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Modelling of nutrient concentrations in roundwood based on diameter and tissue proportion: Evidence for an additional site-age effect in the case of *Fagus sylvatica*

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ABSTRACT

Climate-mitigation strategies encourage the use of forest products and wood energy. This will likely increase the risk of soil depletion through nutrient exportation. Given the high variability in nutrient concentrations within and between trees, it is crucial to better understand the biochemical patterns of nutrient distribution and the related driving factors. Thus, predictions of nutrient concentrations can be improved, and used for assessing nutrient exportation through roundwood exploitation and for developing forest-management rules to maintain soil fertility. Our aims were to better determine (1) the shapes of the relationships between the total concentrations of different nutrients (N, S, P, K, Ca, Mg, Mn) in roundwood and roundwood diameter; (2) the variation of these relationships between different tissues (wood, bark); and (3) potential effects of site conditions and/or stand age on nutrient concentrations. We therefore developed a new modelling approach that relied on empirical and mechanistic relationships, and allowed for sound predictions of both concentrations in individual tissues and in total. We applied the approach to *Fagus sylvatica* using 134 trees from 11 plots that covered large ranges of ecological conditions in terms of geographic region (from the northwest to the northeast of France), site index (from <25 m to >35 m), stand age (form 10 years to 159 years), and roundwood diameter with nutrient concentrations being measured separately for wood and bark tissues partly up to a minimum diameter of 1 cm. Relationships between total nutrient concentrations and roundwood diameter showed several different shapes: a reverse-J-shape for N, S and P; a U-shape for K; and no clear, more complex shapes for Ca, Mg and Mn. These shapes were related to concentration changes with roundwood diameter in both wood and bark for N, S and P (but with low goodness of fit for the models of N and S in the bark), while they were only related to concentration change in the wood for K, and in the bark for Ca and Mn (but with low goodness of fit for the model of Mn in the bark). Moreover, shifts of concentration-diameter curves (additive effect) were likely related to site conditions (chemical fertility), as assessed based on foliar nutrient concentrations. An additional effect of stand age could not be excluded, but so far it appeared difficult to clearly distinguish between influences of site and age. We argue that our modelling approach is particularly suitable to further tackle the issue of site and age effects, by combing data from several studies on the same species and/or on other species (genericness). Comprehensive forest-management rules based on silvicultural scenario simulation and assessment may finally be developed by coupling nutrient, biomass and site-sensitive tree-growth models.

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1. Introduction

The amount of nutrients that a given amount of woody biomass contains can be estimated based on statistical models of nutrient concentrations (e.g. Augusto et al., 2008). Given the high variability in nutrient concentrations (Paré et al., 2013), it is crucial to better understand the biochemical patterns of nutrient distribution within and between trees and the related driving factors, thus allowing for enhanced model predictions. For being applicable to forest management-related issues, nutrient models should rely on dendrometric variables that can be deduced from forest inventories and felling operations (especially diameter of roundwood as a major determinant of bucking rules in forest management), or on variables available in management documents (e.g. stand age, site characteristics), including outputs of growth and yield models (tree growth, volume and biomass predictions). Nutrient estimates combined with biomass estimates (e.g. Genet et al., 2011) for the same roundwood sections allow then to determine the amount of nutrients exported from forest stands due to roundwood exploitation, as part of a more comprehensive assessment of forest nutrient input–output budgets (Laclau et al., 2005). Providing such an assessment is crucial as the risk of soil depletion due to nutrient exportation will likely increase if the use of forest products and wood energy is encouraged, as suggested by climate-mitigation strategies (UNECE, 2005). Especially a raising demand for energy wood may lead to an increase in the exploitation of small trees or of small tree compartments such as tree tops and branches which often show the highest concentrations in nutrients (André and Ponette, 2003; André et al., 2010), thus resulting possibly in an alteration of soil productivity (Thiffault et al., 2011).

Nutrient models have been established for various trees species of temperate forests (e.g. Ponette et al., 2001, and Ranger and Gelhaye, 2001, for *Pseudotsuga menziesii*; André and Ponette, 2003 for *Carpinus betulus* and *Quercus petraea*; Joosten and Schulte, 2003 for *Fagus sylvatica*; Sicard et al., 2006 for *Picea abies* and *P. menziesii*; Augusto et al., 2008 for *Pinus pinaster*; André et al., 2010 for *F. sylvatica* and *Q. petraea*; Rance et al., 2012 for *Eucalyptus globulus* and *Eucalyptus grandis*). The most common approach consists in developing specific models for predefined tree compartments such as stem and branches classified by their bottom- and top-end diameters, and for different tissues such as bark, wood, heartwood and sapwood. Moreover, models for the vertical profile of nutrient concentrations have been developed for the stem compartment (e.g. Rytter, 2002 for *Populus tremula* × *P. tremuloides*; André et al., 2010 for wood and bark tissues of *F. sylvatica* and *Q. petraea*). Rochon et al. (1998) used patterns of horizontal variation in nutrient concentrations to model the nutrient concentration of the bole, while they found no significant pattern of vertical variation in nutrient concentrations for samples located at similar distances inside the bark (species analysed: *Abies balsamea*, *Betula papyrifera*, *Picea glauca* and *P. tremuloides*). The dynamics of nutrient concentrations within the wood of the bole (horizontal and vertical variations at different stand ages) of a *Eucalyptus* hybrid were modelled by Saint-André et al. (2002).

In the study described herein, we further investigated the relationships between nutrient concentrations in different tissues of roundwood and roundwood diameter under different ecological conditions. There seems to be no clear evidence so far about the different shapes of these relationships, and about how they can be explained. A continuously decreasing relationship was found by Augusto et al. (2008) for N, P, K, Ca and Mg in *P. pinaster*. Also, a decrease in nutrient concentrations of the bole (commercial portion) with increasing diameter at breast height (dbh) was found, based on models that integrated two different patterns of horizontal variation in nutrient concentrations with increasing distance from the bole periphery: an exponential decrease followed by no variation for so-called "mobile elements (N, P)" and an exponential decrease followed by linear variation with a positive slope for so-called "nonmobile elements (Mg, Ca, K)" (Rochon et al., 1998, p. 39). However, the decreasing trend in nutrient concentrations with increasing diameter can be more or less pronounced (sometimes it can even be almost absent or inverse) depending on the nutrient and on the species (Chatarpaul et al., 1985; Rochon et al., 1998; André and Ponette, 2003; Augusto et al., 2008; André et al., 2010). Considering more generally the fact that certain nutrients such as Ca tend to accumulate in old wood tissues and also in the bark tissue (Ingerslev, 1999; Sicard et al., 2006; André et al., 2010), another shape could also occur (e.g. with an increasing trend in nutrient concentrations for relatively big diameters). Models relating nutrient concentrations in individual tissues (bark, heartwood and sapwood) to tissue thickness are reported by Augusto et al. (2008). However, they do not explain the partitioning of total nutrient concentrations between tissues within roundwood of various diameters. Models by André et al. (2010) allow distinguishing several types of vertical profiles of nutrient concentrations in wood and bark tissues, but only for approximately the lower half of the bole (bole diameter ⩾ dbh/2). Moreover, for a given diameter, observed nutrient concentrations still show a high variability (André and Ponette, 2003; Augusto et al., 2008; André et al., 2010), suggesting that other factors than diameter are also involved. Possible effects of various other dendrometric variables (e.g. height, age) were tested by Augusto et al. (2008) but not retained in the final models.

To tackle these issues we established a new modelling approach for predicting nutrient concentrations in roundwood of various diameters. Roundwood diameter was used as continuous, explanatory variable. Differences in nutrient concentrations between tissues were taken into account using a simple mechanistic relationship that related concentrations in tissues with the total concentration. We applied this approach to *F. sylvatica* based on a dataset of 134 trees from 11 plots including separate measurements of nutrient (N, S, P, K, Ca, Mg, Mn) concentrations for wood and bark tissues over a wide range of roundwood diameters, partly up to a minimum diameter of 1 cm. In addition, possible effects of geographic location, site index and/or stand age on nutrient concentrations could be explored.

Our aims were to better determine (1) the shapes of the relationships between the total concentrations of different nutrients (N, S, P, K, Ca, Mg, Mn) in roundwood and roundwood diameter; (2) the variation of the relationships between nutrient concentrations and diameter between different tissues (wood, bark); and (3) potential effects of other factors on nutrient concentrations, namely effects of site conditions and/or stand age.

2. Material and methods

2.1. Model construction

Our modelling approach was developed to predict nutrient concentrations in sections of roundwood (hereafter shortly referred to as sections) over bark. For a given nutrient and section, the total concentration, $\widehat{C}_{total}$, and the concentrations, $\widehat{C}_i$, in different tissues, *i*, were modelled using the mechanistic relationship

$$\widehat{C}_{total} = \sum_i (\widehat{C}_i \times P_i) + \varepsilon_{total} \quad \text{with} \sum_i P_i = 1, \qquad (1)$$

where P_i = tissue proportion within the section and ε_{total} = residual term for the total nutrient concentration.