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Norway spruce cone crops in uneven-aged stands in southern Finland: A case study

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Norway spruce cone crops in individual trees from two seed ripening years 2012 and 2014 were studied. Data were collected from five stands in southern Finland, managed by single-tree selection harvests since the 1980s. The upper third of living crown of each individual tree was photographed for digital cone counting with image analysis. The average number of cones per tree for trees bearing any cones was 92 in 2014 and 66 in 2012. Highest cone numbers found per individual tree were 526 in the year 2014 and 364 in the year 2012. Of all trees studied, 55.5% produced cones during both years, 9.6% produced cones once and 34.9% did not produce cones in 2012 or 2014. The number of cones per tree in 2014 was positively correlated with tree diameter at breast height and the presence of cones (at least twenty) in that particular individual two years earlier and negatively correlated with local basal area. The quality of the seed crop in 2014 as determined in two of the stands was poor. Based on X-ray analyses, 44% of seeds were empty, 29% were damaged by insects feeding on seeds (*Plemeliella abietina* or *Megastigmus strobilobius*) and only 25% were full and capable of germination. The results have implications for management practices in uneven-aged Norway spruce stands. It is suggested that at each harvest entry, some large, prolific trees should be retained in order to increase the total number of seeds produced in a stand to enhance regeneration and the recruitment of new seedlings.

1. Introduction

Norway spruce in Fennoscandia shows high year-to-year variation in cone and seed production. In southern Finland, for example, abundant cone crops generally occur only once or twice a decade. In northern Finland, good cone crops are even less frequent (Tiren, 1935; Sarvas, 1957; Koski and Tallqvist, 1978; Pukkala et al., 2010) and seed maturation in this region may be incomplete due to harsh climatic conditions (Opsahl, 1952; Almqvist et al., 1998). Furthermore, Norway spruce seed crops are often of poor quality, as seeds are frequently destroyed by insects (Hokkanen, 2000). Also, in poor flowering years, the number of empty Norway spruce seeds is high, ranging from 50 to 90% (Andersson, 1965; Sarvas, 1968).

Historically, Norway spruce cone and seed crops have been intensively studied in all Nordic countries, though older information is based on data from trees growing in even-aged stands. The results of these studies may not be directly applicable to selection stands because of different stem counts, basal area and stand structure in uneven-aged stands (Valkonen and Maguire, 2005).

Norway spruce cone and seed crops are also characterized by large variations between individual trees in a stand. The percentage trees that flower varies, depending on whether it is an abundant or scarce flowering year. Koski and Tallqvist (1978) found that in abundant flowering years, the percentage of nonflowering trees is between 2 and 10%, whereas during the years of scarce flowering, this percentage is 55–98%. Thus, only a small part of the trees may produce the bulk of cone and seed crops, particularly in poor seed years. During a 12-year monitoring period, in an 80-year-old, even-aged Norway spruce stand in southern Finland, 20% of individuals produced 50% of the total cone crop (Annila, 1981).

Generally, dominant and codominant trees produce heavier and more frequent cone crops than intermediate trees; the latter, in turn, produce heavier and more frequent crops than suppressed trees (Heikinheimo, 1932; Waldron, 1965). Moreover, both cone

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size and the number of seeds in an individual cone are positively correlated with tree size (Heikinheimo, 1932; Andersson, 1965).

The high year-to-year variation in cone and seed production of Norway spruce presents a challenge to all types of natural regeneration of spruce stands. Synchronous production of large seed crops followed by small seed crops, ie. masting (Silvertown, 1980) has special implications on selection stands with generally continuous seed production as well as the establishment of new seedlings are required for sustainable management.

The objective of this case study was to examine the quantity and quality of cone and seed crop in individual Norway spruce trees in stands managed with single-tree selection.

2. Material and methods

The data for this study was collected from permanent sample plots established by the Finnish Forest Research Institute (nowadays Natural Resources Institute Finland), in five stands dominated by Norway spruce in southern Finland and managed by single-tree selection harvests since the 1980s. The stands represent samples of either distinct selection structures due to past selection treatments or different stages of transition from an irregular structure towards some, yet unknown, sustainable selection structure (Saksa and Valkonen, 2011).

The area of each stand was about 2 ha. They were grown on mineral soils, and the forest site type was either mesic *Oxalis-Myrtillus* or submesic *Myrtillus* type. Specifically, we used the multiple density plots (cf. Eerikäinen et al., 2007) established in these stands from 1992–1994. These plots are rectangular ($80\ \text{m} \times 100\ \text{m}$) areas, each divided into 8 subplots ($20 \times 20\ \text{m}$) with 10-m buffer zones. Subplots form a series of four different target basal areas of 8, 12, 16 and 20 $\text{m}^2\ \text{ha}^{-1}$ (Vesijako and Mikkeli) or 10, 15, 20, and 25 $\text{m}^2\ \text{ha}^{-1}$ (Suonenjoki I, II and Evo) (Table 1). In each main plot and stand, subplots are replicated once in two opposed rows in the monitoring plot with buffer zones between rows.

In earlier studies (Saksa, 2004; Eerikäinen et al., 2007; Saksa and Valkonen, 2011), diameter at breast height, coordinates, height, vitality and health and malformed or dead crown of each individual was recorded at 5-year intervals. The last tree measurements were taken in 2012 in Evo and Vesijako stands, and in 2013–2014 in three other stands.

Trees on every subplot were divided into eight diameter classes and every third individual from each class was chosen as a sample tree. The upper third of their living crowns were photographed in June 2014 with a digital camera (focal length of 215 mm at maximum, 35 mm film equivalent 1200 mm) with an optical image stabilizer. Current-year cones and cones from the 2012 crop were counted in the photographs (see Supplementary material) using "ImageJ" (Schneider et al., 2012). Year is referred to as the seed ripening year. In total, 639 trees were photographed. As tree crowns were photographed only from one side, a correction factor given by Machanicek (1973) was used in order to account for the number of cones from the crown's nonvisible side. An unknown, but different proportion of 2012 cones in dominant and codominant trees may have been dropped from the crowns by the time we had done our inventory. Thus, generally the number of cones in that year may have been underestimated.

2.1. Statistical analyses

In the first step of the analysis of cone crop per tree, a generalized linear model with Poisson distribution and log link was fitted to the data. The dependent variable was the number of current-year cones in a given individual.

The fixed, independent variables were tree diameter at breast height (D), local (subplot) basal area (B), a given stand (S) and a binary dummy variable (C) indicating whether a given individual produced cones two years earlier (at least 20 cones, yes/no). The limit of 20 cones per tree was subjectively chosen to divide the data between flowering and nonflowering individuals. This value is approximately one-third of the mean cone number value in the data.

The Poisson model did not fit the data well due to many zero-valued observations. This was indicated by large residual mean deviance 48.36 (30,566 with 632 degrees of freedom). In order to account the large variation in the data, a negative binomial model with an estimated heterogeneity parameter k was used. The fit of this model was satisfactory as indicated by residual mean deviance of 1.092 (690.0 with 632 df).

The final model was:

$$\log(\mu) = b_0 + b_1 \times D + b_2 \times B + b_3 \times S + b_4 \times C \quad (1)$$

$$n_{\text{cones}} \sim \text{NegBin}(\mu, k)$$

$$E(n_{\text{cones}}) = \mu \text{ and } \text{var}(n_{\text{cones}}) = \mu + \mu^2/k$$

where n_{cones} = the number of cones in each individual tree.

Overall fit of the model (1) was examined by looking at graphical summaries of the standardized residuals vs. fitted values and covariates. Pearson chi-square test was used to evaluate the observed cone frequency classes vs predicted values from the model (1). Individual model terms were assessed by comparing the log-likelihood statistics of two nested, candidate models and Wald-significance tests for parameter coefficients. Model terms were considered statistically significant at $p \leqslant 0.05$. For all analyses, Genstat 18 (VSN International...2014) regression procedures were used.

2.2. Analysis of seed quality data

To determine the seed crop's quality, a sample of 162 cones (6 cones per tree on average) was taken from 26 randomly chosen sample trees in Suonenjoki I and II stands. The cones were collected in February 2015. Altogether, 2163 seeds from these samples were X-rayed (Faxitron MX-20, IL, USA, exposure time 18 kV, 4 s; image processing with Agfa CR-30X reader) and classified in three categories: (1) full seeds with properly developed embryos

Table 1
Local basal areas for Norway spruce trees (with diameter at breast height larger than 10 cm) on the multiple density plots in the five experimental stands of the study.

Parameter	Local basal area, $\text{m}^2\ \text{ha}^{-1}$			
	Mean	Median	Min.	Max.
Stand 1 (Evo)	16.6	17.2	9.4	21.9
Stand 2 (Vesijako)	16.2	14.2	9.6	23.2
Stand 3 (Suonenjoki I)	20.7	19.7	14.6	27.6
Stand 4 (Suonenjoki II)	17.3	18.6	9.9	24.4
Stand 5 (Mikkeli)	17.6	16.0	12.5	23.9