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Modeling birch seed supply and seedling establishment during forest regeneration

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ABSTRACT

The seed ecology and regeneration management of birch species in Fennoscandia has been quite thoroughly investigated through decades of forestry research. Nonetheless, there are few methods for precise predictions of spontaneous natural regeneration. In this study a first framework of a model is presented that combines possible seed supply with seed emergence and seedling survival based on GIS data and the results of past experiments. The birch seed supply was calculated by combining spatial data on standing birch volume with birch seed dispersal distributions. The establishment on a site was further estimated based on the effect parameters of soil moisture conditions and soil scarification. This model shows a reduced variance compared to general means of seed supply and partly explains the variation between sites with the same soil scarification treatments. Even though additional management and ecological variables should be incorporated to increase the model's predictive ability, it could already be of use in practical forestry.

1. Introduction

Modeling ecological drivers is important both for enhancing progress in forest management and expanding our understanding of tree species. There is a great need for predictive precision when it is time for forest regeneration after harvest. Regeneration by spontaneous seeding from retention trees or surrounding stands often results in higher risks and uncertainties and raises different research questions than when studying plantations of cultivated material (Puettmann and Ammer, 2007). Estimates of the seed supply might facilitate the choice of management in the establishment phase. Increased knowledge and better predictions could encourage forest owners to explore combined methods of planting and natural regeneration in order to obtain mixed species stands in production-oriented forestry, especially since the use of complementary tree species in plantations has high potential (Ackzell, 1994; Agestam et al., 2005; Hewitt and Kellman, 2002a). The most abundant broadleaved tree species that naturally regenerate in Swedish forests are the two native species of *Betula*, silver birch (*Betula pendula* Roth.) and downy birch (*Betula pubescens* Ehrh.) (Götmark et al., 2005). The two species are also relatively well studied and described in forest literature (Hynynen et al., 2010; Karlsson, 2001; Perala and Alm, 1990a; b; Sarvas, 1948). The species are similar in phenology and traits and are, therefore, seldom separated in Swedish forestry practice or in the Swedish national forest inventory (NFI). In addition, other models of regeneration have revealed no significant difference between the two species (Eerikäinen et al., 2007). Due to inconsistent differentiation of the two species within the source data of this model, they were not separated and hereafter they are both referred to as birch unless otherwise indicated.

Modeling the seed dispersal distributions (dispersal kernels) from seed trees has been undertaken using both empirical seed trap data and by theoretical modeling of the behavior of the propagule and the clearcut air flow (Canham and Uriarte, 2006). The ecology of seed dispersal is a relatively newly revised topic (Fenner, 2005). The dispersal kernel is often described as a lognormal, Gaussian or negative binomial distribution with a fat tail (Bullock and Clarke, 2000; Nathan and Muller-Landau, 2000). The shape of the kernel is of major importance in this study, as well as in others (Allard and Soubeyrand, 2012). Several other studies have revealed a seed dispersal distribution with a high amplitude over short distances from the seed source and a rapid decline with distance from the seed trees for wind-dispersed species in general (Bolker and Pacala, 1999; Nathan and Muller-Landau, 2000; Tamme et al., 2014) and for birch specifically (Fries, 1984; Karlsson, 2001). The spatial matrix of seed density, known as the seed shadow (Fenner, 2005), repre-

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sents the summarized output from calculated dispersals from all available sources.

Estimates of standing tree volume (m^3 ha^{-1}) for the most frequent tree species are available in raster format for all high productivity forested land in Sweden, named k-NN Sweden (Reese et al., 2003). Today spatial distribution data is used to estimate forest development and in particular, probability based k-nearest neighbor techniques (kNN) are often used when multiple continuous attributes need to be estimated (Brosofske et al., 2014; Gilichinsky et al., 2012; Tomppo et al., 2008). In earlier studies, the k-NN Sweden data have been used in ecological explanations of large scale variables of land use and forest structure, e.g. the abundance of saproxylic beetles and amount of wood, (Abrahamsson et al., 2009), allocation of broadleaved forest (Lindbladh et al., 2011) or allocation of old growth forests (Reese et al., 2003; Reese et al., 2002). In addition, methods for retrieving categorical variables from the continuous forest variables have been published on the basis of the raster data (Trubins and Sallnas, 2014).

For many tree species, seed germination rate is higher on bare mineral soil than in undisturbed humus layer (Löf et al., 2012; Willis et al., 2015) since the mineral soil seed bed substrate has a higher moisture content (Oleskog et al., 2000) and several soil scarification techniques have been shown to increase the density of birch seedlings (Karlsson et al., 2002). The use of soil scarification on clearcuts has a positive effect on seedling establishment (Karlsson, 1996; Nilsson et al., 2002). The two main explanations are the increased amount of bare mineral soil and the removal of physical barriers for seeds to reach the soil surface. The positive effect of soil scarification on seed germination may also persists in subsequent years (Johansson et al., 2013). Soil moisture content is an important variable for birch seedling emergence and survival (Frivold, 1986; Sarvas, 1948) both at the stand level and in small-scale micro conditions (Pliura et al., 2000). Increased moisture content in a seed bed increases the germination rate of birch seeds (Ackzell, 1994; Karlsson, 1996). The clearcut size is also important: large areas without seed trees will reduce the seed supply but small gaps in closed canopies may provide insufficient resources for seedling survival (Perala and Alm, 1990a). High basal area of retention trees, so-called shelters, has the same effect, with insufficient resources for seedling growth during the first years after emergence (Laiho et al., 2011; Nilsson et al., 2002).

The main purpose of this study was to obtain predictions of birch regeneration using the output of a model of the mean density of birch saplings four years after clearcutting in southern Sweden. This paper focuses on two important drivers of the outcome: seed supply, for a specific stand during a defined year, and clearcut management, with its implications for seedling establishment. Large scale data, such as spatial distribution of standing birch volume on a regional level, Small scale features, such as soil properties in the seed bed, and regenerative traits of birch were combined to provide an output of the density of vital birch seedlings four years after clearcut (Fig. 1). Previous linking of the landscape matrix with the ecological traits of seed dispersal and regeneration has led to an increased understanding of forest species composition and succession (Papaik and Canham, 2006; Pennanen et al., 2004). In addition to this, an operational motivation for the regeneration model is selection of areas for natural regeneration of birch. The main hypothesis tested was that information about amount and spatial position of seed-source will significantly improve prediction of natural regeneration of birch on clear-cuts in southern Sweden.

2. Material and methods

The model estimates the regeneration success and seedling survival of birch on clearcuts in southern Sweden. The model covers the regeneration process from seed production by birch seed trees and birches in the neighbouring stands, seed dispersal to the clearcut, seed germination and seedling survival (Fig. 1). The model begins with an annual cohort of seeds the year before harvest and thereafter additional annual cohorts during the three following years. The number of surviving seedlings four year after clearcutting is the final output (Fig. 2). In this study, clearcutting was conducted between the growing seasons of years −1 and 0. If slash removal and soil scarification was performed it occurred during year 0, at the latest before seed fall in August. No further soil disturbance was accounted for in the model the following years. Seed germination was estimated from year 0 to year 3. Consequently the seed production was estimated from year −1 to year 2 and seedling survival from year 1–4. The cohorts are denoted by the year i (where $i = -1 \ldots 4$) when the seed landed on the clearcut.

The model incorporates ecological characteristics of birch such as seed production in relation to tree volume, seed dispersal and germination rates. These characteristics were retrieved from earlier experiments and published references. In this study the model has been validated with data from five year-old clearcuts, described under the section validation data. Stand variables describing surrounding seed sources were derived from national GIS spatial data and regeneration treatments (soil scarification type) on the clearcut were entered into the model. The model result; seedling density $^{-2}$, were made for every measured sample plot in the validation data but results are also evaluated as mean values of the sample plots on each clearcut.

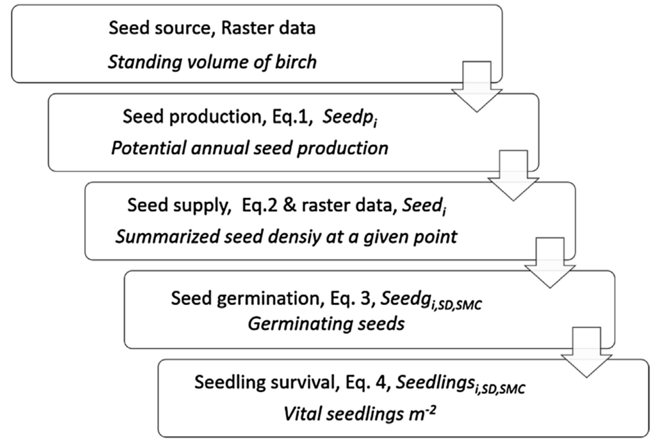

Fig. 1. Flowchart overview of the model.

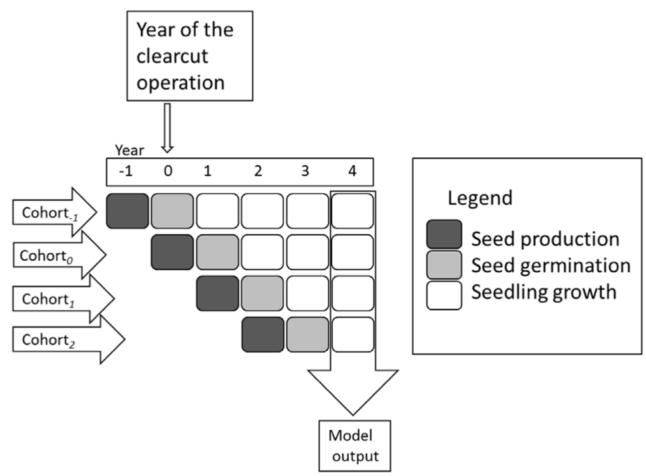

Fig. 2. Cohort succession.