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Abstract:

Scarce and uncertain data on woody debris decomposition rates are available available for calibrating forest ecosystem models, owing to the difficulty of their empirical estimations. Using field data from three experimental sites which are part of the North American Long-Term Soil Productivity (LTSP) Study in south-eastern British Columbia (Canada), we developed probability distributions of standard wood stake mass loss of *Populus tremuloides* and *Pinus contorta*. Using a Monte Carlo approach, 50 synthetic decomposition rate values per debris type were used to calibrate the ecosystem-level forest model FORECAST. Significant effects of uncertainty of pine stake mass loss rates on estimated tree growth were found, especially in moderately managed forests, as estimations of available nitrogen were affected. Consequently, our work has shown that projections of tree growth under management conditions depend on accurate estimations of woody debris decomposition rates, and special effort should be done in create reliable databases of decomposition rates for their use in tree growth and yield modelling.

Recommendations for Resource Managers

1. Maintaining woody debris on site, particularly large roots, should be favored. Significant influences of wood decomposition rates on tree growth were found, especially in moderately managed forests, because belowground woody debris became an important reservoir of nutrients needed to maintain tree growth rates. Forest floor and stump removal are therefore discouraged.

2. When using ecological models for estimating tree growth, uncertainty associated with calibrating woody debris decomposition processes should be taken into consideration if moderate management is planned.

3. Special efforts should be made to gather site- and species-specific woody debris decomposition rates, particularly for medium and coarse roots (diameter above 2.5 cm). Creating a database of standardized branch and root decomposition rates would greatly reduce the uncertainty of model estimations of tree growth.

Key words: ecosystem-level model, sensitivity analysis, uncertainty analysis, forest ecosystem, forest management, FORECAST model.

1. INTRODUCTION

In sustainable forest management it is necessary to define management plans, taking into account the interaction between forestry activities and ecological processes, as well as the predicted long-term outcomes of alternative management plans. One of the best tools for such tasks are ecosystem-level ecological models (Kimmins et al., 2010). However, these models can be difficult to calibrate due to the high number of parameters and the specific scientific-oriented nature of some of them. Ideally, calibration values should come from detailed, carefully-collected field data that adequately estimate the parameter values (Gárate & Blanco, 2013). However, due to common funding limitations for sampling and monitoring programs in most forestry-related institutions around the world, the sampling effort is usually focused on the main model parameters that are more prone to influence model behavior. Such parameters can be identified *a priori* by sensitivity analysis, which consists of creating a ranking of the different factors that influence the chosen target variables (Håkanson, 2003), and possibly identify the most influential factors for model behavior (Kimmins et al., 2010). If the model is run with different parameter values, but the target variable´s trend is similar over time, the model is considered robust to the uncertainty surrounding the parameter calibration value, even though the numerical values are different (Ford, 1999). Such characterization of model behavior improves our understanding and, therefore, can improve the ability of the model to mimic the natural system it is trying to emulate. A rigorous sensitivity analysis also provides guidance on formulating a hypotheses of potential model behaviors under circumstances that would imply recalibrating parameter values, such as when using the model in ecosystems with different values of ecological parameters (portability of the model) or when new or novel ecological conditions are simulated (scenario analysis, e.g. climate change).

Model sensitivity analysis is a fast-evolving field, with major breakthroughs in recent years towards

sensitivity analyses that assess global model behavior when multiple parameters are modified simultaneously. However, more traditional one-at-a-time (OAT) sensitivity analyses still have importance in ecological modelling, as they give detailed assessments on the influence of specific parameters on model behavior (Saltelli et al., 2008). Such studies are very important to help model users find the best tool and method for their needs. This is a common situation in management-oriented forest models. For example, Tatarinov & Cienciala (2006) used OAT methods to develop user guidelines in the BIOME-BGC model (Running & Coughman, 1988) for four major tree species in Europe. Similarly, Rodríguez-Suárez et al. (2010) used OAT methods to estimate the 3-PG model (Landsberg & Waring, 1997) sensitivity to changes in soil fertility. In addition, Blanco (2012) and Gárate & Blanco (2013) carried out sensitivity analysis of the hybrid ecosystem-level forest model FORECAST to changes in the decomposition rates of leaves, fine roots, and coarse woody debris, and indicated that decomposition rates of lignified and fine roots can potentially influence tree growth simulations.

However, relatively few empirical wood decomposition rates are available for many forest ecosystems (Russell et al., 2015; Petrillo et al., 2016) until the recent development of using standardized wood stakes to estimate the effects of climatic and soil conditions on wood decomposition (Jurgensen et al., 2006). The rate of wood decomposition can be used as an index of long-term effect of forest management effects on soil productivity (either negative or positive). This protocol has been included on a number of sites in the North American Long-Term Soil Productivity study (LTSP), which is an international project designed to investigate effects of soil organic matter removal and soil compaction on forest productivity over the long-term (Powers & Avers, 1995). This provides an ideal template for evaluating the influence of stand management on surface and belowground changes in site processes (e.g. decomposition). Organic matter, such as leaves or woody debris from a particular site, gives only location-specific information on carbon (C) and nutrient turnover rates, but differences in organic matter quality (lignin, cellulose: lignin or C:N ratios) make it difficult to compare results among sites. In the context of this research, woody debris refer to lignified material (stems, roots or branches) with diameter 2.5 cm or larger.

By using the same organic material on several sites, organic matter quality is held constant and the decomposition rate becomes a function of soil abiotic and biotic conditions. Therefore, we used wood from two different tree species (trembling aspen [*Populus tremuloides* Michx.] and loblolly pine [*Pinus taeda* L.]) to make stakes that were placed at two different soil locations (soil surface, and buried in the mineral soil), as an index to assess the longer-term (5 year) effects of harvest removal intensity on wood decomposition. These two wood species were selected because they have different wood properties, which favor the development of different wood-decomposing microbial communities (Blanchette, 1984). Woody debris are a normal component of forest soils (lignified surface residue, stumps, roots), and their decomposition is affected by changes in moisture and temperature over long time periods (Chen et al., 2000).

Using the LTSP study plots and wood stakes provides an opportunity to obtain a unique dataset of decomposition of standard woody material exposed to a gradient of forest management intensities, which could be used to obtain a range of wood decomposition rates under different soil micro-climate conditions. Therefore, the objective of the research reported here was to assess the influence of the uncertainty associated with field-based estimations of wood decomposition rates on projections of future tree growth when using the ecological model FORECAST (Kimmins et al., 1999). FORECAST has been used to provide acceptable estimations of tree growth for North American forests, particularly in coastal and interior British Columbia (Seely et al., 2010; Blanco et al., 2007, 2014), as well as tropical plantations (Blanco & González, 2010; Wang et al., 2013; Wu et al., 2015), temperate mixed forests (Lo et al., 2015a; González de Andrés et al., 2017; Candel-Pérez et al., 2017), and sub-boreal and alpine forests (Seely et al., 2010; Jie et al., 2011; Wang et al., 2014).

2. MATERIAL AND METHODS

2.1. Research Sites

Data on wood stake mass loss rates on and within the mineral soil were gathered from three research sites from the LTSP sites in southeastern British Columbia (western Canada), which were established by the BC Ministry of Forests in the 1990s in co-operation with the U.S.D.A. Forest Service (Holcomb, 1996). Research sites were established in the Interior Douglas-fir (IDFdm2) biogeoclimatic zone (Meidinger and Pojar, 1991) in 1999-2001 (Table 1). The IDF is characterized by warm, dry summers and cool winters with mean annual temperatures ranging from 1.6 to 9.5 °C. Mean annual precipitation is between 300 and 750 mm, but can surpass 1000 mm in the wettest subzones, and 20-50% of the precipitation falls as snow. Main tree species are Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), trembling aspen (*Populus tremuloides* Michx.), and lodgepole pine (*Pinus contorta* Doug.). Common understory shrubs are soopolallie (*Shepherdia canadensis*(L.) Nutt.) and kinnikinnik (*Arctostaphylos rubra* (Rehd. & Wilson) Fernald).

Detailed information about the LTSP installations in British Columbia can be found in the establishment report (Hannam et al., 2008). The three LTSP study sites are located in the Kootenay/Boundary Region (British Columbia Ministry of Forests, Lands and Natural Resource Operations) in the southeast corner of British Columbia. Mud Creek and Kootenay East are on the eastern side of the Rocky Mountain Trench and Emily Creek is located on the western side. The three sites are located within 13 km of Canal Flats (north of Cranbrook, BC) and all are on Orthic Eutric Brunisols (Soil Classification Working Group, 1998; Table 1). The closest weather station with full records since 1983 is Wasa (49º 49' 26" N, 115º 37' 53" W, 970 m a.s.l., Figure 1). Average temperature in the region is 6.0º C, but it can reach as high as 37º C in summer and as low as -35º C in winter. Average annual precipitation is 458 mm, with the driest season occurring in late fall and the wettest in mid-spring. Frost can occur any time of the year except in July (Figure 1).

2.1.1. Estimation of wood decomposition rates

At each research site, a 3 x 3 factorial experiment was established in 1999-2001, with three different levels

of organic matter retention and three levels of soil compaction. In the research reported here, only the data

from the no compaction treatments were used, as the FORECAST model does not simulate bulk density

and therefore cannot directly simulate the effects of soil compaction. The organic matter retention levels

were: Control / no management, where the original Douglas-fir dominated stands remain and neither

harvesting nor forest floor or woody debris removal was carried out; M0 / moderate management, where

the original forest was clearcut and only the tree boles were removed; and M2 / intense management,

where the original forest was clearcut and boles, crowns and forest floor were removed. To estimate wood

decomposition rates, wood stakes of aspen (*Populus tremuloides* Michx.) and loblolly pine (*Pinus taeda*

L.) were used as standard substrates, following the protocol described by Jurgensen et al. (2006). We used

stakes placed on the soil surface as an index of branch or twig decomposition on the soil surface. To do

this, 50 stakes of each species (2.5 cm × 2.5 cm × 15 cm) were place on top of the forest floor in 2001

(Mud Creek), 2002 (Emily Creek), and 2003 (Kootenay East). As an index of root decomposition, another

slightly longer set 50 stakes of each species were inserted vertically to a depth of 20 cm in the mineral soil

at each of the study sites, to access for typical soil moisture levels that roots would encounter. To limit

physical damage to the stakes we made a 2.5 cm^2 hole with a metal coring tool and inserted the stake so

that the top was level with the mineral soil surface. If a forest floor was present it was returned to cover

the stakes. Ten stakes of each species from each location were removed from each site yearly in June for 5

years. The stakes were weighed in the field to calculate moisture content, then were air-dried and sent to

Michigan Technological University (Houghton, MI) for final drying and weighing. Decomposition rates

(*k*) were estimated by fitting the weight loss data to a negative exponential model (Olson, 1963), using the

software JMP 12.0 (SAS Institute, Cary, NC, USA).

2.2. The FORECAST model

2.2.1. Model calibration and evaluation

FORECAST is forest ecosystem simulator which operates at annual time steps and at stand level. It is deterministic and management-oriented. A detailed description can be found in the Appendix A.

The datasets used for the research presented here were based on existing calibration datasets assembled as part of the project funded by the Canadian Foundation for Innovation "The Ecosystem Management Simulation Laboratory for research on forest stewardship and sustainability" (Canada Research Chair Infrastructure awarded to Dr. J.P. Kimmins, University of British Columbia). Previous work done with the same datasets showed the capability of the model to acceptably simulate aboveground forest biomass, as well as its capability to simulate different soil types belonging to different biogeoclimatic zones (Blanco et al. (2014, 2015a). However, those works also warned on the potential influence that inaccurate estimations of soil organic matter may have on tree growth estimations, without being able to quantify such influence given the lack of empirical data at that time. Such work has now been possible with the data from the LTSP study. Growth and yield tables for the interior B.C. region were combined with species-specific allometric biomass equations to generate calibration data (biomass accumulation rates, top height, diameter at breast height, and stand density). Nutrient dynamics in this study were restricted to N, the most limiting nutrient at these sites (Blanco et al., 2014). To calibrate N flows and stocks, literature data were used for N concentrations in plant tissues (Kimmins et al., 1979; Peterson & Peterson, 1992; Wang et al., 1996), leaf and needle decomposition rates estimated with litter bags (Prescott et al., 2000a, 2000b; Camiré et al., 2002), litterfall production rates (Kimmins et al., 1979; Peterson, 1988; Li et al., 2003), light transmission through the canopy (Messier et al., 1998; Leifers et al., 2002; Comeau & Heineman, 2003), and light-limited growth rates (Mailly & Kimmins, 1997; Leifers et al., 2002; Claveau et al., 2002). Calibration values are not repeated here as they can be found in those studies.

Previous applications of FORECAST have studied soil productivity and its relationship with soil organic matter (e.g. Morris et al., 1997; Seely, 2005; Seely et al., 2010; Blanco, 2012, Blanco et al., 2015a).

Particularly, the model has been extensively evaluated and validated against independent field data for tree growth and other ecophysiological and soil variables for BC´s Douglas-fir forests, showing acceptable model behavior and accuracy of its estimations (see Blanco et al., 2007; Seely et al., 2008, 2010).

2.2.2. Model initialization

A modified spin-up process was used to reach a stable state to define the simulation´s starting conditions (Hashimoto et al., 2011; Shi et al., 2013). Based on data on fire return intervals in interior BC, the model simulated seven 125-year cycles for a mixture of Douglas-fir (1350 trees ha^{-1}) and trembling aspen (450 trees ha^{-1}). The last run ended with a stand-replacing wildfire (Blanco et al., 2007, 2014). This procedure did not pretend to simulate the past stand history of the sties, but it just allowed the model to reach stable values of litter and humus in soil. The ecosystem state at the end of these initialization runs was used as the starting conditions for the simulation runs.

2.3. Sensitivity analysis of model response to wood decomposition rates

In FORECAST, branches are one unique biomass pool without further differentiation by branch diameter, whereas roots are divided into two different biomass pools: fine roots (diameter ≤ 3.0 mm) and woody roots. Branches and roots were simulated independently for conifers and broadleaves. Therefore, to test the influence of uncertainty of wood stake decomposition rates and their relationship to tree growth, we selected four parameters for further uncertainty analysis: 1) loblolly pine stakes at the forest floor surface were used as an index of conifer branches (*Conif-Branch*); 2) loblolly pine stakes in the mineral soil were used as an index of conifer roots (*Conif-Root*); 3) aspen stakes at the forest floor surface were used as an index of broadleaf branches (*Broad-Branch*); and 4) aspen stakes in the mineral soil were used as an index of broadleaf roots (*Broad-Root*).

To study the influence of wood decomposition rates on tree growth predictions, we carried out an uncertainty analysis (Saltelli et al., 2008). The pre-treatment forest was simulated by using the initial

densities for lodgepole pine, Douglas-fir and trembling aspen of 825, 450, and 222 trees ha^{-1} respectively (following the average densities defined for the same forest types in the region by Blanco et al., 2015a). The pre-treatment simulation lasted for 70 years (a typical harvest interval for Douglas-fir forests, Hermann & Lavender, 1999), with final densities of 648, 359, and 93 trees ha^{-1} of lodgepole pine, Douglas-fir and trembling aspen, respectively. That point was considered the initial starting point for the sensitivity analysis runs. For **control** runs, no management was carried out and therefore the simulation started with 70-year-old trees present in the stand. The **M0 – moderate management** runs were carried out by simulating clearcutting at year 1, followed by stem-only removal and planting 2-year old Douglas-fir seedlings at initial density of 2250 trees ha^{-1}. The **M2 – intense management** runs were carried out by simulating clearcutting at year 1, followed by whole-tree (stem + canopy) and forest floor (all litter types) removal, and planting 2-year old Douglas-fir seedlings at initial density of 2250 trees ha^{-1} (Hannam et al., 2008).

To test for the influence of uncertainty of woody debris decomposition rates on the main variables defining the N and C cycles, empirical data on decomposition rates obtained from stakes of pine and aspen were used respectively to create the distribution functions of the parameters *Conif-Branch*, *Conif-Root, Broad-Branch*, and *Broad-Root*. Using a Monte Carlo approach, 50 synthetic decomposition rates for each combination of wood type and management treatment were generated (Figure 2). Then, for each synthetic decomposition rate generated, a simulation was carried with FORECAST keeping the rest of the parameters with the same value, therefore performing an OAT local sensitivity analysis (Saltelli et al., 2008). We carried a total of 600 simulations, being the target variables soil C, tree C, total stand C, annual N released from litter, annual N released from humus and available N. To quantify the propagation of parameter uncertainty into model output and compare the effects of different input parameters on all target variables, the Uncertainty Propagation Index (UPI) was defined as (Eq. 1):

$$\text{Uncertainty Propagation Index (\%)} = \frac{CV_{\text{target variable}}}{CV_{\text{input parameter}}} \times 100 \quad (1)$$

Where $CV_{\text{target variable}}$ is the coefficient of variation of each of the six target variables, and $CV_{\text{input parameter}}$ is the coefficient of variation of each of the four input parameters. The index compares, in a simple way, if the variability around the average of the target variable is larger or smaller than the variability around the average decomposition rates of each of the four woody materials studied. Therefore, if UPI is larger than 100%, the model amplifies parameter uncertainty when estimating the target variables, whereas if UPI is lower than 100%, it reduces it (Kirschbaumm, 1999). Analogous to the ranges defined by Jørgensen and Fath (2011) for the sensitivity index, ranges of the uncertainty propagation index can be defined as: no propagation (UPI=0%), low propagation (0%<UPI≤10%), moderate propagation (10%<UPI≤50%), equal propagation (50%<UPI≤100%), and high propagation (UPI>100%).

3. RESULTS

The population of synthetic decomposition rates generated logically followed the observed field data, with much lower rates for surface wood (used to calibrate the *Conif-Branch* and *Broad-Branch* parameters) than for wood in the mineral soil (*Conif-Root* and *Broad-Root*), and with lower decomposition rates for pine than for aspen (Figure 3). It also followed the empirical observation that the more intense the management, the faster the roots decompose, but the opposite for branches. Such synthetic distributions were therefore considered an adequate representation of empirically-estimated decomposition rates.

The effect of uncertainty in decomposition rates had a clear interaction with the type of management. For both the control and the intense management (M2) plots, the effect on tree or soil carbon was minimal. The same was observed for most moderate management (M0) simulations, except for conifer roots (Figure 3). Uncertainty in the *Conif-Root* parameter could create differences of up to 12.4 Mg ha^{-1} and 41.4 Mg ha^{-1} for estimations of soil C and tree C, respectively. In relative terms, these results indicate a potential deviation up to 12.3% and 41.7% from the average for soil C and tree C, respectively.

Uncertainty in soil N flows were mostly related to uncertainty in estimation of litter mass and its associated N content; whereas for N released from humus the influence of uncertainty of woody

decomposition rates was almost negligible. Only for low-intensity management (M0) a noticeable influence was observed at about mid-rotation (ages 28-50) for conifer roots, although such differences were dimmed by the end of the simulation. For the same M0 scenario, uncertainty in decomposition rates of conifer roots in N released from litter was important for the first half of the simulation, reaching differences up to 33 kg N ha^{-1}yr^{-1} (41.5% of the average value). More importantly, uncertainty in input in the *Conif-Branch* parameter could cause the model to estimate either net mineralization or net immobilization from litter during the first 11 years (Figure 4).

As for the previous variables, for the control and M2 scenarios the uncertainty in input decomposition rates was minor to almost negligible for available N and total stand C, but for the M0 scenario the uncertainty in *Conif-Root* also created noticeable ranges for the estimations of the target variables (Figure 5). Differences for available N were higher during the first 20 years of the simulation, reaching a maximum of 81.6 kg N ha^{-1}, but later stabilizing in the range of 26-30 kg N ha^{-1} for the second half of the rotation. Such differences in available nutrients had a corresponding effect on tree growth and organic matter accumulation on the forest floor, bringing total ecosystem C to values into a range between 145-197 Mg C ha^{-1}, or in relative terms, approximately ±30.4% of the average C after 70 years of simulation.

The model, in general, showed low values of the uncertainty propagation index for most of the variables (Figure 6). Only for the moderate management scenarios and the *Conif-Root* parameter, values of the uncertainty propagation index were in the region of moderate propagation, with slightly higher values at 35 years of simulation than at the end of the 70-year runs.

4. DISCUSSION

4.1. Effects of type of material

Broadleaf woody debris usually have higher N but lower lignin content than coniferous woody material, and therefore decompose faster (Shoronova & Kapitsa, 2014). These differences in decomposition rates were recorded during other wood stake studies (Jurgensen et al., 2006; Risch et al., 2013; Finér et al., 2016), and they were reflected in the distribution of the synthetic decomposition rates generated for this uncertainty study (Fig. 2). However, conifer-related parameters had higher influence on tree growth projections than broadleaf-related parameters. The explanation is likely related to the minor broadleaf component, as this type of mixed forest is mostly comprised of pioneer species such as trembling aspen, which are shaded out during stand development by coniferous, slower-growing species such as Douglas-fir and lodgepole pine. Therefore, the influence of uncertainty in decomposition rates related to broadleaf material is almost negligible, and only a minor impact can be seen on N released from litter.

Empirically estimated decomposition rates, both for broadleaf and coniferous woody material were affected by management treatment, with a decrease from control to M2 in recorded branch decomposition rates. This is likely caused by the drying effect on wood stakes on the soil surface void of forest floor and without an overstory; thereby reducing decomposer activity. For the stakes buried in the mineral soil there was an increase in decomposition. Such increase was likely caused by increased water and radiation reaching the soil surrounding the decomposing roots, causing an increase in soil temperature and therefore in decomposer biological activity (Crockatt & Bebber, 2015; Fissore et al., 2016; Finér et al., 2016). A clear increase in wood stakes decomposition in the mineral soil as management intensity increased was recorded. Although the population of synthetic decomposition rates followed the same pattern, the clear treatment effect on decomposition rates was not propagated to estimations of tree growth for Control and M2 treatments. The effect of the M0 treatment on decomposition rates was not so evident and is likely associated with an increase in the variability of recorded decomposition rates. The highest dispersion of synthetically-generated root decomposition rates was observed for conifers in the M0 scenario, likely

reflecting the high heterogeneity of micro-climate conditions after harvesting. Higher uncertainty of empirically-measured decomposition rates for M0 compared to control and M2 can also be a factor influencing the higher UPI values estimated for the *Conif-Root* parameter in the M0 scenarios.

4.2. Effects of management treatments

Our results highlight the important interaction that exists between management scenario and uncertainty. Although most of our results show the uncertainty from the input parameters related to wood decomposition rates is scarcely propagated to the target variables, there is one important exception: decomposition of modeled coniferous roots under moderate management. Such scenario (managing coniferous forests in a moderate fashion, removing only the stems but without removing the forest floor layer) is actually the most common form of forest management in most of the Pacific Northwest of North America. The reasons for the observed interaction between management regime and wood decomposition rate are several. In mature stands such as in the control plots, there is already a large amount of biomass accumulated on the forest floor and soil. An important part of this organic matter is composed by organic matter in different stages of decomposition. Mineralization of decomposing leaf litter and humus are the main sources of nutrients for vegetation and the uncertainty of wood decomposition rates does not affect N availability. Similarly, Wang et al. (2013b) also found changes of less than 6% in total C estimated by the CENTURY model in response to uncertainty of woody biomass decomposition and removal. As in our case, Wang et al. (2013b) suggested that such small sensitivity was a consequence of the small N flow that woody residues provided to trees.

In addition, as mature trees grow older, most of their nutrient requirements are met through the resorption of nutrients from leaves and twigs prior to their senescence. This is particularly important in the case of conifers, as they maintain needles for several years, using the old needles as nutrient reservoirs (Blanco et al., 2009). As trees simulated in the control plots gradually reduce growth rates as they slowly reach maturity and old-growth stage, their nutrient requirements also gradually decline. These stages of tree

growth are only slightly dependant on nutrients coming from the mineralization of woody debris. As a consequence, the uncertainty around wood decomposition rates barely influence tree growth.

In contrast, the opposite occurs in stands under intensive management, as was the case of the M2 plots. In these plot, where the organic layer has been removed together with the woody debris on the soil surface, all N released from mineralization comes from the decomposition of dead roots from the trees harvested prior to the establishment of the new plantation. This N is depleted relatively quickly as roots have higher decomposition rates than branches, due to their higher moisture content and contact with soil (Ganjegunte et al., 2003). As a consequence, the impact of uncertainty in woody debris decomposition rates that can be seen in the first 10 years of N release from residual roots (Fig. 4 bottom left) does not translate into additional tree growth because the planted seedlings are small and cannot use all the nutrients that are potentially available.

After the first ~10 years, when most roots from previous trees are likely completely decomposed, most available N originates from three sources: 1) mineralization of humus, which remains unaltered by uncertainty in decomposition because after removing most of the organic layer new humus is formed slowly, 2) mineralization of litter produced after tree establishment, which remains a small pool as newly planted trees need time to produce and accumulate a significant litter layer and the shrub layer is not fully developed, and 3) non-symbiotic N fixation, which also remains relatively low in temperate coniferous forests (Wei & Kimmins, 1998; Blanco et al., 2017). Hence, available N is relatively unaffected by uncertainty and remains limiting for tree growth for all scenarios with different wood decomposition rates. This process is already being documented in the field where periodic measurements of planted trees in the LTSP experimental plots in British Columbia show significantly lower growth rates in M2 plots (Kamaluddin et al., 2005; Ponder et al., 2012; Kranabetter et al., 2017). Therefore, uncertainty in decomposition rates has almost no influence on estimates of tree growth, as also Wang et al. (2013b) have reported for the CENTURY model.

An intermediate case is the situation estimated for the moderate management (M0) plots. This management regime only removed tree boles and left crowns (stem tops and branches) and the entire forest floor (inclusive of the Oa, Oe, and Oi horizons). Therefore, the length of time woody material from tree crowns remains, mostly in the form of branches from coniferous species Douglas-fir and lodgepole pine, is critical. In addition, the parameter *Conif-Root* becomes increasingly important and influential on tree growth. The confluence of N being released from roots together with N released from the decomposing organic horizons make a difference and significantly increase tree growth. Similarly, Krankina et al. (1999) also reported the importance of woody debris as an N source following disturbance. In fact, under the M2 management, the lowest values of *Conif-Root* could cause N immobilization during the first years following harvesting and tree establishment, changing roots from being a source to a sink of available N (Laiho & Prescott, 1999). Similar behaviour has been described in the field by Palviainen & Finér (2015), who reported that most of the N can be still be sequestered in the decaying roots of Norway spruce after 40 years. In the runs with the highest *Conif-Root* decomposition values increases in estimated available N had a direct translation in greater tree growth. This difference has important forest management implications, as differences between the highest and lowest estimation of stand C can be up to 42% after 70 years.

An important management implication from our results is that forest floor (composed of several types of leaf and woody debris in different decomposition stages), even if it represents only a small portion of the total ecosystem C, it can have important influence on forest productivity, as it is the main source of mineralized N (Blanco et al., 2011). Previous studies from British Columbia have shown the importance of forest floor on determining forest productivity (Seely et al., 2002, 2010), and forest floor C has been proposed as an indicator of reductions of ecosystem productivity (Yanai et al, 2003; Blanco et al., 2014). In addition, although forest floor can contain up to 10 times the amount of nutrient than woody debris (Klockow et al., 2013), important interactions between decomposition of woody debris and forest floor

litter have been reported stimulating the release of N from litter in the short term but helping to stabilize more N in the soil in the long term (González-Polo et al., 2013; Kim et al., 2017). Our results corroborate such reports, as shown by the important uncertainty associated to available N under the M0 management. Therefore, given the uncertainties associated with the estimations of wood decomposition rates presented here, the precautionary principle should be followed when managing forest soils, discouraging the removal of forest floor and tree roots or stumps just to remain on the safe side of maintaining forest productivity in the long term.

4.3. Model limitations and further work

The parameters values used to simulate woody material decomposition rates were directly based on field data from wood stakes placed on the surface of the forest floor or buried in the first 20 cm of mineral soil, as described in Jurgensen et al. (2006). Although such standardized material provides an index of the influence of soil micro-climate on wood decomposition, stake decomposition rates do not directly estimate woody debris decomposition rates because stakes have uniform dimensions and lack bark. Relative masses and nutrient concentrations in different woody debris could cause that average actual decomposition rates be slightly different from the ones used here. However, we think that such differences between actual woody debris decomposition rates and the index from wood stakes would be of lower magnitude than the uncertainty ranges already incorporated in our research, and therefore the trends in uncertainty propagation and tree growth would be very similar. In addition, FORECAST has previously shown acceptable agreement with empirical data in young and mature Douglas-fir forests in British Columbia, both for the coastal and interior regions (Blanco et al., 2007; Seely et al., 2010). In particular, model projections have been well in range for empirical estimations of ecosystem C by Harmon et al. (2004) and Sollins et al. (1980). Previous sensitivity analyses have also shown that the model responded with moderate sensitivity to changes in tree and soil parameters (Blanco, 2012). Such moderate sensitivity shows FORECAST´s capability to contain error propagation when simulating the long-time influence of parameter uncertainty (Kimmins et al., 2010). Similarly, previous sensitivity analyses for fine root-related

parameters have shown that the model is able to capture the observed variability without magnifying or minimizing it when estimating tree growth (Gárate & Blanco, 2013). As the model has already shown acceptable performance, we are confident on the estimations of temporal evolution and relative differences among management option. However, as this study involves the simulation of several decades of stand development, the exact values predicted for each variable should be taken with caution.

A final consideration is that FORECAST does not implicitly simulate the effects of microclimate and soil moisture regime. As a hybrid model, its working assumption to estimate tree growth in the future is using data on past tree growth assuming that climate will remain stable inside the same observed range during the period to be simulated. Obviously, if future climate is significantly different from the past such assumption may not be valid. We believe that for the research presented here this is not an issue as we are trying to analyze how the model reacts to different values of empirically-estimated decomposition rates, rather than predicting future tree growth for a specific site. We consider that the influence of climate on decomposition rates is already implicitly included in the simulations through the use of field data which already reflect macro- and micro-climate influence on wood stake decomposition. However, climate change may be an important influencing factor leading to altered woody debris decomposition rates (Risch et al., 2013; Mazziotta et al., 2014). Therefore, when simulating actual management scenarios or predictions of tree growth under potential future climates, an explicit representation of soil moisture regimes will be needed. Given the increased complexity of the potential interactions between climate-related parameters and tree- and soil-related parameters, a global sensitivity analysis would likely be also needed to complement the results of one-at-a-time sensitivity analysis presented here.

5. CONCLUSIONS

The FORECAST model showed a moderate- to low-sensitivity to uncertainty in parameters related to wood decomposition. However, an important interaction between uncertainty and management was found, indicating that uncertainty in model calibration can be propagated more directly into uncertainty of tree growth projections in situations where nutrients from woody debris are critical to reach or maintain high tree growth rates. Therefore, for uncertainty in model predictions of tree growth and C sequestration to be reduced, it is necessary to use empirically-recorded decomposition rates from field studies in which the uncertainty in estimated decomposition is reduced by controlling experimental conditions and standardizing both the woody material and the treatments. Such uncertainty on tree growth is partially caused by uncertainty of available N released from forest floor and woody debris, which can have important consequences on tree growth estimations. A way to deal with such uncertainty in forest management plans is to follow a precautionary principle in which the removal of forest floor and root systems (stumps) is avoided.

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APPENDIX A: BASIC DESCRIPTION OF THE FORECAST MODEL

The FORECAT forest ecosystem model is designed to account for biomass flows among carbon stocks (aboveground biomass, belowground biomass, forest floor, dead wood and mineral soil organic carbon, as defined by Penman et al., 2003). An early version of the model (named FORCYTE) was originally created to estimate the effects of forest harvesting for energy production, as commissioned by the Government of Canada program "Energy from the Forest (ENFOR)", following the energy peak prices that followed the oil embargo in the 70s (Kimmins et al. 1979). It was quickly apparent to the model designers that to understand the impact of intensive tree harvesting, cycles of nutrients in addition to only growth should be included (Kimmins 1993). Over the years, the FORECAST model has outgrown its original purpose and it has been applied to multitude of forest types (from tropical to boreal) and management regimes (from unmanaged old-growth forests to intensive plantations, see Kimmins et al. 2010). Through all these applications, the model suitability to acceptably estimate tree growth and nutrient flows has been established, but also the sensitivity of the model to decomposition rates but the difficulty to obtain accurate estimations for the woody fractions (Blanco, 2012; Gárate & Blanco 2013). It has not been until the recent establishment of the wood stake decomposition protocol, combined with the use of the LTSP network that an accurate, empirical-based sensitivity analysis on woody fractions decomposition rates has been possible, as it is reported in this work.

The model uses a mass balance approach to account for C and nutrients flows through the ecosystem. Although water flows are not simulated, soil moisture is still accounted for by the use of the parameter "maximum leaf biomass", which is directly correlated with soil moisture availability (see a detailed discussion on this topic in Kimmins et al., 1999). Stand growth is calculated by simulating ecosystem dynamics through the representation of the most important ecological processes that regulate competition and availability of natural resources for tree growth (Figure 7). To calculate rates of these key ecological processes, FORECAST uses a hybrid approach combining empirical data on tree growth (from inventories, permanent plots, growth and yield tables, etc.) with calculations of net primary production as

limited by nutrient and light availability (Blanco & González, 2010; Wang et al., 2013). Details and explanations of the algorithms used in the model can be found in Kimmins et al. (1999) and Lo et al. (2015), and only a basic explanation is provided here.

The model works in two consecutive stages. First, the model produces a series of equations for tree growth and ecological processes that include (among others), photosynthesis and light levels through the canopy, litterfall production, mortality, and nutrient uptake. Mortality for each species is estimated depending on species-specific minimum light levels. FORECAST uses data on observed tree growth patterns combined with empirical data on nutrient concentration, biomass distribution among different tree components and mortality to estimate the rates of key ecosystem processes (such as nutrient uptake, litterfall production, litter decomposition, etc.) as they should had happened to produce the observed stand development patterns provided by the model user, including minor vegetation (Kimmins et al., 2008). Detailed descriptions of decomposition, vegetation uptake and biogeochemical cycles have been described before (Kimmins, 1993; Kimmins et al., 1999, 2010). Therefore, for each plant species for which historical data are provided, the total net primary production (TNPP) that occurred for each annual time step (t) is calculated with Equation (2).

$$\text{TNPP}_t = \Delta\text{biomass}_t + \text{litterfall}_t + \text{mortality}_t \tag{2}$$

where $\Delta\text{biomass}_t$ = the sum of the change in mass of all the biomass components of the particular species in time step t; litterfall_t = the sum of the mass of all litter fractions that are lost in time step t; and mortality_t = the mass of plants that die in time step t. Change in biomass ($\Delta\text{biomass}_t$) in each time step is derived from a series of age–biomass curves created with empirical data (see a detailed description of the process in Kimmins et al., 1999).

After the self-calibration of ecosystems processes is finished, the model proceeds to the second stage to simulate the scenarios defined by the user. At this stage, the model adjusts the growth and mortality curves estimated during the first stage to the stand density to be simulated. In FORECAST, foliar N efficiency is used as the driving function, effectively linking C and N cycles (Agren & Bossata, 1996). Such driving function estimates the amount of biomass produced by unit of foliar N, but taking into

account that not all foliage is fully under the sun, and therefore light absorption through the canopy profile is estimated to generate corrected N foliage efficiency. This is the Shade-Corrected Foliage N content (SCFN), which represents the amount of N in fully illuminated foliage that was required to produce the calculated historical total net primary productivity (TNPP), as estimated during the first stage. FORECAST then calculates the equivalent N content after correcting for self-shading (SCFN, Equations 3 and 4).

$$SCFN_t = \sum_{i=1}^{n}(FN_{t,i} \times PLSC_i) \tag{3}$$

$$FN_{t,i} = \text{foliage biomass}_{t,i} \text{ x foliar N concentration} \tag{4}$$

Where $FN_{t,i}$ = mass of foliage N in the *ith* quarter-meter height increment in the live canopy at time *t*, $PLSC_i$ = photosynthetic light saturation curve value for the associated light level in the *ith* quarter-meter height increment in the live canopy, *n* = number of quarter-meter height increments in the live canopy at time *t*. Finally, the adjusted driving function curve for potential growth of a given species in FORECAST is the Shade-Corrected Foliar N Efficiency (SCFNE) calculated for each annual time step (t) with Equation 5:

$$SCFNE_t = TNPP_t / SCFN_t \tag{5}$$

The calculation of N in foliage depends on the capability of trees to uptake N, which depends on nutrient availability. Nutrient availability is calculated with data from litter decomposition rates, inputs and outputs from the biogeochemical cycle (e.g. deposition, seepage, N fixation), and soil and humus chemical features (cation exchange capacity [CEC] and anion exchange capacity [AEC]). In FORECAST, litterfall is divided into different pools (up to 50) each of them simulating different kinds of litter (leaf litter, branch litter, root litter, etc.). Humus is simulated by using two different pools: the "active" humus and the "passive" humus, depending on the level of stabilization reached by the organic matter in each humus fraction. The turnover of active humus was set for the research presented here to 50 years (Seely et al. 2010). The turnover for passive humus, which accounts for organic matter very resistant to decomposition and includes physically and chemically stabilized SOM, was set to 588 years for this research (Seely et al.

2010). Simulating stable soil organic matter by using two different humus pools has also been previously used in models such as CENTURY (Parton et al., 1987), ROMUL (Chertov et al., 2001), or ICBM (Andrèn & Kättere et al., 2001), among others. FORECAST also uses a mass balance approach to track changes in N stocks and flows (Figure 8). In the model, N can be found in the vegetation biomass, the soil organic matter (humus and litter) and the mineral soil (CEC and AEC). In addition, the model simulates external inputs into soil N from nitrogen deposition and biological N fixation (Figure 7). All the interchangeable N present in the soil during one year either as NH_4^+, NO_3^- or labile organic N fractions with turnover rates shorter than one year is clumped as annual available N. How these processes are simulated in FORECAST is described in detail in Kimmins et al. (1999) and Blanco et al. (2012).

The simulation of litter (both woody and non-woody types) in FORECAST is very straightforward, and driven by empirical input data. Each kind of litter type (in the research presented here, 20 types were used) losses weight from the time it is shredded and falls on the soil at a user-defined rate, depending on the decomposing material and its age. Therefore, the model does not explicitly simulates decomposer activity (i.e. microfauna, microflora and microorganisms), only their effects on remaining litter biomass (Kimmins, 1993). Such empirical approach has the advantage of using real data as observed in the field, and therefore the underground nutrient cycles are acceptably estimated (Blanco, 2012; Gárate & Blanco, 2013; Blanco et al., 2014). However, the main limitation is that as no direct decomposer activity is simulated (either with metabolic rates, respiration or by other means), it is not possible to simulate the influence of microclimate (particularly soil moisture and temperature) on decomposition rates. Such limitation would be important when simulating future scenarios of tree growth including climate change. To address this issue, a new version of the model has been developed (FORECAST Climate, see Seely et al., 2015). However, as discussed in the main text, in the research presented here we do not think is an important limitation as our projections are theoretical and just focus on the model sensitivity to observed decomposition rates. Detailed discussions on other strengths and weaknesses of the followed simulation approach and its comparison to other forest models can be found in Kimmins et al. (1999), Blanco et al. (2007, 2015b), and Lo et al. (2015b).

Tables

Table 1. Main features of study sites (adapted from Norris et al., 2015).

Site	Latitude	Longitude	Elevation (m a.s.l.)	Soil texture (% clay)	Soil depth[1] (cm)	Establishment year
Mud Creek	50º 08'N	115º 44' W	1005	Loam (21%)	22	1999
Emily Creek	50º 09' N	115º 59' W	1180	Loam (7%)	48	2000
Kootenay East	50º 11'N	115º 59' W	1030	Silt loam (16%)	24	2001

[1] Depth to carbonates.

Figure legends

Figure 1. Left panel: Position of the reference climate station (study sites in its vicinity) in relationship to North America. Right panel: Climate of Wasa (1983 – 2016). Blue line: mean monthly precipitation (rainfall + snow) Red line: mean monthly temperature; y: number of years used to calculate the normals; T: mean annual temperature (°C); P: mean annual amount of precipitation (mm); T_M : absolute maximum temperature (°C); t_M : mean daily maximum temperature (°C); t_m: mean daily minimum temperature (°C); T_m : absolute minimum temperature (°C). The frost period with an absolute minimum temperature below 0 °C (is indicated by the grey area at the bottom of the figure.

Figure 2. Distribution of synthetic values of wood decomposition rates generated based on field work observations. The values from surface stakes were used to calibrate the branch-related parameters, whereas the values from buried stakes were used to calibrate the root-related parameters. Pine stakes were used to calibrate conifer-related parameters and aspen stakes for broadleaf-related parameters.

Figure 3. Total soil C (left panels) and tree C (right panels) under three types of forest management. The lines of the same color above and below the average indicate the confidence intervals (±95%) of the target variables when each parameter is modified.

Figure 4. Total N released from litter (left panels) and from humus (right panels) under three types of forest management. The lines of the same color above and below the average indicate the confidence intervals (±95%) of the target variables when each parameter is modified.

Figure 5. Available soil N (left panels) and total stand C (right panels) under three types of forest management. The lines of the same color above and below the average indicate the confidence intervals (±95%) of the target variables when each parameter is modified.

Figure 6. Uncertainty Propagation Index of four wood-decomposition related parameters into six target variables under three different types of management.

Figure 7. Diagram of the most important ecosystem processes and interactions among them included in the model (black dotted lines). Mass and nutrient flows connect the main ecosystem pools (black solid lines). Effects of limitation and competition for light and nutrients are explicitly simulated, whereas soil moisture limitation is simulated implicitly.

Figure 8. Order of simulated events to estimate annual available soil N. Step 1: inputs from geochemical flows are calculated, lumping together all different forms of N. Step 2: inputs and outputs of biochemical fluxes. Step 3: Available N is uptaken by the vegetation. Step 4: N is retained in soil CEC (as ammonium) or AEC (as nitrate). If N exceeds soil´s retention capacity, any excess is considered to be lost as leaching and denitrification losses and removed from the soil. After Step 4, any N remaining in the soil then passes to the next year, becoming the initial value of available N for the next year.
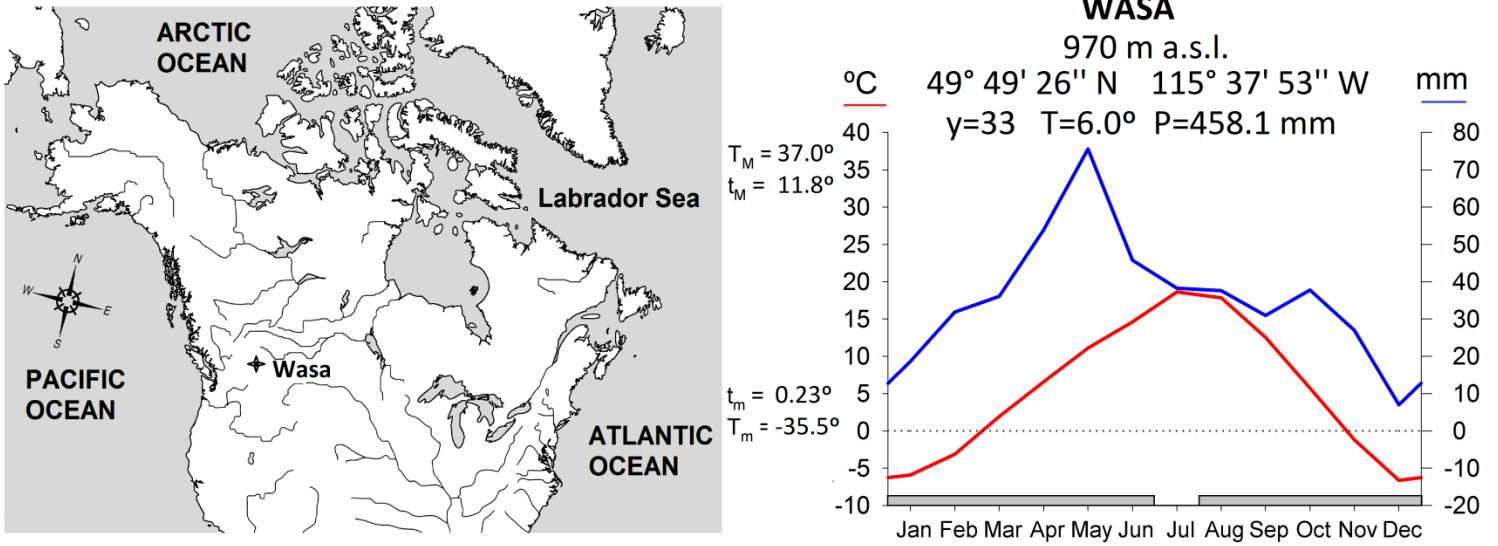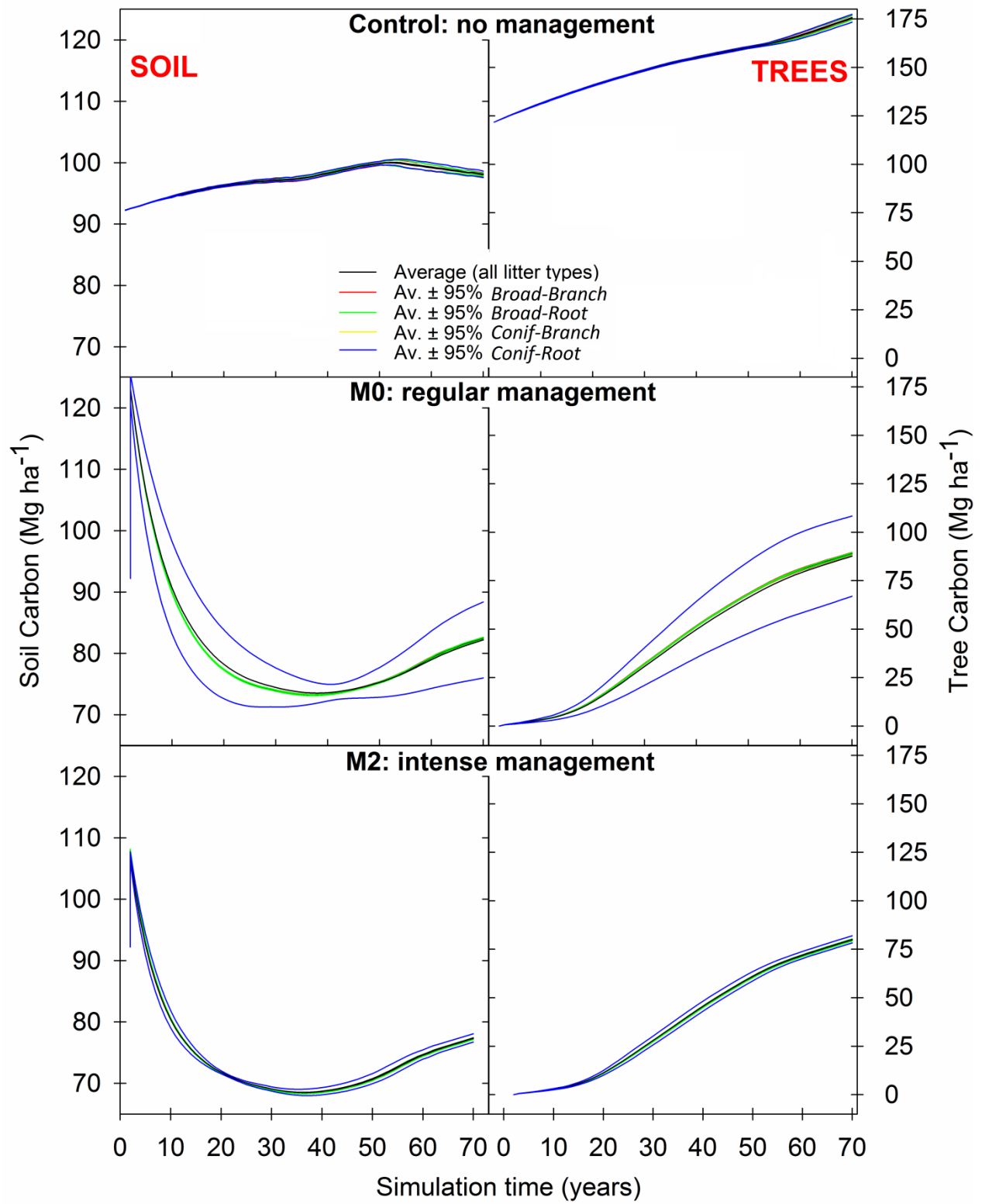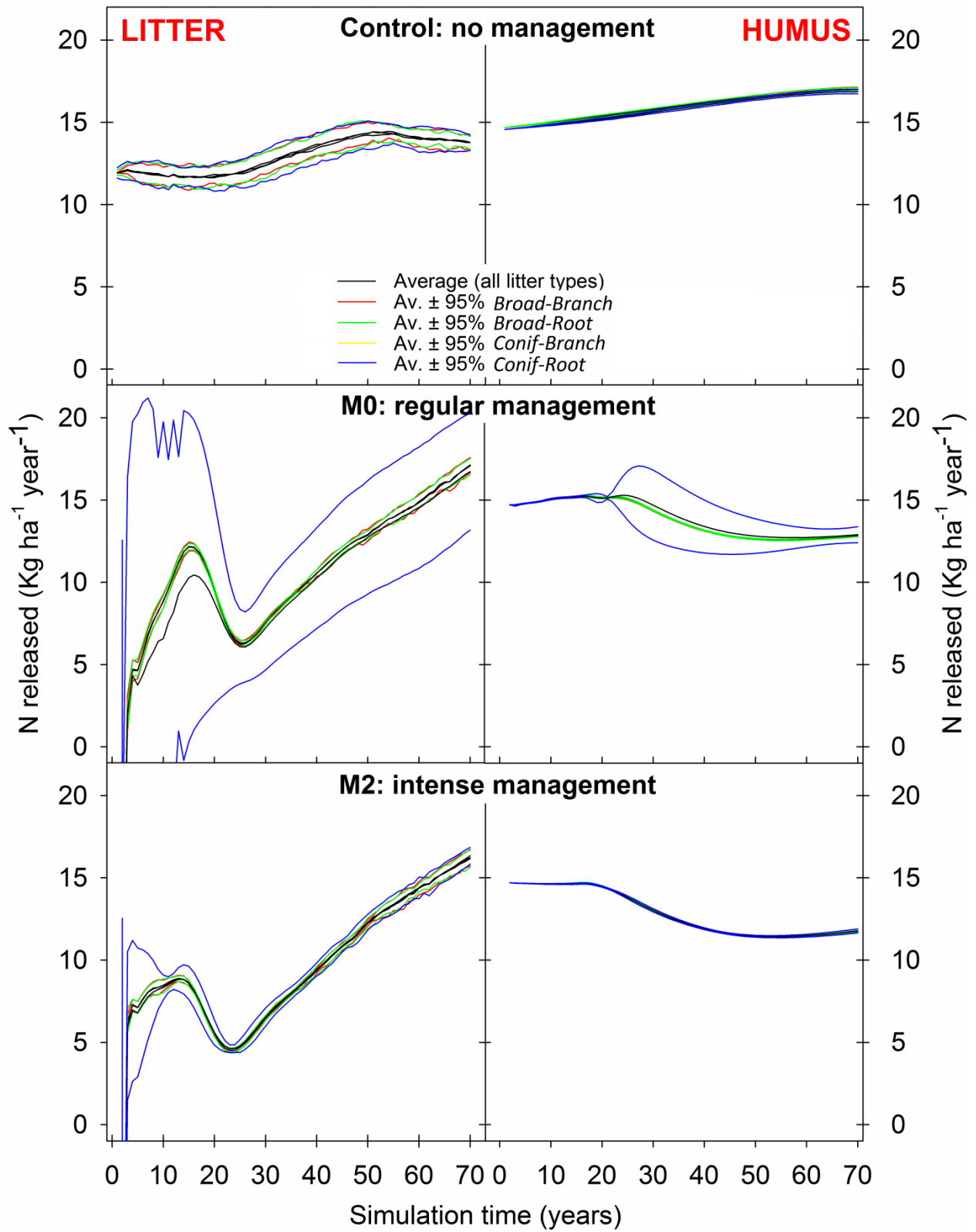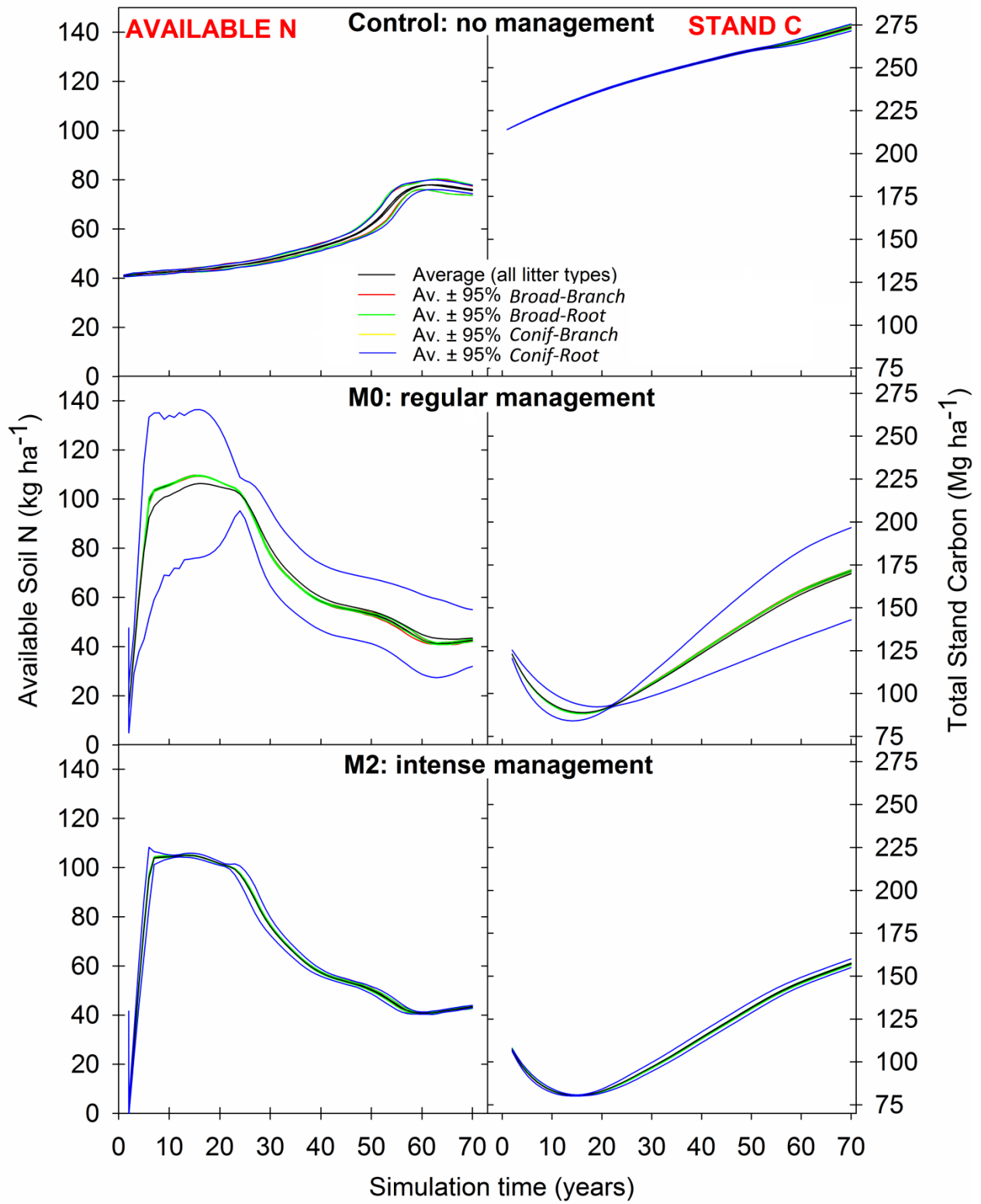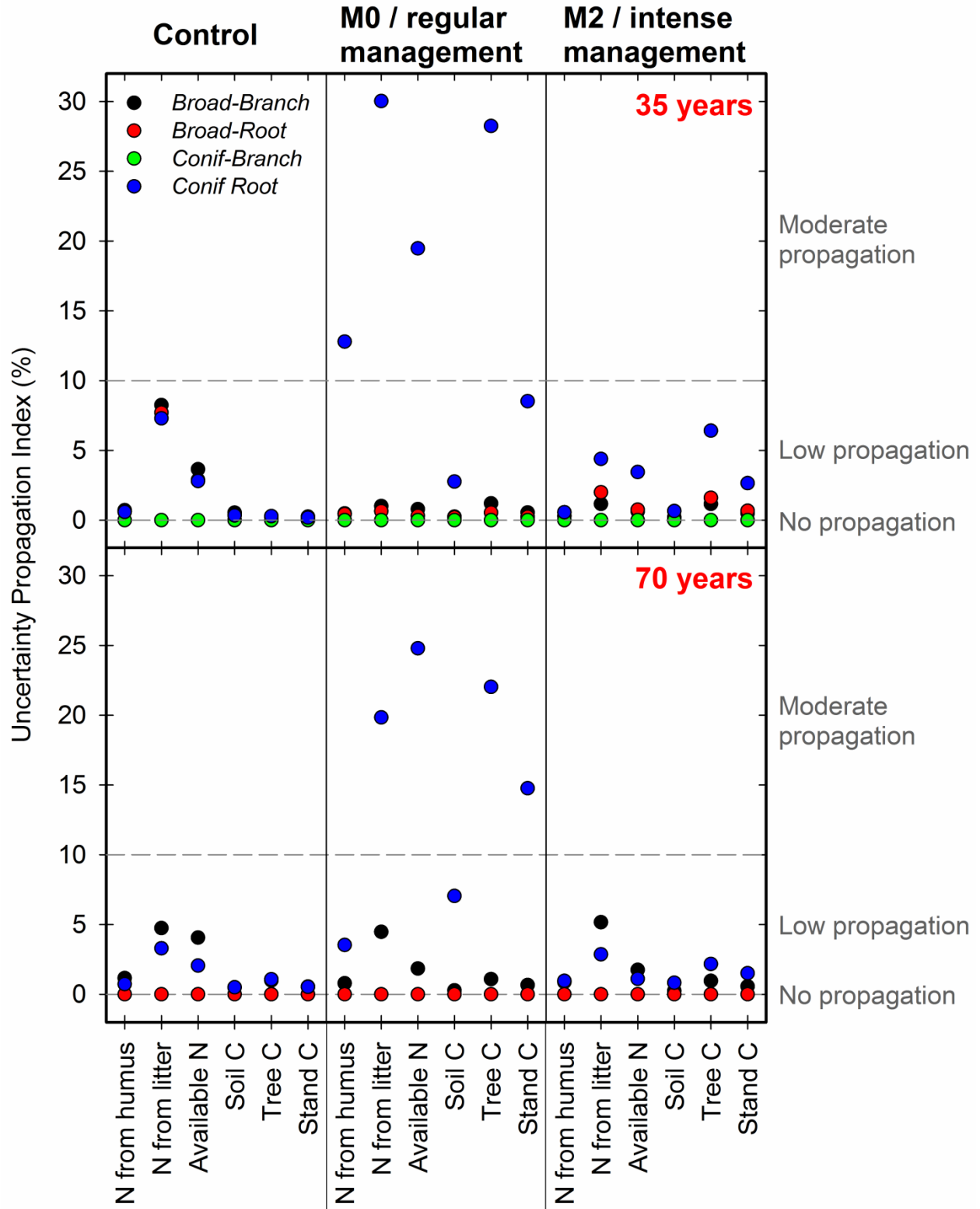
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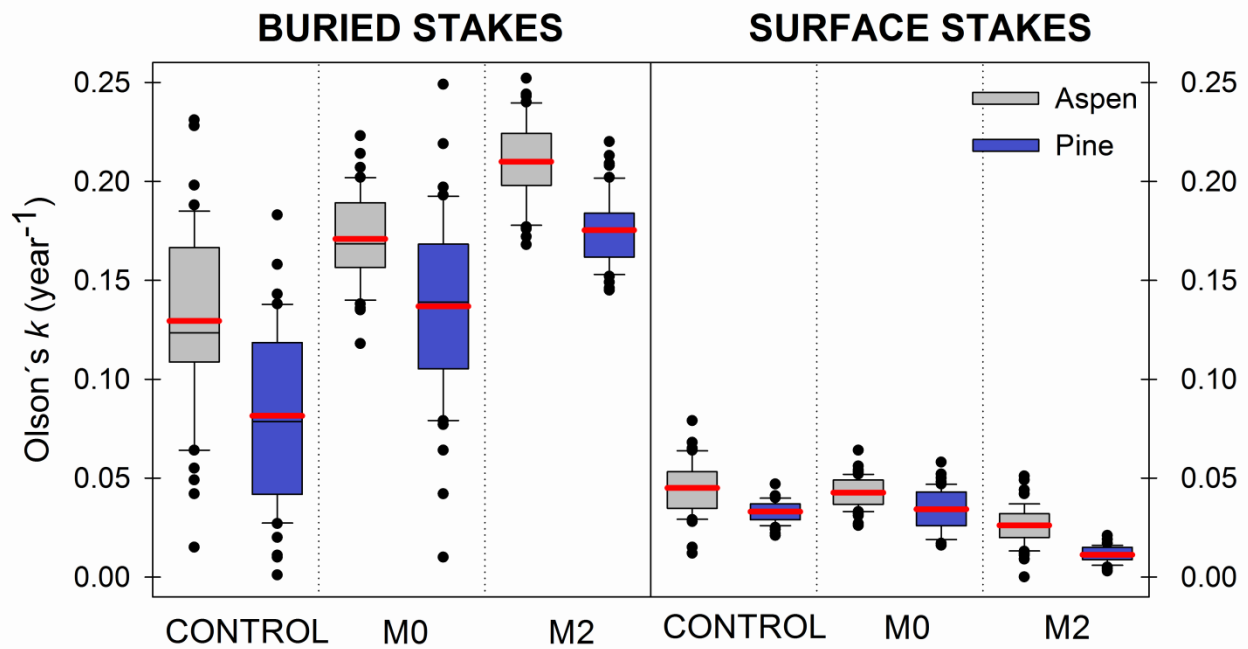
Figure 2.

Figure 3.

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Figure 6.

Figure 7.

Figure 8.