Strong negative impacts of whole tree harvesting in pine stands on poor, sandy soils: A long-term nutrient budget modelling approach

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ABSTRACT

Global environmental changes such as climate change, overexploitation and human population growth increase the interest in woody biomass from forests as a resource for green energy, chemistry and materials. Whole Tree Harvesting (WTH) can provide additional woody biomass, mainly for bioenergy, by harvesting parts of the crown not harvested under conventional Stem-Only Harvesting (SOH). However, WTH also increases nutrient export, potentially depleting soil nutrients and threatening future stand productivity. Here we assess the impacts of WTH in Corsican pine stands (Pinus nigra ssp. laricio var. corsicana Loud.) with a rotation period of 48 years on poor, sandy soils in Belgium. We performed a detailed nutrient budget assessment before and after thinnings and clear-cuts under scenarios of WTH and modelled the long-term changes in ecosystem nutrients under both WTH and SOH. Our results demonstrate a strong immediate impact of WTH on aboveground nutrient stocks (mainly in clear-cuts). In clear-cuts with WTH, half of the base cations (calcium, potassium, magnesium) in the trees and forest floor were exported. The amount of available cations in the soil is not sufficient to immediately compensate for this export. Only one fourth of the amount exported were available for biota in the top 50 cm of the soil. We also modelled long-term development of ecosystem nutrients (available nutrients in the soil and nutrients in trees and forest floor) and found that the available soil calcium, potassium and phosphorus stocks are insufficiently replenished by deposition and weathering to sustain WTH on the long term. We found no indications of potential depletion of ecosystem cations and phosphorus for the next ten rotation periods under SOH management. Our results thus support a less intensive management in pine stands on poor, sandy soils, for instance, by adopting SOH and/or longer rotation periods.

1. Introduction

The use of woody biomass for bioenergy has increased by almost 80% in the 27 European Union member states between 1990 and 2008 (Eurostat, 2011). As a result of the EU 20-20 objectives, demand for woody biomass is expected to keep rising and even double by 2030 (Mantau et al., 2010). At the moment, more than two-thirds of harvested woody biomass originates from forestry (Mantau et al., 2010). Simultaneously, the demand for wood for materials is increasing (Mantau et al., 2010). On the one hand, this accelerating demand resulted in increased import of woody biomass, in western Europe mostly as pellets imported from North-America (Sikkema et al., 2010). The increased demand has also stimulated interest in production of wood chips and pellets in western Europe. Biomass in European forests is mainly produced as stem wood (52%); the remainder are logging residues (26%) and stumps (21%) (Mantau et al., 2010). The main source of biomass for bioenergy from forests originates from leftovers such as crown wood and smaller trees from early thinnings. Stump extraction is currently economically unfeasible in several European regions (including Belgium) with a very low forest cover (e.g., costs mentioned in Berch et al. (2012) largely exceed the current market prices). Stem wood, on the other hand, is primarily used for material purposes and in Belgium kept away from the energy market by legislation (Vangansbeke et al., 2015b).

Enhanced utilization and harvest of whole trees raises questions about the sustainability of this practice and the impact on ecosystem services delivered by forests (Schulze et al., 2012). For example, the additional harvest of biomass in forests on top of the harvest of logs might negatively affect forest biodiversity of...
saproxylics, small mammals and birds and the functioning of associated aquatic ecosystems by increasing acidifying potential and reducing stream productivity (Berger et al., 2013). Also soil microbial properties and activity and related soil productivity and functioning can be influenced (Smäl et al., 2008b). During Whole Tree Harvesting (WTH) more nutrients are exported from the forest than under Stem-Only Harvesting (SOH) (Achat et al., 2015). The additional export could be significant, despite the lower crown biomass compared to stem biomass, because the nutrient concentrations in these tree parts are much higher than in logs (Neirynck et al., 1998). Jorgensen et al. (1975) found that the export of N, P and K under WTH, including the larger roots, was about three times bigger than under SOH in a 16 year old pine plantation. Depending on the forest and soil type, WTH might have a negative impact on the soil fertility of a stand (Jorgensen et al., 1975; Olsson et al., 1996a) and its future productivity (Johnson, 1994; Walmsley et al., 2009; Wall, 2012). A harvesting regime can be considered unsustainable when the ratio between the imports (mainly through deposition and weathering) and exports (mainly through harvest, leaching and run-off) of nutrients is smaller than 0.9, and if the remaining ecosystem nutrient stock is not sufficient for the next ten rotation periods (Göttlein et al., 2007). The ecosystem nutrient stock exists of the nutrients in trees, forest floor and the available soil nutrients (Fig. 1).

Studying the effects of contrasting harvesting scenarios on soil nutrient development can be performed (1) by empirically comparing pre- and post-harvest nutrient stocks, (2) by modelling the long-term impact or (3) by quantifying growth reductions in the stand. Here we give a short literature overview of different studies on the impact of WTH on nutrient status of forest stands.

A first type of WTH nutrient studies focused on the empirical identification of immediate or long-term effects of harvesting intensity on nutrient stocks. For example, Klockow et al. (2013) studied the effect of slash and live-tree retention in Populus tremuloides dominated forests in the USA. They found that a lower harvesting intensity (i.e., SOH vs. two intermediate scenarios retaining some slash on the stand vs. WTH) positively influenced the total nutrient stocks of the stand. Most remarkably, this study mentioned a slash retention of almost 50% under WTH due to harvest losses (Klockow et al., 2013). Olsson et al. (1996b) found a significant effect of harvesting intensity (SOH vs. WTH) on base saturation, especially in the litter layer (L, F and H layer), 16 years after harvest in spruce and pine stands in Sweden. Phillips and Watmough (2012) found a decrease in available soil stocks of calcium (Ca) and potassium (K), by making a detailed nutrient budget before and after stem-only selection cutting in sugar maple stands (Acer saccharum Marsh.) in Ontario, Canada. Jorgensen et al. (1975) found a significant decrease in available soil nutrient pools when WTH was applied instead of SOH. Vanguelova et al., 2010 found an increase in acidity and a decrease of available soil K and phosphorus (P) stocks under WTH in comparison to SOH in Sitka spruce stands in the UK after 28 years and Smäl et al. (2008b) detected a significantly lower biomass and nitrogen content of the litter layer under WTH compared to SOH, 8–16 year after harvest in pine stands in New Zealand. On the other hand, some studies reported little significant differences in nutrient stocks between stands after WTH and SOH. Wall and Hyytonen (2011), for example, studied Norway spruce stands 30 years after SOH and WTH, with needles left on site, in Finland. They found no significant differences between the stands in stocks in forest floor and concentration in foliage of nitrogen (N), magnesium (Mg), P, Ca and K. Wilhelm et al. (2013) compared nutrient budgets and fluxes before and after harvest for 3 harvesting intensities (WTH and treatments leaving most of the crown in the stand) in oak dominated stands on poor, sandy soils in Wisconsin, USA. Only little differences were detected between the treatments in the first 2 years after harvest. In general, these empirical studies offer excellent insights into the immediate impact of different harvest regimes and can be used to test results from modelling work. However, this type of studies does not directly evaluate the long-term perspective of possible soil depletion.

A second type of studies used models to estimate the long-term impact of different harvesting intensities on nutrient stocks. Aherne et al. (2012), for instance, modelled the soil nutrient status under different harvesting intensities and under projected climate change scenarios for Scots pine (Pinus sylvestris), birch (Betula pendula) and Norway spruce (Picea abies) on contrasting soils in Finland. According to the model, WTH (with crowns, excluding stumps) in pine stands increased the removal of biomass by only 24%. Yet, the removal of base cations more than tripled and nitrogen was removed six times more than under SOH. Palviainen and Finér (2012) developed equations to estimate the nutrient content of crowns and stems based on the stand volume for pine, spruce and birch in Fennoscandia. Based on these equations they modelled nutrient exports under SOH and WTH for thinning and clear-cuts. Generally they found negative nutrient balances under WTH for most nutrients and most tree species. The study of Phillips and Watmough (2012) estimated the long term impact of a stem only selection harvest by starting from an empirical dataset on the impact of harvesting and modelling the nutrient import by leaching and atmospheric depositions and the nutrient export by leaching. They found a net loss and a high long-term risk of depletion for bioavailable K and mainly Ca. Zanchi et al. (2014) modelled responses of spruce stands to increased biomass extraction (by residue removal, intensifying thinnings and shortening rotation periods) in southern Sweden. By assuming a fixed harvest loss of 40% of the foliage under all scenarios, they found significant changes in aboveground and belowground stocks and fluxes of carbon. In sum, modelling studies give an interesting overview of impact on a larger space and time scale. Moreover, a well performing model, tested on field data, such as the NuBalM model for nitrogen and biomass pools in pine stands, has the potential of being a useful management tool (Smäl et al., 2011). The drawback is that the data is mostly not empirically generated and sometimes lacking terrain validity, e.g., poorly accounting for the fact that only part of the crowns are exported and that significant harvest losses occur on site.

A third kind of studies directly assessed the impact of different harvesting intensities on future productivity of forest stands. Egnell (2011) found a significant decrease of productivity over 31 years in planted spruce after WTH in northern Sweden. Fleming et al. (2014) compared total aboveground biomass 15 years after harvest in pine stands in Ontario, Canada. The aboveground biomass decreased significantly under WTH with removal of the forest floor. Stands under SOH had a higher aboveground biomass than stands under WTH, but this difference was not

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**Fig. 1.** Overview of the different stocks of ecosystem nutrients and the internal fluxes between these stocks.
significant and mainly caused by a higher natural regeneration. Kaarakka et al. (2014), found no effect of harvesting intensity on growth of the next generation 10 years after clear-cutting in spruce stands in Finland. However, in this study a clear effect of treatment was found on the stocks in mineral soil and litter layer, suggesting that on the longer term WTH could have negative effects on site productivity. Wall and Hytönen (2011) found no decrease in spruce stem volume production between stands under WTH (with crowns left on site for 1 year after harvest, so that needles were not exported) and SOH in Finland, even after 30 years. However, the total site productivity was higher in the sites where only stems were harvested, because of the higher density of the naturally regenerated seedlings. Ponder et al. (2012) compared growth in 45 long-term soil productivity experiments across several climate regions and soil types throughout North-America 10 year after harvest and also found little consistent effects of planted tree biomass in stands under WTH and even under WTH with forest floor removal compared to SOH. Finally, Walmsley et al. (2009) found a reduction in diameter at breast height in Picea sitchensis stands in the UK 23 years after WTH in comparison to SOH. This type of study yields very interesting results reporting on direct change in ecosystem service delivery. Possible drawbacks are the delay between WTH and final results and the many possible confounding factors that can cause growth differences, other than the management regime (Burger, 1996). For a good understanding of the ecological causes of a possible growth reduction, there is a strong need to combine the growth reduction results with a thorough study of the ecosystem nutrient stocks.

Some of the studies from the three types mentioned above detected a reduced ecosystem nutrient stock and tree growth after WTH. A recent meta-analysis by Achat et al. (2015) based on 749 case studies also demonstrated a clear impact of a higher harvesting intensity (removing branches and foliage) on nutrient export leading to reduced available and total nutrient stocks in soils and, subsequently, growth reductions in the short or medium term.

Different management practices have been described to remediate this. The first, most straightforward decision could be to reduce intensity of harvesting. This could be done by adopting SOH, by leaving the foliage in the stand (Wall and Hytönen, 2011; Achat et al., 2015), by exporting only part of the harvestable crown (Klockow et al., 2013) or by switching between WTH and SOH in consecutive rotations. Another possibility is to change the forest management type by adopting a so-called ecological length of rotation, a longer rotation period that gives enough time to natural processes such as weathering and deposition to compensate for the export of nutrients through harvesting (Achat et al., 2015). Another option is to adopt other harvesting systems, such as selection cutting instead of clear-cutting (Phillips and Watmough, 2012). A last method to compensate for the increased nutrient exports is to apply specific fertilization (Brandtberg and Olsson, 2012). N and K fertilization has been put forward to sustain forest growth under WTH in Finland (including stump extraction) (Aherne et al., 2012). However, Small et al. (2008a) found that the N fertilization effect was strictly additive to the effects of increased organic matter removal and thus that fertilization did not appear to counteract all the effects of additional biomass harvest. Moreover N fertilization leads to a lower pH and a possible increase in leaching of base cations (Ballard, 2000).

As mentioned earlier, impact assessments of additional biomass harvests on ecosystem nutrient stocks and long-term soil fertility are complex and have resulted in contrasting findings (Riffell et al., 2011). Results are dependent on forest stand type, soil type, climate and amount of atmospheric deposition. Therefore, it is important to synthesize relevant knowledge of each geographic area where biomass is extracted and to draw more general conclusions whenever possible (Abbas et al., 2011).

Here we investigate, for the first time, the impact of WTH on nutrient budgets of pine stands on poor, sandy soils in North-Western Europe. This is a highly relevant study system for numerous reasons. The poor sandy soil type we studied is widespread in the region and typically contains low stocks of exchangeable base cations (Neirynek et al., 1998). Moreover the study region has a strong history of acidifying deposition, in contrast with Scandinavia where most studies to date were performed. The total N-deposition levels in Belgium for example were on average 5.3 times higher than N-deposition levels in Sweden in 2013 (data obtained from the European Monitoring and Evaluation Programme database (EMEP; http://www.emep.int)). These high levels of acidifying deposition can result in a strong leaching of base cations, further depleting the available soil stocks (Verstraeten et al., 2012). Consequently, our study system represents a worst case scenario. In addition, the demand for renewable energy sources in this densely populated and strongly industrialized region is especially high. Pine stands make up a large part of the forests in this region (e.g., 39% in Flanders (Division of Forest and Nature, 2001) and 33% in the Netherlands (Dirkse et al., 2007)), especially on the sandy soil types. Hence, currently there is already a very high interest to harvest additional biomass from these stands. Our understanding of the consequences on nutrient budgets, however, is still incomplete.

We performed a detailed inventory of nutrient exports and stocks before and after a thinning and a clear-cut, taking away whole trees. We used these empirical data in a long-term nutrient budget modelling. We thus combined the first and the second type of WTH impact studies described above, building on an empirical basis to maximize ecological understanding and estimate long-term impact. We hypothesized that WTH depletes ecosystem stocks of base cations and possibly phosphorus on the long term under the studied circumstances (short rotation period, poor soils and high acidifying deposition loads) significantly more than SOH. Based on the results, we formulated recommendations for sustainable forest management.

2. Methods

2.1. Study region

The study was performed in Bosland, covering a total surface area of 22,000 ha of which approximately 45% nature and forest area. Bosland is a statutory partnership of four public owners and two non-profit organizations in north-eastern Belgium (center of the study region: 51.17°N, 5.34°E). The soils are characteristically dry, sandy and nutrient poor and were classified as Carbic Podzols (IUSS Working Group WRB, 2007). Until the middle of the 19th century, Bosland was mainly covered by an extensive heathland. Afterward, gradual afforestation with conifers took place with Scots pine (P. sylvestris) and Corsican pine (Pinus nigra ssp. laricio var. Corsicana Loud.) as dominant tree species (Vangansbeke et al., 2015a).

2.2. Management of pine stands

To develop our harvest scenarios, we interviewed two Bosland forest managers about the standard management of pine stands for wood production. In these stands, pines are left alone for about 30 years after planting or natural regeneration. Then harvester passages are created and a first thinning is executed, taking away about 20% of the total volume. Subsequently, every 6 or 9 years after the previous thinning a large part of the stand increment is taken away by a new thinning (Jansen et al., 1996). The rotation period is classically ended by a clear-cut at a stand age between

40 and 100 years, depending on the management regime. We chose to study a management regime with a relatively short rotation period of 48 years. A shorter rotation period is most suited to optimize biomass production (Dwivedi and Khanna, 2014). The management applied in Bosland, as described above, is comparable with the management of pine stands in other countries. Thinned after around 30 years and clear-cut after 40–110 years in Finland (Pussinen et al., 2002); clear-cut after 10–40 years in USA when focussing on biomass production (Dwivedi and Khanna, 2014); clear-cut after 77 years in Finland when focussing on timber and additional biomass and after 82–118 years when carbon storage was adopted as one of the management goals (Pihlainen et al., 2014).

2.3. Stand selection

We selected eight monoculture stands of Corsican pine with a similar size (1.13 ± S.D. 0.22 ha; Table 1) where whole trees were harvested between November 2012 and January 2013 according to the management plan and in the context of a biomass harvesting experiment. This harvesting was closely monitored and slightly different harvesting practices were used in the different stands to compare efficiency and cost-effectiveness (Vangansbeke et al., 2015b). The stands in this harvesting experiment were selected based on their similarity in soil type, tree species and management and were chosen to be representative for the region.

All stands occurred on typically dry to very dry sandy soils and were situated in Overpelt and Lommel. Four stands with a stand age of 33 years were selected in Overpelt (stands O1–O4; center of stands 51.21°N, 5.36°E); These stands were originally planted on former heathland in 1922, but destroyed by fire in 1976 and replanted in 1979 with a planting density of 6666 trees per ha. Four older stands with an age of 48 years were selected in Lommel (stands L1–L4; center of stands 51.18°N, 5.30°E), also planted on former heathland with the same planting density. The stands in Lommel had been thinned twice. In stands O1–O4 we executed a thinning, stands L1–L4 were clear-cut.

All clear-cuts were performed with a harvester and logs were extracted using a forwarder. The tree-tops were chipped inside the stand with a mobile chipper for stands L3 and L4 and were extracted using a forwarder and logs were separated by a forwarder and the tree tops were chipped at the roadside. In three of the thinned stands, and L4 and at 12 cm for stands L1 and L3. Three of the stands in Overpelt were thinned by a harvester, stand O4 was thinned by an excavator with a pinching head. In three of the thinned stands, all trees were chipped: in stand O1 the trees were extracted with help of a forwarder and chipped at the roadside; in stand O2 the trees were chipped in the stand by a mobile chipper; in O4 the trees were extracted by a tractor with a trailer and chipped at the roadside. In stand O3 the logs and tree tops were extracted separately by a forwarder and the tree tops were chipped at the roadside. For more information about the different harvesting practices we refer to Vangansbeke et al. (2015b), where differences between stands were used to compare efficiency of the different practices.

2.4. Data collection

In every stand, samples were taken from different ecosystem compartments before and after the harvest. We randomly laid out 3 square plots of 400 m² in every stand in which we measured the diameter of all trees before and in the thinnings also after harvest. The fresh mass of all lying coarse dead wood with a diameter over 5 cm was determined before and after harvest and subsamples were taken. Within every plot, we systematically laid out 5 square subplots of 1 m² in which we collected all fine dead wood (with a diameter under 5 cm) before and immediately after harvest and determined the fresh weight. To avoid the impact of previous sampling, we altered the exact location of the subplots sampled after the harvest from the subplots sampled before the harvest. In the middle of each of the subplots, we took a sample of the mineral soil until 50 cm depth before the harvest, separated in five subsamples of 10 cm layers. Additionally, before and immediately after the harvest, we collected all species present in the understory (woody and non-woody species) and a 0.25 × 0.25 m² sample of the whole litter layer (L, F and H layer) in the middle of each subplot. The samples for each soil layer were pooled at the plot level, resulting in five mixed soil samples per plot, one for each 10 cm layer. To quantify the standing stocks of trees, we cut five trees in both regions selected with a stratified sampling design: three trees with an average diameter of the stands were selected, plus one tree having the first and one tree having the third quartile diameter (after Neirynck et al. (1998)). We randomly selected trees with the desired diameter, keeping a distance of more than 10 m from the forest edge. For these trees, the exact height was determined with a measuring tape and stem disks were sampled at 1 m height and of every third meter higher (1 m, 4 m, 7 m, etc.). Of each of these model trees 20 fresh grams of the current needles were sampled to assess the nutrient status of the trees (Rautio et al., 2010). Finally we also collected a sample of the harvested tree chips and pooled ten subsamples of 0.5 dm³ for each exported chip container. A total of 79 containers were sampled.

2.5. Soil and wood chemical analyses

Soil samples were dried at 40 °C until a constant weight was obtained and passed through a 1 mm sieve. pH-H₂O was measured using a glass electrode (Orion, Orion Europe, Cambridge, England, model 920A) following the procedure described in ISO 10390:1994(E). Total N and C contents were measured by dry combustion using an elemental analyser (Vario MAX CNS, Elementar, Germany). Exchangeable K, Ca, Mg, Na and Al content was measured by atomic absorption spectrophotometry (AA240FS, Fast Sequential AAS) after extraction in BaCl₂ (NEN 5738:1996). This method was used as an estimation of the available cation concentrations in the soil. For calculation of effective cation exchange capacity (CEc) of the soils, all extracted exchangeable cations (K, Ca, Mg, Na and Al in meq kg⁻¹) were summed. Total P concentrations were measured after complete destruction with HClO₄ (65%), HNO₃ (70%) and H₂SO₄ (98%) in Teflon bombs for 4 h at 150 °C. Concentrations of P were measured according to the malachite green procedure (Lajtha et al., 1999). Available inorganic soil P within one growing season was measured by extraction in NaHCO₃ (Olsen-P according to ISO 11263:1994(E) and colorimetric measurement according to the malachite green procedure (Lajtha et al., 1999)). This directly available soil P pool is replenished by

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Stand and soil characteristics of the thinned stands in Overpelt (O1–O4) and the clear-cut stands in Lommel (L1–L4).</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (ha)</td>
<td>Year of planting</td>
</tr>
<tr>
<td>O1</td>
<td>1.05</td>
</tr>
<tr>
<td>O2</td>
<td>1.00</td>
</tr>
<tr>
<td>O3</td>
<td>1.35</td>
</tr>
<tr>
<td>O4</td>
<td>1.55</td>
</tr>
<tr>
<td>L1</td>
<td>1.15</td>
</tr>
<tr>
<td>L2</td>
<td>1.17</td>
</tr>
<tr>
<td>L3</td>
<td>0.89</td>
</tr>
<tr>
<td>L4</td>
<td>0.92</td>
</tr>
</tbody>
</table>
the slowly cycling active P pool (Richter et al., 2006), consisting of phosphate that reacted with aluminum (Al\(^{3+}\)) and iron (Fe\(^{3+}\)). The slowly cycling P pool was calculated based on the relationship: slowly cycling P = Olsen – P × 3.0736. This relationship was revealed from a large database of sandy soil measurements of both Olsen-P and slowly cycling P, measured as oxalate-P according to NEN 5776:2006.

Samples of wood chips, needles, dead wood, understorey and litter layer were dried at 65 °C to constant weight and the dry weight was determined. Subsamples of the coarse and small dead wood and the stem disks were dried at 65 °C to constant weight, weighed and ground to particles <0.5 mm (Retsch, SM200). Total N and C concentrations were measured by high temperature combustion using an elemental analyser (Vario MACRO cube CNS, Elementar, Germany). Concentrations of P, K, Ca and Mg were obtained after digesting 100 mg of sample with 0.4 ml HClO\(_4\) (65%) and 2 ml HNO\(_3\) (70%) in Teflon bombs for 4 h at 140 °C. P was measured colorimetrically according to the malachite green procedure (Lajtha et al., 1999). Concentrations of K, Ca and Mg were measured by atomic absorption spectrophotometry (AA240FS, Fast Sequential AAS).

2.6. Data analysis

2.6.1. Differences between stands within locations

To test for differences between the stands and harvest practices within both locations (Lommel and Overpelt) we applied mixed-effect models for each location with stand as a fixed effect term and plot (and subplot nested within plot, if applicable) as random-effect terms for each response variable using the nlme package in R 3.0.1 (R Core Team, 2013). The response variables were biomass and nutrient stocks for the different elements of the ecosystem compartments in the forest floor and mineral soil. The standing stock did not differ significantly between stands within one location (Vangansbeke et al., 2015b). Differences in soil characteristics and nutrient pools of the forest floor between the different stands of each location were small (Table A1). However, there was significant variation between stands in soil C in deeper soil layers in Lommel and of soil pH and exchangeable Mg stocks in soils in Overpelt. These initial differences might confound results of the impact assessment. Here we expect a limited impact, as the stands within one location were quite uniform in general. Moreover we found no other significant differences between stands after harvest than those present before harvest. The small differences between the harvest practices did thus not affect the nutrient pools and nutrient export. The four stands within each location were therefore considered as replicates.

2.6.2. Differences between locations

Since the stands in the two locations had contrasting stand age and density, significant differences existed between the nutrient pools in trees and forest floor e.g., more biomass in the stems and thicker litter layer in the older stands. We thus mainly focused on the soil differences between locations (Lommel and Overpelt) (Table A2). As all stands in both locations were classified within the same sandy soil type on the soil map we expected very similar soil conditions, a prerequisite to estimate future ecosystem nutrient stocks with a space for time substitution. To check this hypothesis we first made a pedological description up to 50 cm depth (cf. Davis et al. (2004)). The soil profiles were very similar in all stands of both locations and typical for carbic podzols with an obvious E-horizon on sandy parent material. To further test for differences between locations, we applied mixed-effect models with location as a fixed effect term and stand and plot, nested within stand, as random-effect terms for different response variables using the nlme package in R. The tested response variables were the stock of C, the stock of exchangeable Al and base cations, the CECe and the ratio between base cations (Ca, Mg, K) and Al.

We found significantly higher concentrations of exchangeable Al and base cations in the stands located in Lommel, resulting in a much higher CECe in the top soil, in comparison with the younger stands in Overpelt (p < 0.001). Yet, the CECe was strongly correlated with the amount of soil organic material (analyzed as % C as measure for % organic material) (r = 0.94, n = 24, p < 0.001). We also found a much higher C content in the older stands located in Lommel. Moreover, the ratio between exchangeable base cations (Ca, K, Mg) and Al was not significantly different between both locations (p = 0.16). As soils in both locations had a very similar texture, history and total nutrient stock, it can be expected that a large part of the difference in organic matter content and related CECe might disappear with the aging of the Overpelt stands. In this respect, the Overpelt stands can be considered as a younger version of the Lommel stand.

Studying long-term changes in soil productivity always implies some uncertainties. When using permanent plots, diverging growth patterns due to differing management regimes can easily be confounded by other factors (Burger, 1996). Inappropriate use of space-for-time substitution procedures on the other hand can lead to false conclusions about ecological processes. Space-for-time substitutions procedures remain an important tool for studying temporal dynamics of soil development (Walker et al., 2010) and are most appropriate for studying simple systems following temporally linear trajectories (Walker et al., 2010), such as the pine stands we studied.

2.6.3. Impact of harvest on aboveground nutrient stocks

The volume and biomass of stems before harvest was calculated based on the ten harvested model trees, following studies by Neirynck et al. (1998) and Berben et al. (1983) in the same area. The amount of nutrients in the stems was then calculated by using the concentration of the model trees and the stand biomass per hectare. The initial biomass of the crowns was estimated based on the fresh weight of the harvest for every stand and the moisture content of the chips, increased with the assumed harvest losses. To estimate these harvest losses, we calculated the difference between the biomass of the litter layer and the fine and coarse dead wood before and after the harvest. The amount of nutrients in the crown was then calculated using the estimated crown biomass and the concentrations of the wood chips. The root biomass and root nutrient stocks were estimated using the ratio of aboveground to belowground biomass and nutrient amount of the trees (Neirynck et al., 1998). The nutrient stocks of the understory, the coarse and fine dead wood and the litter layer were calculated as their nutrient concentration times their dry mass. The amount of nutrients in the mineral soil (0–50 cm) was estimated using the measured nutrient content and the bulk density. We used the bulk density of each 10 cm layer from a nearby level II plot of the

<table>
<thead>
<tr>
<th>Element</th>
<th>Overpelt Available</th>
<th>Overpelt Total</th>
<th>Lommel Available</th>
<th>Lommel Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca</td>
<td>13.9 (5.8)</td>
<td>404.1 (31.2)</td>
<td>65.3 (16.5)</td>
<td>517.7 (388.1)</td>
</tr>
<tr>
<td>Mg</td>
<td>5.2 (0.6)</td>
<td>988.5 (70.7)</td>
<td>9.6 (2.7)</td>
<td>894.4 (186.9)</td>
</tr>
<tr>
<td>K</td>
<td>31.7 (3.6)</td>
<td>1747.8 (122.1)</td>
<td>32.2 (4.5)</td>
<td>1778.1 (302.1)</td>
</tr>
<tr>
<td>Al</td>
<td>350.2 (32.2)</td>
<td>11796.6 (962.4)</td>
<td>704.6 (118.3)</td>
<td>11483 (1540.9)</td>
</tr>
<tr>
<td>P</td>
<td>638.2 (20.1)</td>
<td>2590.1 (179.0)</td>
<td>875.5 (23.6)</td>
<td>3513 (46.1)</td>
</tr>
<tr>
<td>N</td>
<td>3237.2 (215)</td>
<td>4270.3 (804.1)</td>
<td>4207.3 (804.1)</td>
<td>80474.3 (19377.6)</td>
</tr>
<tr>
<td>C</td>
<td>40307.2 (3631.1)</td>
<td>80474.3 (19377.6)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The export of biomass and nutrients under WTH was calculated with the weight of the harvested stems and the concentration in the stems of the model trees and with the weight and the nutrient concentration of the wood chips. The amount of nutrients that would have been exported under SOH was calculated using the weight of the harvested stems and the nutrient concentration in the stems of the model trees. The SOH was thus not actually executed, but the theoretical export was readily calculated based on the WTH and the assumption that all crowns would have been left in the forest, as is normally performed.

To evaluate the magnitude and immediate impact of the export by harvest we compared the amount of exported nutrients with the aboveground nutrient stocks and the available nutrients in soil that together make up the ecosystem nutrient stock (Fig. 1). Different methods exist to analyze the available nutrient stocks in soils. Here we used the term available soil P for the slow cycling P pool, available soil cations were measured after BaCl2-extraction and the total N pool in the soil was considered as available soil N (see soil and wood chemical analysis).

2.6.4. Nutrient budget modelling

To model the future impact of WTH and SOH on ecosystem nutrient stocks we considered all aboveground nutrients included in trees and in the forest floor as bio-available. Moreover, we neglected all the internal fluxes (fine root turnover, growth, litterfall and decomposition), as these do not change the amount of ecosystem nutrients (Fig. 1).

To model the future ecosystem nutrient budgets, we defined a simple standard management scenario with a first thinning creating harvester passages at 33 years, a second thinning at 39 years and a clear-cut at 48 years (based on the interviews with the forest managers, see above). To evaluate the total impact of this management regime, we estimated the stem volume of the thinning at 39 years stand age using the yield table of Jansen et al. (1996). Different methods exist to analyze the available nutrient stocks in soils. Here we used the term available soil P for the slow cycling P pool, available soil cations were measured after BaCl2-extraction and the total N pool in the soil was considered as available soil N (see soil and wood chemical analysis).

Future nutrient budgets are modelled by summing the yearly fluxes for weathering, deposition and leaching and the exports of thinnings and clear-cuts. The nutrient budget modelling was executed for a period of 100 years (2011–2111). The situation in the clear-cut stand just before the harvest in 2011 (harvest was in 2012) was adopted. Afterward thinnings were modelled at a stand age of 33 and 39 and a next clear-cut at a stand age of 48, thus in 2060 and repeated through each subsequent rotation. We also took part of the uncertainty of the model into account based on the best available S.D. of the respective fluxes. For example the S.D. of the ecosystem potassium on time i is calculated as follows: $S.D.(K_i) = \sqrt{(S.D.(K_L_i)^2 + S.D.(K_D_i)^2 + S.D.(K_E_i)^2 + S.D.(K_F_i)^2)}$ (abbreviations given in caption of Fig. 2).

3. Results

3.1. Pre-harvest nutrient status

The soils at both locations were relatively acidic (average pH H2O 4.33). The amount of base cations in the soil was low, especially in the Overpelt stands (0.27 meq kg$^{-1}$) compared to Lommel (0.63 meq kg$^{-1}$). Both soils had a similar ratio of base cations to Al (0.054 meq meq$^{-1}$). To estimate the pre-harvest nutrients status, the available and total stocks in the soils of both locations were determined (Table 2). The available soil stock of base cations and P was relatively small.

Corsican pine is, well adapted to these nutrient poor soil conditions, but not too very acidic situations (Hill et al., 1999). To estimate the current nutrient status of the stands, we compared the needle nutrient concentrations to the concentrations described as “low” and “high” in the ICP Forests manual (Rautio et al., 2010) (Table 3). The observed Mg concentrations in both Lommel and Overpelt were below the 5 percentile of the ICP Forests Level II dataset. Also for Ca (mainly in Lommel) and K (in Overpelt) the observed needle concentrations were on the lower side of the plausible interval, suggesting that base cation concentrations at our study sites were close to the lower limit of the species.

3.2. Immediate impact of harvest on aboveground nutrient stocks

In the clear-cut stands L1–L4, aboveground stocks amounted to 396.4 ton ha$^{-1}$ before the harvest; whole tree harvesting reduced this to less than half of the initial stock with an export of 206.4 ton ha$^{-1}$ (Fig. 3). In the thinned stands O1–O4, the initial aboveground stock was 349.3 ton ha$^{-1}$ and only 43.5 ton ha$^{-1}$ was exported. Not all material from stems and crowns was
Forests values were highlighted in bold.

harvest and concentrations for Corsican pine, based on the ICP Forests dataset (Rautio et al., 2010). Nutrients that differed significantly between locations are marked with a

Needle nutrient concentrations (/C0

every compartment).

exports of the thinned vs. clear-cut stands (error bars mark standard deviations for

Fig. 3. Impact of harvest on different compartments of aboveground stocks and exports of the thinned vs. clear-cut stands (error bars mark standard deviations for every compartment).

and SOH was proportionally small, with an export of 170.5 ton ha−1 under SOH, which is 82% of the biomass exported under WTH. In the thinned stands, the difference was proportionally larger, with an export of 26.2 ton ha−1 under SOH, which is only 60% of the biomass exported under WTH. The trees in the younger thinned stands had deeper crowns than the mature pines in the clear-cut stand. In general, when solely looking at the mass of the stocks, a clear-cut had a strong impact on the aboveground stocks but the extra impact of WTH seemed relatively small.

To evaluate the direct impact on the nutrient stocks in trees and forest floor we looked into the export of the base cations, and N and P (Table 4). In the thinned stands about 11% of the aboveground base cations was exported and about 8% of the aboveground stock of N and P. The reduction of the export of nutrients under SOH was quite similar to the reduction of biomass export (variation between 40% and 70% of export compared to WTH for different nutrients and 60% for biomass).

Under clear-cuts, again the heavy impact of WTH on the aboveground stocks was evident. For base cations, half of the aboveground pool was exported under WTH, and for N and P one third. This relatively large export of nutrients could easily affect future tree growth and site productivity, when available stocks in the soil are small and/or insufficiently replenished. The export of base cations under WTH in the clear-cuts exceeded the available stock in the top 50 cm of the soil more than fourfold (compared to a little less than threefold under SOH). Under WTH, for P the export in clear-cuts was about equal to the slow cycling soil stock and for N to one fifth of the soil N (compared to 58% for P and 15% for N under SOH).

Leaving the crowns in the stand after clear-cut had a significant reduction on impact as on average only 67% of the base cations, 69% of the N and 55% of the P was exported in comparison with WTH, but the extra impact of WTH seemed relatively small.

By only considering the stem export, we estimated the impact of SOH in which crowns are left in the forest stands. In the clear-cut stands the difference in biomass export between WTH

and SOH was proportionally small, with an export of 170.5 ton ha−1 under SOH, which is 82% of the biomass exported under WTH. In the thinned stands, the difference was proportionally larger, with an export of 26.2 ton ha−1 under SOH, which is only 60% of the biomass exported under WTH. The trees in the younger thinned stands had deeper crowns than the mature pines in the clear-cut stand. In general, when solely looking at the mass of the stocks, a clear-cut had a strong impact on the aboveground stocks but the extra impact of WTH seemed relatively small.

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Leaving the crowns in the stand after clear-cut had a significant reduction on impact as on average only 67% of the base cations, 69% of the N and 55% of the P was exported in comparison with WTH, while 82% of the biomass under WTH was taken away under SOH.

3.3. Long-term impact on ecosystem nutrient stocks

The modelling showed that the clear-cut reduced the stocks of all nutrients, both under SOH but more strongly under WTH (Fig. 4). In the next 33 years, the different stocks become replenished by deposition and weathering while the stand matures until the first thinning. After a modelled second thinning and a new

| Nutrient | Overpelt | Lommel | ICP Forests manual
<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>S.D.</td>
<td>5 percentile, lower limit</td>
</tr>
<tr>
<td>Ca</td>
<td>1631</td>
<td>413</td>
<td>1141</td>
</tr>
<tr>
<td>Mg</td>
<td>520</td>
<td>104</td>
<td>506</td>
</tr>
<tr>
<td>K</td>
<td>4730*</td>
<td>857</td>
<td>7881*</td>
</tr>
<tr>
<td>N</td>
<td>14998</td>
<td>1853</td>
<td>16518</td>
</tr>
<tr>
<td>P</td>
<td>1021</td>
<td>105</td>
<td>1098</td>
</tr>
</tbody>
</table>

Fig. 2. Scheme of the nutrient budget modelling approach. The amount of ecosystem nutrients is influenced by the balance of four external fluxes: imports (in green) by atmospheric deposition (ID) and weathering (IW) and exports (in red) by Harvest (EH) and Leaching (EL). The period and the source of the data is given for each flux. (*p < 0.05; nutrient concentrations that were below the lower boundary of the ICP Forests values were highlighted in bold.)

This study

Lommel

Mean | S.D.

5 percentile | 95 percentile

Ecosystem nutrients

- Consists of nutrients in trees, forest floor and available soil nutrients
- Measured. Except for nutrients in roots (estimated).

Harvest

- On stand age 33, 39 and 48
- WTH vs SOH
- Export of T33 and CC measured, T39 estimated

Weathering

- Yearly
- Estimated from literature

Leaching

- Yearly
- Adopted from measurements in nearby level II plot

clear-cut in 2060, the first rotation is finished and it is possible to evaluate the evolution of the ecosystem stocks for the different nutrients. The ecosystem stock of Mg is predicted to increase over the rotation period while the ecosystem stock of P and Ca is expected to decrease under both WTH and SOH. Differences between SOH and WTH were most obvious for K and N with a long-term decrease under WTH and an increase under SOH.

### 4. Discussion

#### 4.1. Nutrient exports

It is clear that, except for N, the stocks in the soil were insufficient to sustain the same growth levels under WTH (and SOH) if not sufficiently replenished by deposition and weathering. Compared to the literature, the differences between WTH and SOH were much smaller than described for pine stands in Finland (Aherne et al., 2012). In their study, the export of cations under WTH was more than three times higher than with SOH, while we found a ratio of 1.5. This difference was probably due to the fact that the models used in Aherne et al. (2012) did not take harvest losses into account. We found harvest losses of 40% of the crown in the clear-cuts and 46% in thinning. These harvest losses probably contained more twigs and needles and thus represented an even larger share of the nutrients. When comparing our results to the findings of Palviainen and Finér (2012) we found higher ranges for export of most nutrients for SOH, probably because of the higher productivity under a Belgian climate compared to the situation in Fennoscandia. We found strikingly higher N exports in our study. This difference was most likely related to the high N availability in Belgium, with a history of very much higher N deposition rates than in Fennoscandia (see Waldner et al. (2014)). The modelled export through WTH of Palviainen and Finér (2012) was within the same range as in our study. The difference between WTH and SOH in this study was thus again larger than the observed difference in our study. This can be explained because the harvest losses were not included in the modelling study of Palviainen and Finér (2012).

The impact of thinnings was smaller and less drastic than the impact of clear-cuts, with only ca. 12% of the aboveground base cations and 8% of the aboveground N and P stock exported under WTH (6% and 4% respectively under SOH). Nonetheless, export of base cations under WTH (with only 20% of the trees removed) equalled the available soil stock for base cations in soil (see also Palviainen and Finér (2012)).

### Table 4

Aboveground nutrient stocks and export from the thinned and clear-cut stands under whole tree harvesting (kg ha⁻¹). The stock after harvest under stem-only harvesting was calculated by adding the export of crowns to the other organic stock, as the crowns would stay in the forest floor after stem-only harvesting.

<table>
<thead>
<tr>
<th>Stock before</th>
<th>Whole tree harvesting</th>
<th>Stem-only harvesting</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trees</td>
<td>Forest floor</td>
</tr>
<tr>
<td>Thinned</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>185.7</td>
<td>134.1</td>
</tr>
<tr>
<td>Mg</td>
<td>57.2</td>
<td>24.7</td>
</tr>
<tr>
<td>K</td>
<td>318.1</td>
<td>83.7</td>
</tr>
<tr>
<td>N</td>
<td>1096.1</td>
<td>1091.7</td>
</tr>
<tr>
<td>P</td>
<td>40.2</td>
<td>44.3</td>
</tr>
<tr>
<td>Clear-cut</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>340.2</td>
<td>208.1</td>
</tr>
<tr>
<td>Mg</td>
<td>63.0</td>
<td>32.0</td>
</tr>
<tr>
<td>K</td>
<td>268.0</td>
<td>98.5</td>
</tr>
<tr>
<td>N</td>
<td>1398.9</td>
<td>1531.0</td>
</tr>
<tr>
<td>P</td>
<td>46.9</td>
<td>54.7</td>
</tr>
</tbody>
</table>
4.2. Future modelling and impact on long-term soil fertility

4.2.1. Long-term impact

The modelled long-term changes in ecosystem nutrient stocks varied greatly among nutrients and treatments. For example, ecosystem Mg stocks tend to strongly increase, while P and Ca stocks always decreased. On the other hand, ecosystem K and P stocks only increased under SOH. When ecosystem nutrient stocks are decreasing, there is a risk of a shortage over the short or long term. In these cases it is important to estimate the possible impact and time-frame and to evaluate if current harvesting regime could be continued. Göttlein et al. (2007) defined a harvesting regime as “problematic” when the ratio between the imports (mainly through deposition and weathering) and exports (mainly through harvest, leaching and run-off) of nutrients is smaller than 0.9, and if the remaining ecosystem nutrient stock is not sufficient for the next ten rotation periods. Under WTH, the ratio between imports and exports was smaller than 0.9 for each nutrient except Mg, indicating a possible significant decrease in stock (Göttlein et al., 2007). For Ca, K and P, the current ecosystem stock was only sufficient to support four future rotation periods under the current circumstances. The ratio of N import/export is also smaller than 0.9 for WTH, but the current ecosystem stock is sufficient to sustain 16 more rotation periods under current circumstances. Under SOH, the ratio import/export is only smaller than 0.9 for Ca and P. However, current ecosystem stocks suffice for fourteen and ten future rotation periods respectively, making the situation less critical than under WTH. These results largely coincide with the findings of Palviainen and Finér (2012), who also found deficiencies of P, K and Ca under WTH for pine or spruce stands. In addition they also found shortages of N for spruce and birch stands. As mentioned earlier, the deposition of N in Belgium is and has been larger than for Fennoscandia, resulting in a build-up of N in the forest floor and in soils in the former region. Under a system of SOH, however, Palviainen and Finér (2012) did not detect a decrease in ecosystem nutrients, except for P and K under some circumstances. Hence, our results stress the strong negative impacts of WTH on ecosystem stocks of Ca, K, and P and the possible drawbacks on future productivity.

The modelled increase of Mg in time is somewhat contradictory to the low levels of ecosystem Mg in soils and to the low levels in the needles, indicating a possible deficit. One possible explanation could be that the weathering rate for Mg is an overestimate. Another explanation could be that the current Mg status reflects the situation of the previous decades with even higher acidifying deposition and leaching of base cations, such as Mg (Fig. A1).

4.2.2. Uncertainties

For the modelling we used the best available data and methodology, but some uncertainties and assumptions were inevitable, as described in the methods section. One of the most important assumptions was that the standard deviations of the data on the fluxes reflect the uncertainty of the fluxes. Determining this uncertainty in budget closure, including external fluxes such as weathering, leaching and deposition remains very challenging (Yanai et al., 2012). Another uncertainty is the transfer from data of nearby stands to our study area. However, these stands were very nearby and very similar, which should limit this spatial variability. Extrapolating the results to other pine stands, other regions and other stand types implies higher uncertainty.

Moreover, we only considered the top 50 cm of the soil, while most trees might root deeper and can use available soil nutrients from deeper layers. However, we found a sharp decrease in available soil nutrients with depth and Cermak et al. (1998) demonstrated a paraboloid root architecture for pine trees (with a decreasing amount of roots with depth). Based on these arguments we believe that the uptake below 50 cm is very limited.

When extrapolating current fluxes to future situations, not only the current variation in fluxes but also possible future changes may need to be taken into account. Yet, these estimates are extremely difficult to quantify and were thus not included in our simple model. For example, new technologies might cause harvest losses to decrease and exports to increase. Increasing tree growth (McMahon et al., 2010; Pretzsch et al., 2014) under influence of a changing climate or decreasing tree growth under decreasing available nutrient stocks in soil could also influence exports. New legislations or expansion of agriculture and industry might cause a decrease or an increase in N deposition rates, respectively, which is directly linked to changes in leaching rates. In turn, weathering rates can be affected by climate change (Sverdrup and Warfvinge, 1993). As another example, it has also been demonstrated that fluxes could be influenced by the event of harvesting itself, for example increased nitrogen leaching after harvest (Devine et al., 2012). Thus, the modelling result after 100 years is an indication of the evolution in ecosystem stocks when continuing on the current management path rather than a precise prediction of the ecosystem stocks in each year.

4.3. Other sustainability issues

Apart from soil nutrient depletion, intensified forest management with short rotation periods and WTH cause other sustainability issues. Also soil microbial properties and activity and related soil productivity and functioning can be influenced (Smaill et al., 2008b). From an economic point of view, Vangansbeke et al. (2015b) demonstrated that WTH is hardly profitable in this region under current market conditions. Moreover there are different studies that demonstrate a negative impact of WTH on biodiversity of saproxylics, small mammals and birds (Berger et al., 2013). Other studies challenge the idea of bioenergy from forestry biomass as a carbon neutral alternative (Schulze et al., 2012). These issues are beyond the scope of the current study, but should also be kept in mind when applying WTH.

4.4. Management recommendations

According to our long-term modelling, poor, sandy soils cannot sustain a WTH system of Corsican pine in this region without intervention. Based on our data, we thus recommend to apply SOH, under the current circumstances to reduce impacts on soil fertility. In addition, longer rotation periods can lower the impact on available soil nutrient stocks (Zanchi et al., 2014; Achat et al., 2015). Older trees have slower growth rates and a larger stem to crown ratio, thereby reducing export of base cations and nutrients per unit of time with harvesting. Moreover under longer rotation periods leaching and deposition can more sufficiently replenish ecosystem nutrient stocks (Achat et al., 2015). Currently most stands in Bosland are managed under longer rotation periods and thus with a less narrow focus on production. Under these longer rotation periods, WTH might be considered in some thinnings or clear-cuts, for example, once every three to four rotation periods. Another measure to reduce nutrient export with WTH is to leave the crowns in the stand for 1 year such that the majority of the needles are shed before the crowns are exported (Wall and Hyytönen, 2011). This is also beneficial for the energy content due to lower loss in dry mass in comparison with drying at the terminal (Edwards et al., 2012). In the near future, about half of the pine stands in Bosland will be transformed to native broadleaf species such as oak and birch (Moonen et al., 2011). This new management context for these stands also opens up possibilities for different silvicultural systems, such as selective cutting instead of
clear-cutting with possibly less profound implications on nutrient cycling (Phillips and Watmough, 2012). Apart from reducing the export of nutrients, one could also compensate nutrient exports through fertilization to sustain WTH and short rotation periods. However, a well-balanced (different element concentrations in relation to local shortages), slowly releasing and stand-wide application would be necessary to avoid an increase in leaching and a possible shift in soil biota and vegetation (Hedwall et al., 2014). Some past studies also demonstrated that fertilization cannot replace nutrient loss from greater harvest exports and leads to a lower pH (Ballard, 2000; Smaill et al., 2008a). Moreover, it is very difficult to predict the specific fertilization requirements without thoroughly screening soil or needle nutrient levels and fertilization is expensive (Eisenbjes et al., 2009). It is thus very questionable if WTH including this remediation measure could be cost-efficient in the Flemish forest context, given the current small margin of profit (Vangansbeke et al., 2015b).

5. Conclusions

Our results reveal a strong negative impact of WTH on ecosystem nutrient stocks, definitely for clear-cuts. According to our knowledge of the fluxes that influence the available nutrient stocks in the sandy soils in our study area, an intense harvesting regime with WTH cannot be sustained. Shortages of Ca, K and P will most likely occur, decreasing soil fertility and reducing tree growth. The uncertainty associated with ecosystem future stocks adds to the conclusion that a less intensive system with longer rotation periods would be necessary to avoid an increase in leaching and a possible shift in soil biota and vegetation (Hedwall et al., 2014). Scaling up from the individual tree to the stand level in Scots pine. Needle distribution, overall crown and root geometry. Ann. Sci. Forest. 55, 63–88.


