thead>
<tr>
<th>Decay Class</th>
<th>Small branches</th>
<th>Bark</th>
<th>Penetration of knife blade</th>
<th>Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Present with dried leaves</td>
<td>Intact</td>
<td>Several mm</td>
<td>Circle</td>
</tr>
<tr>
<td>1</td>
<td>Present</td>
<td>Intact</td>
<td>Several mm</td>
<td>Circle</td>
</tr>
<tr>
<td>2</td>
<td>Absent</td>
<td>Loose, begins to peel off</td>
<td>Max 1 cm</td>
<td>Circle</td>
</tr>
<tr>
<td>3</td>
<td>Absent</td>
<td>Mostly peeled off</td>
<td>Several cm, mainly sapwood</td>
<td>Circle</td>
</tr>
<tr>
<td>4</td>
<td>Absent</td>
<td>Absent</td>
<td>Heartwood also soft</td>
<td>Flat elliptic</td>
</tr>
<tr>
<td>5</td>
<td>Absent</td>
<td>Absent</td>
<td>All remaining wood is soft</td>
<td>Small fragments; divergent vegetation</td>
</tr>
</tbody>
</table>

Table 2: Description of the decay classes of CWD (De Keersmaeker et al., 2005).

An estimation of the canopy cover was made for the 45 logs, where soil samples were taken. This was done
for a rectangular plot of which the borders were situated 6 m from the log. A distinction was made between
the shrub (woody vegetation between 1 m and 7 m high) and tree layer (woody vegetation >7 m). These values were aggregated according to Fischer (2015). Furthermore, the share of the different tree species to
the total coverage was estimated to calculate a litter quality score according to Verheyen et al. (2012). Finally,
the position and orientation of the log was registered in the field, and from that, the angle to the dominant
wind direction (relevant for litter accumulation at the log) was calculated in ArcGis. An overview of these
variables is given in Table 3.

2.4. Sampling

2.4.1. Wood

To investigate the concentration of chemical elements in the logs at different decay stages, two superficial
wood samples up to 4 cm deep were taken for each of the 148 logs with a hole saw after removing epiphytes
and bark. Both samples were pooled for analysis.

To also have an idea of the average concentrations of chemical elements throughout the whole crosscut of
the log (sap and heart wood), we took additional samples for a limited number of trees (5 in Sonian and 4 in
Wijnendale) with a wood corer. The methodology and results of these additional cores are not used in the further analysis but can be found in Appendix A.

2.4.2. Soil

For 45 logs two soil samples were taken and pooled at five different distances to the log and two depths. The first sample, at 0 cm, was taken from underneath the log. The other samples were taken at distances of 10 cm, 30 cm, 100 cm, and 300 cm to the log. Samples were also taken at two depths, one of the organic soil layer (F and H layer) and one of the mineral soil layer (0 – 10 cm). In this way, we can investigate the horizontal and vertical range of the effect of CWD on the chemical soil composition.

2.5. Chemical analyses

All samples were bagged and stored at 4-6°C to reduce microbial decomposition. The C, N, P, S, Ca, K, Mg, Mn, Al, and Fe concentration of the superficial wood and soil samples was determined. The superficial wood samples and soil samples were dried at 40°C until a constant weight was reached, ground, and homogenised. Total C and N concentrations were determined with the CN-analyser PrimacsSNC100 (Skalar). P, S, Ca, K, Mg, Mn, Al, and Fe were brought in solution by microwave digestion with the milestone Ethos 1 microwave in an acidic solution (Aqua regia for the soil samples and Hydrogen peroxide for the wood samples). Concentrations of all elements were measured with the Optima 8300DV optical emission spectrometer (Perkin Elner) by inductively coupled plasma atomic emission spectrometry in 12% nitric acid. The plant available P in the soil samples was extracted with an Olsen extraction (Olsen et al., 1954) and measured with a spectrophotometer. To assess the pH 20 g of soil was extracted with 100 ml 1M KCl-solution. The pH-KCl was determined with the T90 titrator (Mettler Toledo). The wood cores were air dried and subsequently ground and homogenised. For these cores, only total C and N concentration were determined with the vario MACRO cube CNS (Elementar).

2.6. Statistical analysis

To test our hypotheses, we modelled the nutrient concentrations and ratios in function of the variables found in Table 3. The variables were first standardised, since they act on different scales. Observations of the nutrient concentrations below the detection limit are replaced by the value of half of this detection limit (USEPA, 2000).
<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Range</th>
<th>Unit</th>
<th>Transformation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angle</td>
<td>Angle of the log to the dominant wind direction (Southwest) (0° is parallel to SW; 90° is perpendicular to SW)</td>
<td>3.23 – 88.33</td>
<td>°</td>
<td>-</td>
</tr>
<tr>
<td>Cover</td>
<td>Aggregated value of the cover of the shrub (&lt;7m) and tree layer (&gt;7m)</td>
<td>0.53 – 0.97</td>
<td>%</td>
<td>-</td>
</tr>
<tr>
<td>DC</td>
<td>Decay class</td>
<td>0 – 5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Diam</td>
<td>Diameter at 1 m from the base of the log</td>
<td>40 – 140</td>
<td>cm</td>
<td>-</td>
</tr>
<tr>
<td>Dist</td>
<td>Distance to the log</td>
<td>0 – 300</td>
<td>cm</td>
<td>ln (X)</td>
</tr>
<tr>
<td>LQ</td>
<td>Litter quality score</td>
<td>1 – 2.65</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Site</td>
<td>Forest site</td>
<td>Sonian Forest Wijnendale Forest</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 3: Overview of the explanatory variables, with their description, range, unit and applied transformation for statistical analysis.

To test our first hypothesis, whether the concentration of elements in CWD increases with decay, we modelled the element concentrations and ratios of the superficial wood samples in function of the decay class, the log diameter at 1m from the base, and the site (Sonian Forest or Wijnendale Forest) with an interaction between site and the other variables, to check whether there are different patterns in the two sites. The response variables were log transformed to satisfy the model assumptions.

\[
\ln(\text{Conc}) = (\text{DC} + \text{Diam}) \times \text{Site} + \text{Site}
\]

For our last three hypotheses ((2) decreasing soil concentrations with distance to the log and increasing soil concentration with (3) decay and (4) nutrient stock), generalised linear mixed effect models were estimated for the nutrient concentrations in the organic and mineral soil layer separately using a log-link gamma distribution. The fixed variables include the natural logarithm of the distance to the log, the decay class, the diameter at 1m from the base, the angle to the dominant wind direction, the litter quality score, and site. We include the decay class, because we expect an increase of nutrient concentration in the soil with the
decay class (Hypothesis 3). The diameter is used as a proxy for the nutrient stock of the log to test Hypothesis 4 (Brown et al., 1996). The angle is considered to account for the accumulation of litter at the log. We also included an interaction effect between the distance and the decay class to check whether the distance effect changes during the decay, and site and the other variables, which allows us to see whether there are different trends in both sites. The log identity (Log) is included as the random effect.

\[
\ln (\text{Conc}) = (\text{Dist} + \text{DC} + \text{Diam} + \text{Angle} + \text{LQ} + \text{Cover}) \times \text{Site} + \text{Site} + \text{Dist} \times \text{DC} + 1|\text{Log}
\]

The statistical analyses were executed in R version 4.3.3 (R Development Core Team, 2018). All statistical tests were performed on a 0.05 significance level. The superficial wood models and the soil models were constructed using the \textit{lm} function and \textit{glmer} function of the \textit{lme4} package respectively. The optimal model was selected with the \textit{dredge} function from the \textit{MuMin} package using the Akaike Information Criterion. The marginal (\(R^2_m\)) and conditional (\(R^2_c\)) coefficient of determination were calculated (Nakagawa & Schielzeth, 2013).

Finally, we estimated the distance to the log up to where the effect of the log decomposition on the chemical composition of the organic soil is significantly different from the concentration at 3 m from the log, where we assume there is no effect from the log. We calculated this value for the two reserves as the X coordinate of the intersection of two functions. For the first function, a linear model of the organic soil concentration in function of the natural logarithm of the distance is fitted. In addition, the average concentration and the standard deviation at 300 cm are calculated and summed, when concentrations are expected to increase with the distance (C, N, P, S, Ca, Mg, K) or subtracted when we expect a decrease (H, Al, Fe) to create the second function. Where the fit passes this value, the effect beyond that distance is not significantly different to the concentration at 300 cm. We then averaged the distance values for all nutrients for which the relation between the distance and the concentration is significant (Sonian: C, N, P, S, Ca, Mn, and H; Wijnendale: C, P, Olsen P, Ca, and Al), to compose an aggregated value of the distance with significant soil effects. This value was then used to calculate what percentage of the forest floor is within the area of influence of the CWD, for its nutrient status. This was done in ArcGIS.
3. Results

All wood nutrient concentrations, except for C and K, increased with increasing decay class (Table 4). For most nutrients there is also an effect of site. We found higher concentrations of N and Al and lower concentrations of S and Mn in Wijnendale. For P, Ca, and Mg there was an interaction effect between the decay class and the site, indicating lower values for less decayed logs in Wijnendale, but these became more similar in both forests as the decomposition continues (Figure 1).

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>C:N</th>
<th>P</th>
<th>S</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>Al</th>
<th>Fe</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>6.22</td>
<td>1.49</td>
<td>4.74</td>
<td>5.24</td>
<td>5.87</td>
<td>8.29</td>
<td>6.82</td>
<td>6.22</td>
<td>4.18</td>
<td>3.15</td>
<td>1.37</td>
</tr>
<tr>
<td>DC</td>
<td>0.34</td>
<td>-0.34</td>
<td>0.25</td>
<td>0.38</td>
<td>0.26</td>
<td>-0.07</td>
<td>0.36</td>
<td>0.22</td>
<td>0.72</td>
<td>0.33</td>
<td></td>
</tr>
<tr>
<td>Diam</td>
<td>-0.01</td>
<td>-0.24</td>
<td>0.25</td>
<td>0.14</td>
<td>-0.20</td>
<td>-0.13</td>
<td>0.11</td>
<td>1.73</td>
<td>-0.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>0.02</td>
<td>0.25</td>
<td>0.14</td>
<td>-0.20</td>
<td>-0.13</td>
<td>0.11</td>
<td>1.73</td>
<td>-0.33</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DC:Site</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diam:Site</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.06</td>
<td>0.48</td>
<td>0.48</td>
<td>0.20</td>
<td>0.48</td>
<td>0.17</td>
<td>0.02</td>
<td>0.24</td>
<td>0.71</td>
<td>0.46</td>
<td>0.43</td>
</tr>
</tbody>
</table>

Table 4: Coefficients of the linear models with the logarithm of the nutrient concentrations of the superficial wood samples as dependent variable and decay class (DC), diameter (Diam), and site (with Wijnendale as reference) as the independent variables (p-value: 0***0.001**0.01*0.05).
Figure 1: Linear models of the nutrient concentrations of the superficial wood samples plotted in function of the decay class and site as group variable. The dark green circles and the light green triangles represent the observations in Wijnendale and Sonian Forest, respectively. The shading shows the 95% confidence interval.
In the organic soil layer there was a decrease for most nutrients at further distance to the log, except for Al, which had a lower concentration close to the log (Table 5, Figure 2). Similar to the wood samples, we found overall higher N concentrations and lower concentrations of the base elements in Wijnendale. Decay class was negatively correlated with the base elements and Al, and there existed a negative interaction effect with the distance for the C:N ratio and Mn. The diameter showed a negative relation for most elements. For C, N, Olsen P, S, Ca, and H this was accompanied by an interaction effect with the site. In the mineral soil, the concentration of C, P, S, Ca, K, and Mg were still negatively correlated with the distance. The effect of distance on element concentrations was however less pronounced compared to the organic soil layer (Table 6, Figure 3). For the other significant variables such as diameter and decay class, effects on element concentrations in organic and mineral soil were mostly comparable, in some cases even more explicit for mineral soils (Table 6). For Ca and Mn there was an interaction effect as well, which indicates that the distance effect becomes more pronounced with increasing decay class.
Table 5: Coefficients of the generalised mixed effect models with nutrient concentrations of the organic layer as dependent variable and decay class (DC), cover, diameter at 1m (Diam), natural logarithm of the distance to the log (Dist), angle, litter quality score (LQ), and the site (with Wijnendale as reference) as fixed variables and the log identity as random variable (p-value: 0***0.001**0.01*0.05).
Figure 2: Linear models of the nutrient concentrations of the organic soil samples (Table 5) plotted in function of the distance (cm) to the log and site as group variable. The dark green circles and the light green triangles represent the observations in Wijnendale and Sonian Forest, respectively. The shading shows the 95% confidence interval.
<table>
<thead>
<tr>
<th>C</th>
<th>N</th>
<th>CN</th>
<th>P</th>
<th>P Olsen</th>
<th>S</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
<th>Mn</th>
<th>Al</th>
<th>Fe</th>
<th>H</th>
</tr>
</thead>
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<td>-0.03 *</td>
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<td>0.62 **</td>
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<tr>
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<td>0.74</td>
<td>0.92</td>
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</table>

Table 6: Coefficients of the generalised mixed effect models with nutrient concentrations of the mineral layer as dependent variable and decay class (DC), cover, diameter at 1m (Diam), natural logarithm of the distance to the log (Dist), angle, litter quality score (LQ), and the site (with Wijnendale as reference) as fixed variables and the log identity as random variable (p-value: 0***0.001**0.01*0.05).
Figure 3: Linear models of the nutrient concentrations of the mineral soil samples (Table 6) plotted in function of the distance (cm) to the log and site as group variable. The dark green circles and the light green triangles represent the observations in Wijnendale and Sonian Forest respectively. The shading shows the 95% confidence interval.
4. Discussion

4.1. Nutrients in CWD

The chemical composition of the recently downed trees is comparable to results of previous studies reporting the composition of living beech trees (André et al., 2010; Augusto et al., 2000; Hagen-Thorn et al., 2004; Penninckx et al., 2001). We found higher concentrations for N at both sites than Hagen-Thorn et al. (2004); for Ca and Mg higher concentrations were registered in Sonian Forest than reported by Augusto et al. (2000) and Penninckx et al. (2001) and lower concentration for Mn in Wijnendale compared to André et al. (2010) and Penninckx et al. (2001).

As we hypothesised, the nutrient concentration increased with decay in CWD (Hypothesis 1). Similar results were reported in previous studies (Arthur & Fahey, 1990; Fahey, 1983; Holub et al., 2001; Krankina et al., 1999; Kuehne et al., 2008). The small number of logs sampled in decay class 5 makes it difficult to predict the change in nutrient concentrations in very advanced stages of decay. Initial concentrations of the base elements and P were higher in Sonian Forest, but the P, Ca, and Mg concentrations of both forests became more similar during decay. This indicates that the rate of the changes in the nutrient concentrations were related to their initial concentrations and ratios. Laiho & Prescott (2004) observed a negative correlation between the rate of the increase of the P, Ca, and Mg concentration and the initial concentration and a positive correlation with the initial N:nutrient ratio. This corresponds to our results, since the N:nutrient ratio was also higher in Wijnendale for these nutrients.

The increase in concentration is mainly due to mass loss, because of microbial respiration and organic matter leaching (Holub et al., 2001). However, mass loss can also be a result of fragmentation, a process where no change in nutrient concentration is involved. Additional processes do occur for different nutrients. The decay of CWD is an N limited process, as lower C:N ratios are required by wood decaying organisms than naturally occurring in fresh dead wood. In logs, N accumulation is partly done by nitrogen-fixing bacteria that colonise decaying wood (Jurgensen et al., 1984; Roskoski, 1980; Spano et al., 1982), but mainly by transmission of N from soil-foraging fungi to the wood decaying fungi (Mäkipää et al., 2017; Rinne et al., 2016). The accumulated N is subsequently recycled internally by the fungi during the further decay process (Watkinson et al., 2006). When CWD further decays, soil inhabiting fungi also start to colonize the soft decomposing
wood itself alongside to the dead wood inhabiting fungi and in the last stages of decomposition mycorrhizal fungi are established as well (Lindahl & Tunlid, 2015; Rajala et al., 2012). This shift in fungal communities possibly has an impact on the N concentration in the CWD as well.

Likewise, there is also evidence for other nutrient transfer between mycorrhiza and wood decaying fungi (Leake et al., 2001; Lindahl et al., 2001) and import of photosynthates by mycorrhiza in the late stages of decay (Mäkipää et al., 2017). According to Wells & Boddy (1995), cord-forming fungi even manage to transport P towards logs over large distances. K concentration decreases with the decay mainly due to leaching, because of the high mobility of this element. Losses of Ca could be due to leaching of labile Ca fraction present in the vascular components, while the structural Ca is mainly retained (Holub et al., 2001).

The C concentration does not change during the decay, since the mass loss is mainly due to loss of lignin and carbohydrates that contain high concentrations of C. So, both the total wood mass and the carbon mass change in a similar way.

4.2. The effect of CWD on the soil

Our results indicate an increase in the concentrations of the essential nutrients, the pH and a decrease in the Al concentration in the proximity of CWD, as we hypothesised (Hypothesis 2). The pH-KCl increased from 2.7 far away from the log to 3.1 underneath the log on average in Wijnendale and 3.1 to 3.3 in Sonian Forest. Accordingly, CWD contributes to a higher soil fertility underneath and in the proximity of the log. This coincides with the results reported by Kappes et al. (2007). Opposite results were described by Krzyszowska-Waitkus et al. (2006) and Spears & Lajtha (2004), who found a lower pH below CWD, as a result of an acidic leachate. The last two studies examined coniferous species, whilst Kappes et al. (2007) studied CWD of beech as we did. Differences in wood composition and wood decaying organisms are a possible explanation for the contrasting results. Softwood species are more associated with brown-rot fungi in contrast to hardwood species where white-rot fungi are the main wood decaying fungi (Atlas & Bartha, 1998). Brown-rot fungi produce more organic acids, causing a decrease in pH (Shimada et al., 1997; Takao, 1965). In our case, the beech wood in mainly decayed by *Ganoderma applanatum* and *Fomes fomentarius*, both white-rot fungi.

In this study we measured the total N concentration in the soil, which does not give a good indication of the availability of this element. Previous studies (Hafner et al., 2005; Zimmerman et al., 1995) showed a decrease
in availability of N, due to an increase in the C:N ratio and higher concentrations of organic C underneath CWD, which leads to a higher N immobilisation (Hart et al., 1994; Magill & Aber, 2000). This effect can help reduce the negative impact of N deposition, which is also reflected in the higher pH in the vicinity of the logs as was observed in this study.

The effect of CWD can be a direct cause of leaching of elements to the soil (Hafner et al., 2005). This relation was examined using the variables ‘Decay class’, ‘Diameter’, and ‘Distance’. The decay class and diameter were not as strongly related to the soil concentrations as expected, but we found significant correlations for some elements (Hypothesis 4 and 5). Most logs that were selected for soil sampling were in average decay class 3 to 4, since we expected that the effects would be negligible nearby fresh CWD and due to limited resources. So part of the variation for this variable was missing. In future studies, soil samples close to less decayed logs should be analysed, to further understand the mechanisms by which CWD affects the soil.

Since we only measured the nutrient concentrations and not the nutrient stocks of the CWD, we are not able to quantify fluxes between the logs and the soil. However, using densities measured for decaying beech wood by Müller-Using & Bartsch (2009), we can make an approximation of the change in stock per unit of length of the beech logs, assuming the densities per decay class obtained by Müller-Using & Bartsch (2009) are representative for our two sites. Since not only the density, but also the volume changes during the decay, we calculated the stock per unit of length instead of per unit of volume. Accompanying graphs can be found in Appendix B. Looking at decay class 0 to 4, we found a significant decrease of C, P, Ca, K, and Mn in both forests and of N, S, and Mg in Sonian. Al increased significantly in Wijnendale. For the other nutrients no significant change was observed. This suggests that there is indeed a flux of nutrients going from the dead wood towards the soil. This is supported by several studies that also found declining stocks for most nutrients (e.g. Ganjegunte et al., 2004; Krankina et al., 1999). However, many others found an increase or no clear trend at all (e.g. Alban & Pastor, 1993; Arthur & Fahey, 1990; Brown et al., 1996; Busse, 1994). The opposite results could be due to failing to take the volume loss into account (Krankina et al., 1999).

Next to the direct effect, CWD indeed can also have a structural effect. CWD creates a physical barrier, where litter can accumulate in broadleaf forests (Orndorff & Lang, 1981). Since this accumulation is presumably greater when the log is directed perpendicular to the dominant wind direction, we can expect an increase of
nutrients with an increase of the variable ‘Angle’, since litter is an important source of nutrients in the soil (Sayer, 2005). For C, Ca, K, Mg, and Al we notice this effect in Sonian Forest, but an opposite effect in Wijnendale. The leaves in Sonian Forest contain considerably more Mg and Ca and less N than those in Wijnendale Forest (Cosyns et al., 2015). This may lead to an enriching effect of the litter in Sonian Forest as opposed to a more acidifying effect in Wijnendale Forest, which would explain the opposite result in the two forests. These results are in accordance with the records of Verstraeten (2018), who reported a decrease in acidity of the organic layer in Sonian Forest and an ongoing acidification in Wijnendale.

4.3. Site-specific effects

The nutrient concentration in both the CWD and the soil showed differences between both study sites, the main difference being the higher concentration of N, the lower concentrations of the base elements, and the lower pH in Wijnendale Forest. This can partly be explained by the different soil textures, as Wijnendale Forest is situated on a sandy soil, whereas Sonian Forest is located on a loamy soil. An additional explanation however can be found in the higher N deposition load in Wijnendale (Verstraeten, 2018). The difference in N concentration in the wood of CWD between the two sites persists for a long time, as we found no convergence during the decay. The different N concentrations give rise to a difference in wood quality and decomposition rate. An elevated N concentration may accelerate the wood decomposition process (Bebber et al., 2011) and affect the species composition of the decomposer community (Moorhead & Sinsabaugh, 2006).

The more sandy acidic substrate in Wijnendale can explain the initial lower concentration of P, Ca, K, Mg, and Mn in CWD. The pH in Wijnendale is situated in the Al buffer range (pH-H₂O < 4.2), whereas Sonian Forest is situated in the Mn buffer range (pH-H₂O < 5) (Ulrich, 1991). The higher concentration of available Al in Wijnendale causes a reduced uptake of Ca, Mg, and P in beech (Bengtsson et al., 1988). In addition, the nutrient concentrations of these elements and Olsen P are lower in Wijnendale. Verstraeten et al.(2012) reported an exceedance of the critical ratio of base cations (Ca, K, Mg) and Al in the soil solution, determined by Sverdrup & Warfvinge (1993) and UNECE (2004) in Wijnendale, but not in Sonian Forest. Beech is rather tolerant to Al (Vanguelova et al., 2007), since Al is precipitated in the root zone, which causes a reduced
uptake of this element (Brunner & Sperisen, 2013). This can explain the many observations for several elements below the detection limit in the wood samples.

The difference in soil characteristics was also reflected in the foliar composition of beech trees in the reserves. Cosyns et al. (2015) found a luxury consumption of N in both forests. Other nutrient concentrations and ratios were normal in Sonian Forest, in contrast to Wijnendale Forest, where deficiencies for Ca and Mg and high N:P, N:K, N:Ca, and N:Mg ratios were found. In forests like Wijnendale, where there are nutrient imbalances, CWD can play a crucial role in buffering and provision of essential nutrients that are in limited supply to the ecosystem. Even in sites where no imbalances are registered, but where the concentration of basic elements is limited (acidocline forest types such as both studied sites), the presence of CWD can significantly influence the soil condition. Especially for the essential basic element Ca, the effect was very significant in both the organic and mineral soils at both studied sites, illustrating the crucial role CWD can play, not only for biodiversity (e.g. Vandekerkhove et al., 2011) but also for the fertility and overall performance of the ecosystem.

4.4. Spatial impact

Since the effect of CWD is only local, the impact on the forest soil will be more substantial, when large volumes of CWD are present. This was the case for the two considered study sites (44 m³ ha⁻¹ in Wijnendale (De Keersmaeker et al., 2009) and 110 m³ ha⁻¹ in the core area of Kersselaerspleyn (Vandekerkhove et al., 2012). In beech forest reserves in Europe the average amount is 130 m³ ha⁻¹ (Christensen et al., 2005).

However, in managed forests this is only 2 to 20 m³ ha⁻¹ on average (Hahn & Christensen, 2004).

We investigated the vertical range of the effect in relation to the distance. The strongest effects were found in the organic soil layer, whilst in the mineral soil layer less significant relations between the concentrations and the distance were found. This is in contrast to similar studies, where significant effects were reported for different depths: the first 5 cm (Busse, 1994; Krzyszowska-Waitkus et al., 2006), up to 15 cm (Panayotov, 2016), or even 50 cm (Pichler et al., 2013). However, the last study was conducted in an andosol, a soil type that is able to accumulate a large amount of organic material. Spears et al. (2003) did not find a significant effect on the C and N concentration, similar to our results for N.
Soil samples were taken at five distances to the log. This enables us to make an estimation of the (horizontal) spatial range of the effect of the presence of CWD on the soil, on top of the magnitude of the effect. The differences between the first three distances (0 cm, 10 cm, and 30 cm) are generally small in comparison to the variation between the observations, indicating that the effect is equally present both below and at short distance from the log. The distances of 100 cm and 300 cm also show little difference, and clearly differ from the concentrations close to the log. At distances of one meter and beyond the effect of decomposing logs appears to be small or non-existing. Since CWD appears frequently clustered, this can lead to biogeochemical hotspots (McClain et al., 2003). In addition, we estimated the average distance range of the effect, as described at the end of Section 2.6. The average significant distance range of the effect for the different nutrients is estimated at 10.3 cm in Sonian and 10.5 cm in Wijnendale. This is smaller than the 30 to 100 cm as stated above and can be interpreted as the range where the effect is definitely significant, whereas for most nutrients the range will be between 30 and 100 cm.

For both sites, a full inventory of all logs over 40 cm is available. By adding a buffer 10.3 cm and 10.5 cm for Sonian and Wijnendale respectively to the area covered by these logs, an ‘area of influence’ of the logs for most essential elements can be calculated and related to the total area of the site. The relative area affected by logs with a diameter of more than 40 cm was 0.92% and 0.36% in Sonian and Wijnendale, respectively.

Taking the 30 and 100 cm into account, the range would expand between 1.55% and 3.77% in Sonian and 0.63% and 1.67% in Wijnendale. Important to note is that we did not study the effect of the crown, which appears more dispersed and expands over a larger surface than the stem. Also smaller wood fragments are not considered. Compared to large logs, they only represent small amounts of dead wood, but with relatively higher concentrations of nutrients, and higher frequency and decay rates. Even without taking these in consideration, CWD can significantly influence soil conditions on a substantial area of the forest floor when large volumes are present. Both study sites were managed up to 30 years ago, with most of the dead wood removed, so build-up of dead wood is still ongoing (Vandekerkhove et al., 2009). Therefore, we can assume that this spatial effect will further increase in the next decades. Since CWD can have a very long lasting effect on the soil (Manies et al., 2005), we can expect that this range will eventually cover most if not all of the forest soil.
In both reserves, a large portion of the base cations is stored in the living biomass. In Wijnendale, the total amount of K and Ca available in the litter layer and mineral soil up to 80 cm together is smaller than in the woody biomass (Cosyns et al., 2015). This implies that CWD can be an important source of these nutrients and that the harvest of both living and dead wood in nutrient poor or acidic managed forests may lead to critical loss of essential nutrients and enhance soil acidification. Limiting the amount of harvested wood, removing only the most valuable boles but leaving low value trees and the crown wood will increase the amount of CWD and can reduce the risk of depletion of essential nutrients and help improve and often restore the soil fertility.

5. Conclusion

The results of the present study show that the concentrations of most nutrients in the decaying wood increase during the decay of CWD and hence indicate that CWD retains essential nutrients, which are gradually released into the soil. In addition, we found an increase in concentration of essential and in some cases limiting macronutrients and a number of micronutrients in the proximity of CWD in the organic soil layer. In the mineral soil layer, we also detected this effect for a subset of the examined nutrients, such as Ca. CWD contributes in this way to the improvement of soil fertility, in particular in forests on poor soils that are acidified by nitrogen deposition. Hence, the implementation of management systems incorporating the conservation of CWD is recommended to keep limiting nutrients inside the ecosystem and locally prevent acidification. This study one of the first steps to explaining patterns in changes in nutrients in wood and soil during wood decomposition in different forests. Subsequent studies are necessary to gain a deeper understanding of the processes at play. Examples are additional analyses of the wood density and nutrient stocks, leachate or long term in situ analysis of the logs and the surrounding soil.

6. Acknowledgments

The authors would like to thank the Flemish Agency for Nature and Forest (ANB) for allowing us access to the forest reserves. We would also like to thank Peter Van de Kerckhove, Marc Esprit, Stefaan Goessens, Siska Van Parys, and Kris Ceunen for collecting parts of the data and the support during the fieldwork. We also thank the analytical laboratory team of INBO who performed the chemical analysis of soil and wood samples,
and Luc Willems for the chemical analyses of the wood cores. Also, many thanks go to Hans Van Calster and Haben Blondeel for their statistical support. We also want to thank the two anonymous reviewers for their insightful and constructive comments.

7. References


Hahn, K., & Christensen, M. (2004). Dead wood in European forest reserves - a reference for forest management. In M. Marchetti (Ed.), Monitoring and Indicators of Forest Biodiversity in Europe - from Ideas to Operationality (pp. 181–191). Saarijärvi.


Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P., & Verschelde, P. (2009). When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-


A. Appendix A

Additional to the superficial wood samples, wood cores were sampled of 4 logs in Wijnendale and 5 in Sonian Forest with different decay classes varying from 1 to 4. We wanted to investigate the difference in nutrient concentration in different wood compartments, ranging from the bark up to the heart of the log. The sampling was done with a wood corer at the same locations of the log as the superficial wood samples. Two cores were taken at each location and pooled. The samples were divided in three subsamples (sapwood, heartwood, and a transition zone). If present, the bark was analysed separately. Differences between nutrient concentrations in the wood cores were calculated using a one-way ANOVA.

In the wood cores we did not find a significant difference in C concentration of the different wood components (Table A.1). The N concentration is significantly higher in the bark and the C:N ratio is significantly lower in the sap wood and the bark. There are no significant differences between the decay classes, except in the sap wood, for N and C:N.

<table>
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<tr>
<th>DC</th>
<th>C [g kg⁻¹]</th>
<th>N [g kg⁻¹]</th>
<th>C:N [-]</th>
<th>Number</th>
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<td>8.27 + 3.66 a</td>
<td>68.28 + 25.42 a</td>
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<td>12.48 + 4.39 a</td>
<td>44.14 + 14.14 a</td>
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<td>3</td>
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<td>4</td>
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<td>4.74 + 1.04 ab</td>
<td>111.13 + 23.76 ab</td>
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<tr>
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<td>6.41 + 2.27 b</td>
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<td>174.64 + 28.33 a</td>
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Table A.1: The average and standard deviation of the concentrations of the wood compartments for the different decay classes (DC). The right column gives the number of observations. Common letters denote no significant difference between the average values at $p=0$.

<table>
<thead>
<tr>
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<td>2</td>
<td>505.78 + 8.79 $^a$</td>
<td>3.15 + 0.47 $^a$</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>517.69 + 9.88 $^a$</td>
<td>2.71 + 0.18 $^a$</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>522.4 + 18.9 $^a$</td>
<td>3.69 + 1.05 $^a$</td>
<td>4</td>
</tr>
</tbody>
</table>

The N concentration is not distributed homogeneously in the wood (André et al., 2010; Meisch et al., 1986; Penninckx et al., 2001). Because beech does not form typical heartwood, the contrast in concentrations in sap and heartwood is not sharp (Penninckx et al., 2001). However, we did find a greater concentration of C in the bark and sapwood, although that last one is not significant. The N concentration of decay class 4 is greater in all wood compartments, but this is only significant in the sapwood. This indicates that not only the concentrations are different in the various wood compartments, but also the rate at which they change during the decay. A similar increase was also reported by Schowalter et al. (1998), although they also found a significant increase in the bark. Recent studies indicate differences in C concentration between wood compartments (Bert & Danjon, 2006; Thomas & Martin, 2012). The small amount of observations prevents us from seeing these differences in our study. André et al. (2010) also didn’t find a significant difference between bark and wood.
### B. Appendix B

<table>
<thead>
<tr>
<th>Density (g cm$^{-3}$)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.58</td>
<td>0.37</td>
<td>0.21</td>
<td>0.28</td>
</tr>
</tbody>
</table>

*Table B.1: The density of beech wood per decay stage obtained by Müller-Using & Bartsch (2009).*
Figure B.1: Linear models of the nutrient stocks in the logs per unit of length plotted in function of the decay class and site as group variable. The dark green circles and the light green triangles represent the observations in Wijnendale and Sonian Forest, respectively. The shading shows the 95% confidence interval.