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Modelling natural recruitment of European beech (*Fagus sylvatica* L.)

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ABSTRACT

In the study, data from a Slovenian forest inventory (67,563 plots, 200 m^2 each) were used to develop a two-stage beech recruitment model. In the first stage a probability model of beech recruitment was estimated with binary logistic regression, while in the second stage a conditional model for beech recruitment rate was derived. A tree was classified as recruited if it had crossed a threshold of 10 cm in its diameter at breast height. On average, 2.5 beech ha^{-1} y^{-1} overgrew the measurement threshold, representing 38% of the total recruitment. High variability in beech recruitment was observed (CV = 274%). Among 21 variables selected for possible inclusion into the models, three stand, one site, two climate, two forest management, and one wildlife variable were chosen; eight were included in the probability model, seven in the conditional model, six of which were included in both models. Beech recruitment was negatively related to stand basal area and mean diameter and positively related to the proportion of beech in the stand basal area. Beech recruitment was most successful in young even-aged and uneven-aged stands and on sites of medium productivity. Tree mortality in a stand, resulting mainly from harvesting, was positively related to beech recruitment, while the opposite was true for large ungulate density index. Among climate variables, mean annual temperature and mean annual precipitation influenced the probability of beech recruitment, a result that could be useful for exploring the future potential of beech in a changing environment.

1. Introduction

European beech (*Fagus sylvatica* L.) is the most abundant broad-leaved tree species in Europe and dominates the potential natural vegetation in a large part of Central Europe (Bohn et al., 2004). It is characterised as a late-successional, shade-tolerant species with a broad ecological amplitude (Ellenberg, 1996). The growth and dynamics of European beech (hereinafter: beech) have been investigated in numerous studies across much of its distribution range. Some have reported beech's reduced competitive capacity (e.g. Gessler et al., 2007; Jump et al., 2006), whereas others have documented its progression as a result of its high adaptive ability and phenotypic plasticity (e.g. Bolte et al., 2007; Poljanec et al., 2010). Based on climate change predictions (IPCC, 2007), it is expected that the distribution range of beech in Europe will expand at its northern edge and shrink at its southern and southeastern edges (Bolte et al., 2007; Czucz et al., 2011; Kramer et al., 2010; Penuelas et al., 2007).

Changes in tree species abundance and spatial distribution are a consequence of many interrelated processes in forest ecosystems (Oliver and Larson, 1996), the main ones being regeneration, recruitment, growth, and mortality. Among these, natural beech regeneration has been exhaustively studied (Jarcuska, 2009; Wagner et al., 2010), with the influence of canopy opening size and light intensity, but also soil moisture, on regeneration growth and morphology receiving particular attention (Ammer et al., 2008; Collet et al., 2001; Czajkowski et al., 2005; Madsen, 1994; Petritan et al., 2009; Stancioiu and O'Hara, 2006; Wagner et al., 2010). Many studies have investigated the growth of beech trees and beech stands, with the most recent mainly focusing on the influence of different silvicultural treatments (e.g. thinning regime) and climate conditions (Grundmann et al., 2011; Lebourgeois et al., 2005; Pretzsch, 2005; van der Maaten, 2011). Some studies, which have been carried out mainly in the regeneration and mature phases of managed beech forests, have explored tree mortality in beech-dominated stands (Jarcuska, 2009; Monserud and Sterba, 1999; Petritan et al., 2007). Beech recruitment, which is understood as the process by which trees overgrow a particular measurement threshold value, has received very little attention, and there are very few examples of studies that have focused on it (e.g. Penuelas et al., 2007). The measurement threshold value is arbitrarily defined and may differ between and within countries. Additionally, recruitment rate is a quantification of the recruitment process and is defined as the number of trees (or sometimes as their basal area) reaching or exceeding a particular measurement threshold over a certain period of time (Lexerød and Eid, 2005). In this study, a tree was classified as recruited if it had crossed a

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threshold value of 10 cm in diameter at breast height (dbh). The recruitment of a particular tree species is the link between its regeneration and the formation of a mature stand. The establishment of natural tree species regeneration requires favourable conditions in an appropriate time and spatial constellation (Jarcuska, 2009). The survival and growth of regeneration is highly dependent on site and stand conditions, mainly due to the influence of the latter on light availability (e.g. Barna, 2008; Madsen, 1994; Wagner et al., 2009). The survival rate of different tree species in the regeneration may differ significantly (Petritan et al., 2007), hence tree species composition may change noticeably during the regeneration period. The recruitment, on the other hand, is the final result of the regeneration process. Therefore, the recruitment rate of individual tree species might better point to the future performance of this species in a given stand than the structure and composition of the regeneration. As such, the recruitment, by itself or in combination with other stand parameters, indicates the future potential of particular tree species.

The recruitment of tree species can be studied on different spatial and temporal scales and in relation to different influential factors. Stand variables, especially stand density and mean stand diameter, are considered the most important in predicting recruitment rate, but tree species composition and intertree competition may also be significant (Hao et al., 2005; Lexerød, 2005; Trasobares et al., 2004; Yoshida et al., 2006). Stand parameters strongly depend on the silvicultural system applied. In potential beech sites, beech usually regenerates and recruits successfully in the various stand conditions created by different silvicultural systems – ranging from regular and irregular shelterwood systems to uneven-aged single or group selection systems. In some regions, the successful regeneration and recruitment of beech has also been observed in coppice and coppice-with-standards systems. The clear cutting system, however, is less appropriate, since beech only rarely regenerates and recruits well in the early successional stages (Barna, 2008). The recruitment rate of beech can also be influenced by site conditions. The response of the recruitment rate of some tree species to site variables such as soil pH, altitude, latitude, vegetation type, fertility, and moisture has been studied in mixed stands (e.g. Bendzsak, 2004; Lexerød, 2005), but there has been a lack of such studies for beech. However, many studies have explored the influence of site variables on beech growth. Since growth and recruitment are closely interrelated, the results are also relevant for beech recruitment. Recently, the influence of climate conditions on beech growth has received a great deal of attention. A number of studies have shown that variation in temperature and precipitation has a significant influence on beech regeneration (e.g. Czajkowski et al., 2005) as well as on the growth of adult beech trees (Grundmann et al., 2011; Jump et al., 2006; Lebourgeois et al., 2005; Pretzsch, 2005; van der Maaten, 2011).

Several methodological approaches have been used to model the recruitment of tree species in response to influential factors, from Markov chains to single equation non-linear and linear models (e.g. Hao et al., 2005; Trasobares et al., 2004). Currently, a two-stage modelling approach (Vanclay, 1992) is most often used for predicting recruitment rate. Recruitment is closely related to regeneration establishment, which is a rather stochastic process. Therefore, much of the variability within recruitment reflects the fact that during any time period regeneration may or may not establish in a stand. Consequently, it is important to estimate the probability of recruitment occurrence first and predict the recruitment rate afterwards, given that some is known to occur. If such data are treated as a two-state system, the ability of the model to correctly predict the recruitment rate is enhanced (Vanclay, 1992). In the two-stage approach, binary logistic regression is typically used in the first stage to predict the probabilities for recruitment occurrence, and various linear or log-linear regression procedures are used to predict its expected amount in the second stage.

To our knowledge, the main factors influencing the recruitment of beech have not been studied in Central Europe. Furthermore, there have been no attempts to model beech recruitment in Europe to date. Thus, the main objective of our study was to develop a model to examine the mutual influence of stand, site, climate, forest management, and wildlife variables on beech recruitment. Several hypotheses were tested: (1) among variables, stand density, measured by stand basal area, is the main predictor in the model of beech recruitment; (2) warmer and dryer climate conditions negatively affect recruitment processes; and (3) beech recruitment can be regulated by the silvicultural system used and is reflected in the stand type.

2. Methods

2.1. Data collection

The study was conducted on a large part of the entire beech distribution range in Slovenia (Fig. 1). Beech forests represent the most widespread forest communities in the natural forested landscape and are currently found on 89% of the total forest area (Dakskobler, 2008). The study area is characterised by considerable variation in relief and climatic conditions. Mean annual precipitation decreases from west to east. Temperature follows a similar pattern, but elevation is an additional factor which significantly influences the distribution of temperature. The analysed beech forests are characterised by small-scale forest management, with the irregular shelterwood system being the prevailing silvicultural system. At the last forest inventory (SFS, 2010), the mean stand basal area in the analysed plots amounted to 31.8 $m^2\ ha^{-1}$ and the mean stand volume was 352 $m^3\ ha^{-1}$. The mean proportion of beech amounted to 31.8% with a standard deviation of 33.6%. The other important tree species in these forests were Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.), and sycamore (*Acer pseudoplatanus* L.), but several other broadleaved and coniferous tree species also occur sporadically.

The data used in the study were provided by a forest inventory done by the Slovenian Forest Service (SFS, 2010). The forest inventory was carried out by sampling a systematic grid of permanent plots (Fig. 1), each consisting of two concentric circles with areas of 200 and 500 m^2, respectively. In the smaller circle, all trees (dbh $\geqslant$ 10 cm) were surveyed, while in the larger area only large trees (dbh $\geqslant$ 30 cm) were registered and measured. Plots were mainly distributed on a 250 $\times$ 500 m grid, but in certain areas, other grids were also used (e.g. 200 $\times$ 200 m). The majority of plots were established between 1993 and 2002, but some had already been established in the 1970s. The remeasurement interval was 10 years and a scheduled number of plots were surveyed each year. By 2010, 64% of established plots had been remeasured at least once. Thus, 67,563 plots were included in the analyses. On each plot, every sample tree was spatially referenced according to its polar coordinates (i.e. distance and azimuth from the plot centre) and several individual tree data were recorded in every measurement, including tree species, dbh, and tree identification code (i.e. standing tree, standing dead tree, thinned tree, recruited tree).

Since close-to-nature forestry is practiced in nearly all of the forest area of Slovenia, the only criterion for plot to be included in the study was that a remeasurement had already been performed. This enabled the calculation of the recruitment within a plot and made model development and evaluation possible.

Beech recruitment rate was assumed to depend on various variables (Table 1). Independent variables were gathered from several sources. Stand, forest management, and some site variables were