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Bridging empirical and carbon-balance based forest site productivity – Significance of below-ground allocation

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ABSTRACT

In forestry, site productivity is commonly described using the concept of site index (SI) and its effect on the potential mean annual increment. Although a unified causal explanation between SI and productivity is still missing, operational methods have been developed to determine SI on the basis of the existing tree crop or other indirect indicators of environmental drivers. In ecology, progress has been made in deriving productivity from the carbon balance, including photosynthesis, respiration and tissue longevity, but considerable gaps remain in quantifying the impact of soil processes on below-ground carbon allocation which would be crucial for closure of the total carbon balance. Recent empirical studies in Finland have found significant and consistent differences in the foliage to fine-root ratio and fine-root lifetime between the conventional SI based on field layer vegetation in geographical vegetation zones. In this study, we utilised this information to bridge the gap between the large body of empirical information on SI and productivity, and productivity as derived from the carbon balance. We incorporated assumptions concerning the climate and soil response of the carbon balance components in a process-based model, PipeQual, and applied the approach to Norway spruce stands in Fenno–Scandian conditions. The results agreed well with an empirical growth and yield model and provided fairly accurate projections for two contrasting test sites. The study provided insights into the role of the component processes of productivity. Importantly, the north-south gradient of productivity was equally attributed to a northward decrease in temperature and an increase in carbon allocation to fine roots. This cautions against climate change projections on the basis of current growth variation with temperature and calls for improved mechanistic models incorporating plant, soil and microbial interactions in regulating the soil-forest carbon and nitrogen fluxes.

1. Introduction

In forestry, site production potential is conventionally described by a species-specific site index, expressed as the height of dominant trees at a specific age (Eichhorn, 1904; Assmann, 1961; Skovsgaard and Vanclay, 2008). Once the site index has been determined, related dominant height and potential volume growth curves as functions of stand age follow. The relationship between the growth of dominant height and stand volume has been one of the corner stones in forest growth and yield study, corroborating the proposition that the impacts of variable edaphic and climatic factors on site productivity can be integrated by the concept of site index. Sites may also be classified on the basis of an independent (set of) variable(s) connected to the site-index-specific height-age curves (Hägglund and Lundmark, 1977; Vuokila and Väliaho, 1980).

In Finland, conventional site classification is derived from the theory of site types by Cajander (1949). It is based on ground and field layer vegetation, and separate site classes have been developed for four different vegetation zones in Finland (Fig. 1, Kalela, 1960; Hotanen et al., 2008). Understorey species composition on a given site reflects the requirements of the species for nutrients and water, and large soil surveys have shown the relation of organic layer nitrogen content and C:N ratio to site type (Tamminen, 1998). Each site type represents a mean site index, measured as dominant height at the age of 100 years, with an uncertainty range of *ca.* 3 m (e.g. Vuokila and Väliaho, 1980). Virtually all empirical information about forest growth and productivity in Finland complies with this system of site classification, including growth and yield studies, descriptive ecological studies (e.g. Mäkinen et al., 2006; Helmisaari et al., 2007) and empirical growth

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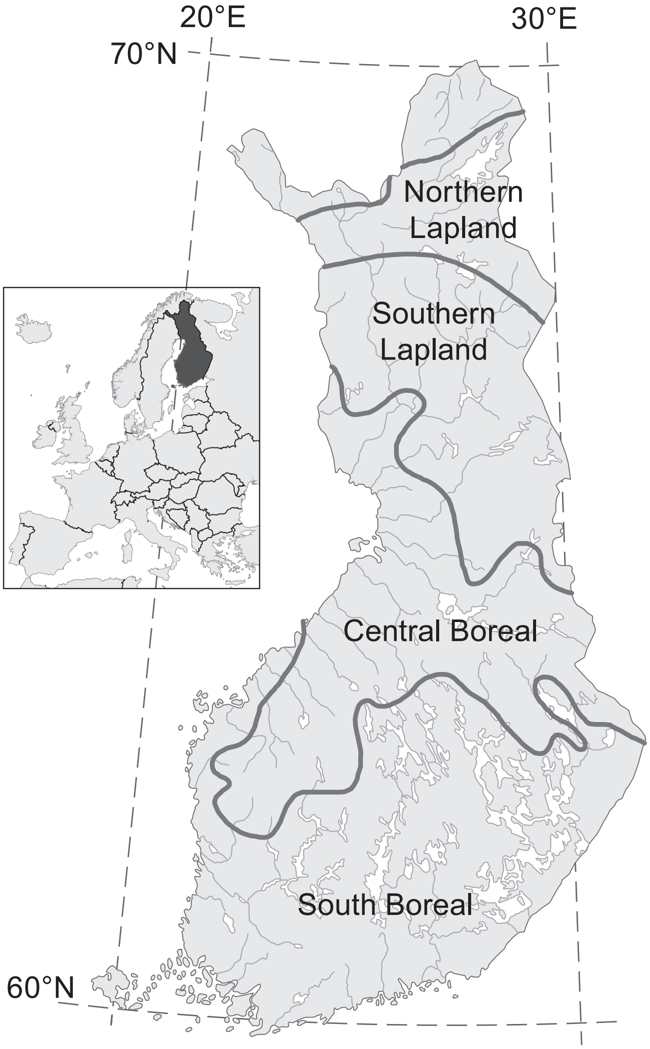

Fig. 1. Vegetation zones in Finland. The northernmost border line approximates the timberline.

models that have been constructed with site class as the key input describing the environment and growth potential (Hynynen et al., 2002, 2005).

The description of site production potential in process-based models is based on climatic driving variables and site-specific parameters that characterise, e.g., water and nutrient availability (reviews by, e.g., Mäkelä et al., 2000; Fontes et al., 2010). In order to run these models for a given site, several input variables at high resolution are required, which is often difficult in a large area with a lot of variability in climate and site conditions (Dewar et al., 2009). Furthermore, it is often not straightforward to define a mapping from the empirical site type classification to the process-based model inputs, as the site types appear to be a result of many factors acting in concert (Tonteri et al., 1990). This would be crucial, however, in order to be able to utilise the large body of empirical studies on productivity in testing and calibrating process-based models.

The PipeQual model is a process-based model that derives tree growth and stem structure from carbon acquisition and allocation (Mäkelä, 1997, 2002). Key factors affecting forest productivity in the model depend on climatic and edaphic factors, comprising the mean annual availability of photosynthates for growth, and the site-specific allocation of carbon to fine roots and the crown. The model has been parameterised for conifers in southern Finland (Mäkelä and Mäkinen, 2003; Kantola et al., 2007) with special focus on stem structure for wood quality applications (Cao et al., 2008; Niinimäki et al., 2012). In a recent study the model was tested against long-term thinning and fertilization trials of Norway spruce (*Picea abies* (L.) Karst.) (Kalliokoski et al., 2013).

From the carbon balance point of view, site productivity is a result of the interplay between gross photosynthesis, growth and maintenance respiration, litter fall and carbon allocation. While PipeQual provides the general rules for carbon allocation and stand structure, the dependence of the metabolic rates on soil and climate must also be available for a regional application of the model. Modelling efforts based on eddy covariance data have shown that a Light Use Efficiency (LUE) type model of Gross Primary Production (GPP) is widely applicable for boreal conifers (Mäkelä et al., 2008a; Peltoniemi et al., 2012, 2015; Minunno et al., 2016) and can be summarised as a dependence of potential GPP on Effective Temperature Sum (ETS) and foliar nitrogen content in the current climate (Härkönen et al., 2010). Temperature and tissue nitrogen content also regulate the regional trends of respiration and tissue turnover (Ryan, 1991; Reich et al., 1998, 2014; Kikuzawa and Lechowicz, 2011; Leppälammi-Kujansuu et al., 2014a). Recent advances in empirical research into the carbon demand of fine roots have produced results that allow us to relate fine root allocation and tissue nitrogen content directly to site type in the Finnish classification system (Helmisaari et al., 2007; Leppälammi-Kujansuu et al., 2014a,b). This means that key impacts of nitrogen limitation can be analysed without explicitly including a model of nitrogen dynamics.

So as to test the above reasoning, the objective of this study was to parameterise the Norway spruce version of the PipeQual model so as to make the model applicable to any forest stand in Finland (and similar climatic areas), given its geographical location and site type class. This consisted of identifying those parameters in the model that show dependence on climate and/or soil processes, and quantifying them in terms of related available inputs. To this end, we utilised the recent advances in empirical research into the regional variation of GPP (Mäkelä et al., 2008a; Peltoniemi et al., 2015) and the carbon demand of fine roots in boreal conifers (Helmisaari et al., 2007; Leppälammi-Kujansuu et al., 2014a,b). The parameterisation was tested against a geographically extensive empirical stand-level productivity and harvest model for Norway spruce by Vuokila and Väliaho (1980). In this model, the growth equations are based on site index, H_{100} (dominant height, i.e., height of 100 thickest trees ha^{-1}, at age 100 years), with a separate analysis of how the dominant height curves depend on site type (Cajander, 1949) and climatic region. Additionally, two individual sites of contrasting site productivity with time series information of inputs and growth was utilised for model testing, one in southern Finland and one in north-eastern Sweden.

2. The model

2.1. Model overview

This study used the PipeQual model version by Niinimäki et al. (2012) and Kalliokoski et al. (2013). Below, the components of the model that are affected by climatic and edaphic conditions are presented, and new equations for estimating these parameters from environmental variables are proposed. The environment-sensitive parameters include (1) metabolic parameters related to carbon assimilation and use, and (2) structural parameters that affect on the variation of carbon allocation between fine roots and crown in different environments. The model operates with an annual time step, but the metabolic parameters related to photosynthesis were calculated using a daily time step model. For a detailed explanation