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Prediction Models for the Annual Seed Crop of Norway Spruce and Scots Pine in Finland

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Many studies indicate that the flowering abundance of boreal trees strongly correlates with the weather conditions of the previous summer. This study developed prediction models for the seed crops of Norway spruce and Scots pine using weather variables one and two years prior to flowering year as predictors. Weather data, systematically recorded at many weather stations, were obtained from the Finnish Meteorological Institute. Seed crop monitoring data came from 22 spruce stands and 44 pine stands. In every stand, seed crop has been monitored for many years, the longest continuous period being 45 years. Monthly mean temperatures, monthly rainfalls, and periodical temperature sums were used as predictors in the seed crop models. Generally, both tree species flowered abundantly one year after a warm summer and two years after a cool summer. While the models only explained about 45% of the variation in the annual seed crop, they accurately predicted good and bad seed years: when the models predicted good seed crops the likelihood to have at least a medium seed crop was very high and when the models predicted small seed crops, the likelihood to obtain medium or good seed crop was very low. Therefore, the models reliably predict if a particular year will be a good seed year or a poor seed year. These predictions can be used in forestry practice for proper timing of natural regeneration activities, and when activities in seed orchards are planned.

Keywords flowering, cone crops, seed years, mixed model
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1 Introduction

Prediction of the seed crops of forest trees is required for the proper timing of the seed and shelter tree cuts for natural regeneration, and the consequent site preparation. For successful seed germination and seedling establishment the site should be disc ploughed or otherwise prepared just before seed fall. This is because the site and the exposed soil are quickly invaded by ground vegetation which decreases the chances of tree seedlings to germinate and survive. Good timing is especially important in the northernmost parts of boreal forests where good seed years are rare. In Finland, there are two main forest tree species; Norway spruce (*Picea abies* L. (Karst.)) and Scots pine (*Pinus sylvestris* L.). Both are important for timber and fibre production and are the focus of this paper. Maximal utilization of good seed years would improve the average outcome for the natural regeneration of both species following shelter and seed tree cuts. Seed crop forecasts are also needed to help the planning of seed collection activities in forests and seed orchards. The chain of treatments aiming at natural regeneration of Scots pine and Norway spruce includes a seed or shelter tree cut leaving 50–200 parent trees per hectare, and removal of parent trees once the regeneration is established. Soil preparation is regularly done in pine stands in summer following the seed tree cut.

A straightforward way to predict seed years is to observe the amount of flowers and cones. The drawback of this method is that the predictions are obtained quite late. For a regular seed crop prediction service this method is impractical since flower and cone counts must be performed annually across many stands. Other potential methods for predicting seed crops include microscopic bud analyses and prediction models based on past weather conditions. A seed crop forecast can be obtained about six months earlier using bud analyses compared with a prognosis based on flowering observations. However, the method is laborious and time-consuming, which means that large-scale analyses cannot be easily done (Hokkanen 2000).

Since weather variables are systematically recorded at many weather stations a prediction service that is based on weather conditions would be cheap. Also planning and scheduling regeneration operations can begin much earlier as seed crop predictions using weather based models can be obtained one year (spruce) or two years (pine) earlier than estimates based on cone counts. This is because the buds of the shoots and flowers of the next growing season have already developed on both spruce and pine before the onset of winter. Differentiation into shoot and flower buds depends of the weather conditions of the year during which the buds develop. Therefore, seed crop predictions can potentially be made at the end of the summer preceding the flowering year. In spruce, this is more than one and a half years before seed fall, because majority of the seed falls during spring one year after the flowering year. In pine, the predictions are obtained one year earlier, i.e., more than two and a half years before seed fall. This is because it takes two summers for pine cones to develop viable seed.

Several studies indicate that boreal conifers flower abundantly after a summer which is warm, dry and sunny (e.g., Tirén 1935, Daubenmire 1960, Matthews 1963, Eis 1973, 1976, Fober 1976, Leikola et al. 1982, Pukkala 1987a, Nikkanen and Ruotsalainen 2000). However, with the exception of seed orchards (Nikkanen and Ruotsalainen 2000) flowering is seldom abundant in two successive years. In an evolutionary context, prolific flowering in several consecutive years could be seen as a sub-optimal strategy since pests and diseases specializing in seed predation would quickly multiply and destroy much of the seed in the years subsequent to the initial productive seed year (e.g. Tillman-Sutela et al. 2004). In many boreal tree species seed production diverts significant resources away from growth. The diameter growth of spruce may be 15–25% reduced in the best flowering and cone producing years (Chalupka et al. 1975, Pukkala 1987b). Greene and Johnson (2004) studied 22 North American tree species and found that there are no discernible endogenous cycles in seed crops but there is a tendency for a high seed production year to be followed by an unusually low production year. Herrera et al. (1998) conclude that in many species the seed crops exhibit a marked trend toward bimodality, with prevalence of either high or low reproduction years and a scarcity of intermediate ones.

It has been suggested that trees have developed adaptations, which prevent abundant flowering in two successive years and this is controlled and cued by the weather (e.g. Eis et al. 1965, Eis 1973, Pukkala 1987a). For example, Pukkala (1987a) found that Norway spruce and Scots pine flower most profusely after a warm summer when the previous year has been cool. Abundant flowering also reduces next year's flowering since it both consumes resources, and the presence of cones reduces the number of potential new flower bud sites. Conversely, potential flowering abundance is high after sparse flowering. The negative autocorrelation between two consecutive years' flowering suggests that weather conditions one and two years prior to the flowering year should be used in the prediction of seed crops.

In Finland, there is a unique empirical seed crop database that has been collected over a 54 year time span (Koski and Tallqvist 1978). Seed crop has been measured over several decades in many stands, in different parts of Finland using special litter funnels (Sarvas 1962, 1968). Since weather statistics across the same time span are also available, the potential to develop empirical models that relate seed crops to weather variables are exceptionally good in Finland. One set of such models has already been developed (Pukkala 1987a). The predictions of these models correlate strongly with the observed female flowering of seed orchards and also with the seed crop of natural stands (Nikkanen and Ruotsalainen 2000). However, disagreement has been found between model prediction and the observed number of flowers in seed orchard in cases of two successive good flowering years.

The above-mentioned model set (Pukkala 1987a) has some limitations which prevent its use in a regular seed crop prediction system. First, the models for pine do not cover the northern part of Central Finland (UTM y coordinate > 7000 km), and the models for spruce may not be reliable for the northernmost part of the country, because too few observations were available in the first modeling effort. In addition, the weather variables and seed crops were expressed as percent of the mean value in the stand during the observation period, to eliminate stand effects. This may create some bias because the observation periods were not the same in different stands. Since the weather variables used in the models were monthly mean temperatures, the models do not take into account the possibility that the period which is critical for bud differentiation may vary between years and locations.

This study aimed at developing improved models for predicting the seed crops of Scots pine and Norway spruce stands anywhere in Finland, using weather variables of years that precede the flowering year as predictors. The models should show reliably whether a particular year is a good or poor seed year. The same data as in Pukkala (1987a) were used, together with new seed crop and weather data collected or recorded after 1987. A mixed modeling technique (random parameter models) was used to account for the stand effect. Such a model type was tested in which the period from which the model predictors were calculated depends on the accumulation of temperature sum, i.e., the period is not the same in every year.

2 Materials

The seed crop data comprised measurements of seed crops over the time period 1956–2006 by the Finnish Forest Research Institute. The total number of stands in which seed crop had been measured was 22 for spruce and 44 for pine. The number of litter funnels was usually 10 per stand, but in some cases it was only two and the maximum was 15. The surface area of a funnel was 0.5 m^2. All caught seeds were counted without assessing seed quality. The counts were converted into per square metre and per calendar year values.

The seed crop monitoring stands cover the entire range of geographical distribution within Finland; the pine stands range in latitude (UTM y coordinate) from 6651 km (south coast) to 7755 km (Utsjoki, the northernmost municipality), and the spruce stands range from 6651 km to 7552 km (Kittilä). The stands were mature, the stand age ranging from 60 to 200 years, and dominant height from 18 to 30 m. The length of the measurement period is different in different stands, the longest continuous measurement periods in the same stand being 45 years. The maximum number of stands were assessed during the period 1960–1975 (Fig. 1), after which the

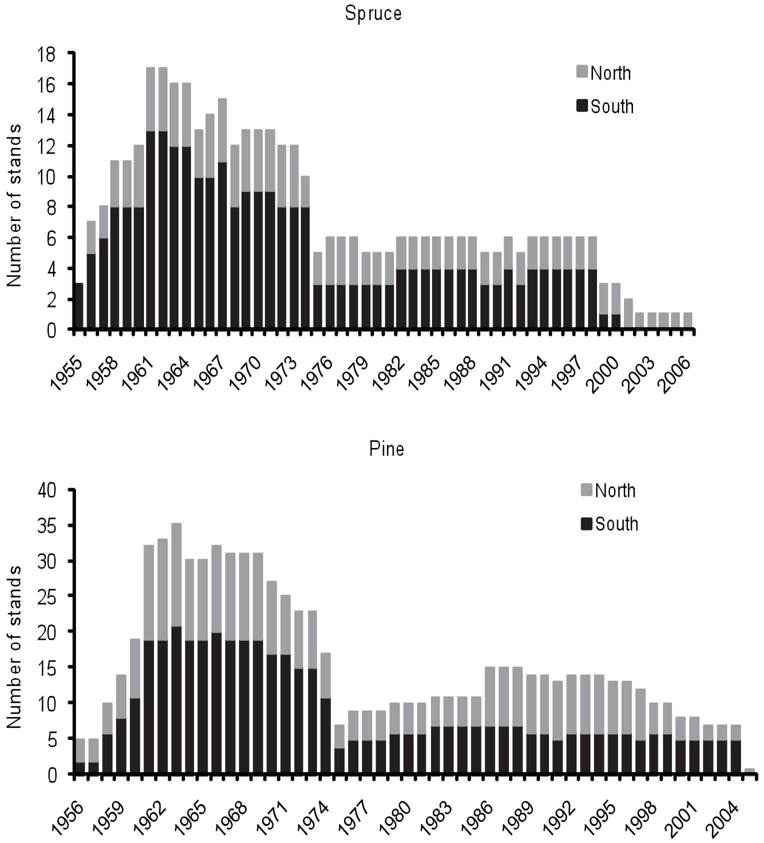

Fig. 1. Number of stands in which seed crop was measured in different years. 'North' = north of 7000 km (UTM y); 'South' = south of 7000 km.

number of pine stands was decreased to 10–15 and the number of spruce stands to 5–6. In the peak years, seed crop was measured in about 35 pine stands and 15 spruce stands.

The total number of seed crop measurement was 785 in pine and 395 in spruce. This was also the number of observations in modeling. However, when temperature sum was used to predict seed crop, the number of observations was less, 644 in pine and 317 in spruce. This is because the daily temperatures, which were required for calculating temperature sums, were not available for the years 1952–1958.

The weather data were obtained from the Finnish Meteorological Institute. Data from the weather station closest to each seed crop stand were used. Daily and mean monthly temperatures measured at 14:00 hrs "winter time" were used, i.e. the solar time was always the same. In addition to temperatures, cumulative monthly rainfall data were obtained, as well as the average cloud coverage of every summer month. However, cloud cover data were not used since cloudiness correlated strongly with temperature and rainfall, and the models would be more difficult to use with cloudiness as a predictor. Monthly and daily temperatures and total rainfall for the months May to September were used in the modelling.

3 Modelling

Three model types were tested. Monthly mean temperatures and total monthly rainfalls were used as predictors in the first model type (referred to as Model 1). This is the simplest model type to use, but the use of data resolved to the month assumes that the time period which is critical for bud differentiation is the same every year and is best explained within the context of monthly intervals. When selecting the combination of predictors, correlations of the mean temperature and total rainfall for May to September with seed crops were calculated, separately for Southern (UTM y coordinate < 6800 km), Central (6800–7200 km) and Northern (> 7200 km) Finland, to see which weather variables were most strongly related to seed crop and whether there were interactions between latitude and weather variables. Moreover, the weather variables of all summer months (May–September) were forced into preliminary models to evaluate the importance of different months. All these preliminary analyses were used to deduce the contribution of the temperature and rainfall of different months to flowering and the consequent seed crop.

In the second model type (Model 2), periodical temperature sums were used as predictors. The temperature sum of a period was denoted as $D^{x,y}$, where x is the temperature sum which must be reached before starting to calculate $D^{x,y}$, and y is the number of days included in the periodical temperature sum. For example, $D^{425,70}$ is a 70-day temperature sum starting the day on which temperature sum reaches 425 d.d. Abbreviation d.d. stands for "degree days" which is the sum of mean daily temperature less 5 °C of those days in which the mean temperature exceeds 5 °C. Many different starting temperature sums and period lengths were tested in modelling.

The third model type (Model 3) used modified periodical temperature sums as predictors. It was assumed that trees complete their annual cycle of growth processes earlier in the year as we move to higher latitudes, which means that counting of $D^{x,y}$ must begin with a smaller temperature sum in the north. The formula for the modified periodical temperature sum was $D^{Mx,My}$, where Mx is the temperature sum which must be reached, and My is the number of days included in the temperature sum. M is a multiplier which depended on latitude

$$M = (7000 - 4000) / (UTMy - 4000) \tag{1}$$

where UTMy is the UTM y coordinate of the stand in kilometres. Modifier M is about 1.2 in South Finland and 0.8 in North Finland.

Mixed modeling technique with a random stand factor was used

$$\ln(S_{tk} + 1) = f(\mathbf{x}_{tk}) + u_k + e_{tk} \tag{2}$$

where S_{tk} is the seed crop of stand k in year t (seeds/m^2), $\mathbf{x}_{tk}$ is a vector of weather variables for stand k and year t, u_k is a random stand factor and e_{tk} is residual. The random stand factors account for the within-stand correlations among observations. The predicted variable was the logarithm of seed crop. The logarithmic transformation ensures that the model never gives negative predictions. One was added to the measured seed crop to avoid taking logarithms of zero. A Snowdon (1991) correction factor was calculated for each model to avoid bias due to the logarithmic transformation of predicted variable.

The year in which the majority of the seed crop corresponding to a particular flowering falls was taken as the reference year. If this year is denoted as t, then the year that precedes the flowering year of spruce is t-2 and the previous year (two years prior to flowering) is t-3. In pine, the corresponding years are t-3 and t-4. Therefore, spruce seed crop in year t was predicted using weather variables of t-3 and t-2, and pine seed crop in year t was predicted using weather variables of t-3 and t-4.

4 Results

4.1 Models for Seed Crop

Model 1 for spruce was based on monthly mean temperatures and monthly rainfalls. The model for spruce seed crop was as follows:

$$\begin{aligned}\ln(S_{t,k}) = {} & 2.373 + 0.1431 Ta_{t\text{-}2,k} - 0.1502 Tb_{t\text{-}3,k} Y \\ & - 0.0828 T^{\mathrm{Sep}}{}_{t\text{-}2,k} + u_k + e_{k,t}\end{aligned} \tag{3}$$

with

$Ta = T^{\mathrm{Jun}} + 2T^{\mathrm{Jul}} + 3T^{\mathrm{Aug}}$

$Tb = T^{\mathrm{Jun}} + 2T^{\mathrm{Jul}} + T^{\mathrm{Aug}}$

Y = UTMy (km) / 10000

where $S_{t,k}$ is seed crop of stand k in year t (seeds/m^2), T^{Jun}, T^{Jul}, T^{Aug} and T^{Sep} are, respectively, the mean temperature of June, July, August and September (°C), u_k is random stand effect, and $e_{k,t}$ is residual. According to the model, seed crop is good if June, July and August (summer) of the year prior to the predicted flowering year are warm and September of the same year is cool. Low summer temperatures in the previous year (t-3) increase seed crop, more so in the north. All predictors of this and all other models were highly significant ($p<0.001$). Generally, spruce flowered abundantly after a warm summer that followed a cool summer. The monthly weather data for July and August in the two years prior to flowering were the most useful for predicting seed crop.

Model 1 for pine was

$$\ln(S_{t,k}) = 0.244 + 0.05948\ Tc_{t\text{-}3,k} - 0.01174 Td_{t\text{-}4,k} + 0.04042\ T^{Jun}{}_{t\text{-}3,k}\ Y - 0.001698\ R_{t\text{-}3,k} - 0.002598\ R_{t\text{-}4,k} + u_k + e_{k,t} \quad (4)$$

with

$Tc = T^{May} - T^{Jun} + 2T^{Jul} + 3T^{Aug} + T^{Sep}$

$Td = T^{May} + T^{Jun} + 2T^{Jul} + 3T^{Aug} + T^{Sep}$

$R = R^{Jun} + 2R^{Jul} + R^{Aug}$

where T^{May} is the mean temperature of May (°C) and R^{Jun}, R^{Jul} and R^{Aug} are, respectively, the rainfall of June, July and August (mm). Also pine flowers abundantly after a pair of years of which the first is cool and the second is warm. Flowering and the consequent seed crop are enhanced if both of these years are dry. It is noteworthy that the sign of T^{Jun} in the formula for Tc is negative which means that June of the year preceding flowering year should be cool for a good seed crop (the same result as in Pukkala 1987a). This interesting effect disappears towards the north (positive regression coefficient of $T^{Jun}{}_{t\text{-}3,k}\ Y$), which means that in northernmost Finland, the entire period from May to September should be warm for pine to flower profusely next summer. Contrary to spruce, May temperature and summer rainfall were also significant predictors of pine seed crops.

Model 2, based on periodical temperature sums, was as follows for spruce:

$$\ln(S_{t,k}) = 2.318 + 0.099906\ D^{200,50}{}_{t\text{-}2,k} - 0.005118\ D^{200,50}{}_{t\text{-}3,k} + u_k + e_{k,t} \quad (5)$$

where $D^{200,50}$ is 50-day temperature sum (degree days) starting on the day when temperature sum exceeds 200 d.d. The main conclusion that can be drawn from this model is the same as obtained with Model 1: the seed crop is abundant two years after a warm summer that is preceded by a cool summer. The most important temperature sum period lasts less than two months, and begins with temperature sum of 200 d.d. The date on which 200 d.d. is reached is often mid-June, but it can range from late May (warm summer, South Finland) to late July (cold summer, North Finland).

Model 2 for pine was

$$\ln(S_{t,k}) = 3.891 + 0.005351 D^{400,45}{}_{t\text{-}3,k} - 0.001578 D^{400,45}{}_{t\text{-}4,k} - 0.002663 R_{t\text{-}3,k} - 0.002924\ R_{t\text{-}4,k} + u_k + e_{k,t} \quad (6)$$

where $D^{400,45}$ is 45-day temperature sum (degree days) starting on the day when temperature sum exceeds 400 d.d. This model can be interpreted as follows: pine flowers abundantly after two dry summers if the first summer is cool towards the end of the season and the second summer is warm towards the end of the season. The temperature sum of 400 d.d. is typically reached between mid-July and early August.

Model 3 for spruce is based on modified periodical temperature sum:

$$\ln(S_{t,k}) = 2.065 + 0.09462\ D^{M200,M70}{}_{t\text{-}2,k} - 0.004701\ D^{M200,M70}{}_{t\text{-}3,k} + u_k + e_{k,t} \quad (7)$$

with $M = (7000 - 4000) / (UTMy - 4000)$

where $D^{M200,M70}$ is $M\times70$-day temperature sum starting on the day when temperature sum exceeds $M\times200$ d.d. and $UTMy$ is the UTM y coordinate of the stand (km). This model is rather similar to Model 2, except that the critical temperature sum begins later in Southern Finland (M=1.2 for South Finland and M=0.8 for North Finland), and the period included in $D^{M200,M70}$ is longer.

Model 3 for pine was

$$\ln(S_{t,k}) = 3.9559 + 0.004359 D^{M425,M70}{}_{t\text{-}3,k} - 0.001465 D^{M425,M70}{}_{t\text{-}4,k} - 0.002728 R_{t\text{-}3,k} - 0.002855 R_{t\text{-}4,k} + u_k + e_{k,t} \quad (8)$$

This model is also rather similar as Model 2 for pine, except that the period for which the temperature sum is calculated is longer. M×70-day temperature sum starting with temperature sum M×425 d.d. represents late summer.

4.2 Evaluation of the Models

Table 1 shows some fitting statistics calculated for each model. According to several of the evaluation criteria, Model 2 seems to be the best performing model for pine and Model 3 the best performing model for spruce. However, some criteria contradict with this conclusion. For example in pine, the R^2, when calculated in original units (seeds/m^2) is much higher for Model 1 than for Model 2. In spruce the RMSE, calculated from original units, is better for Model 1 than for Model 3.

Taking into account these discrepancies and the fact that an important property of the seed crop prediction model is its ability to predict reliably, which year is a good seed year and which is poor, ranking of the models is difficult on the basis of Table 1 alone. In the practical context of forest management we are risk adverse – i.e. we are sensitive to the possibility of false signals either positive or negative – as responding to the model in these contexts could cost the forest manager time and money. As such we are more interested in some regions of the model predictions than others. In order to analyse this we discretised the predictions into classes that were meaningful in terms of seed supply to natural regeneration. The probability that the measured seed crop was "poor", "rather good" or "good" was calculated as a function of the predicted seed crop for each model (Fig. 2). "Poor" seed crops for both species were those with less than 50 seeds/m^2. For pine, >100 seeds/m^2 was considered "rather good" and >200 seeds/m^2 "good". In spruce, "rather good" was >400 seeds/m^2 and "good" was >800 seeds/m^2.

Fig. 2 reveals that the probability of obtaining poor pine seed crops despite the model predictions of a good crop, was clearly lower for Models 2 and 3 than for Model 1. Model 1 sometimes predicted good seed crops although the actual seed crop had been poor. On the other hand, Model 1

Table 1. Fitting statistics for the seed crop models.

	Model 1	Model 2	Model 3
		Spruce	
Observations	395	317	317
Residual variance	1.716	1.634	1.593
Between-stand variance	0.480	0.698	0.708
F	148.8	149.6	159.0
R^2 (logarithmic units)	0.464	0.488	0.503
RMSE (logarithmic units.)	1.276	1.240	1.225
R^2 (original units)	0.340	0.402	0.406
RMSE (original units)	468	478	476
Snowdon correction	1.744	1.530	1.514
		Pine	
Observations	785	644	644
Residual variance	0.845	0.732	0.749
Between-stand variance	0.241	0.170	0.173
F	148.8	156.6	148.8
R^2 (logarithmic units)	0.487	0.496	0.483
RMSE (logarithmic units)	0.896	0.834	0.843
R^2 (original units)	0.411	0.273	0.327
RMSE (original units)	96.2	83.53	97.9
Snowdon correction	1.341	1.321	1.343

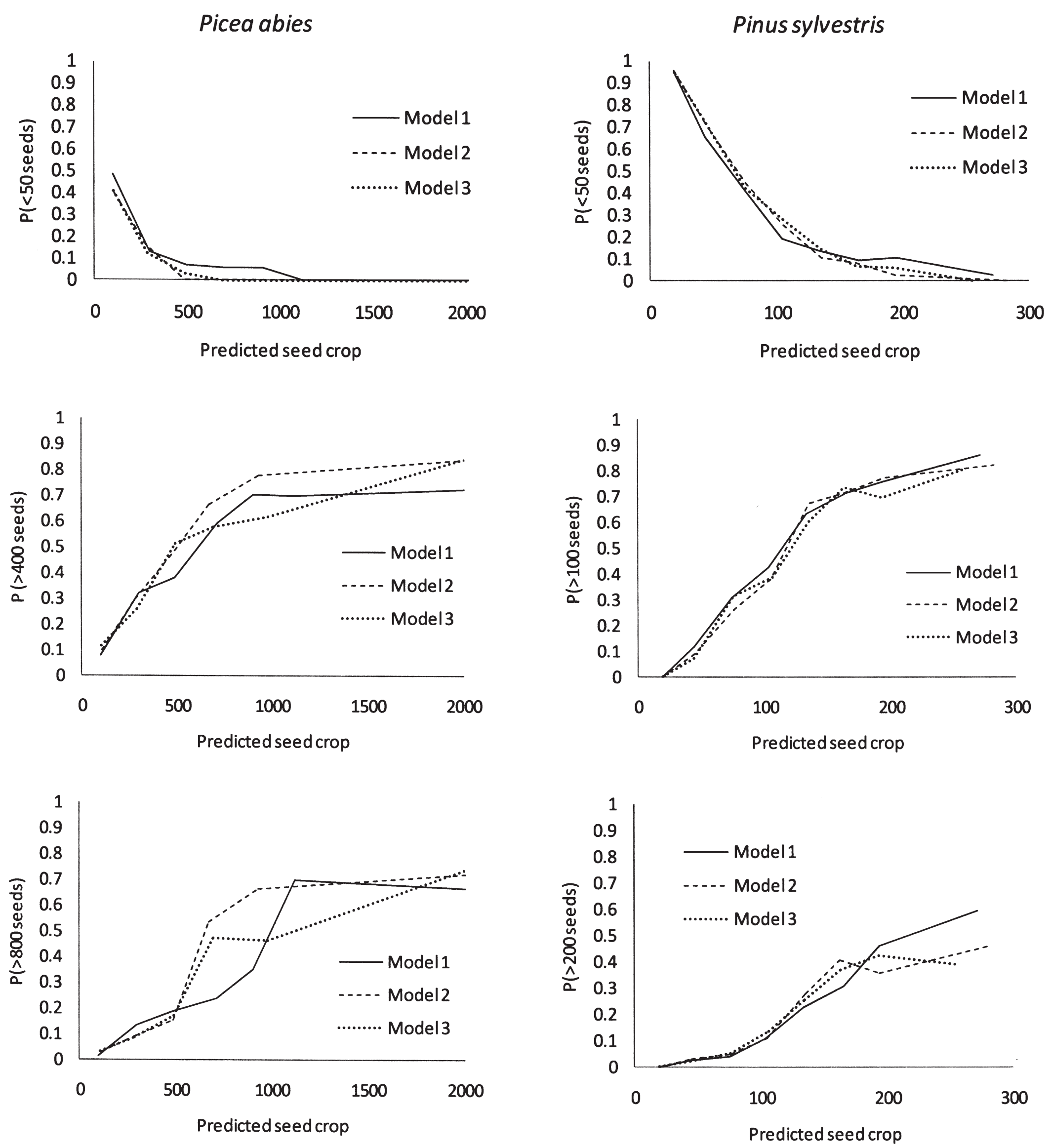

Fig. 2. Probability to obtain <50 seeds/m^2 or more than 100, 200, 400 or 800 seeds/m^2, as a function of predicted seed crop.

seems to be somewhat better than Models 2 and 3 in predicting good seed years correctly.

Model 1 for spruce suffers from the same problem as the corresponding model for pine: it sometimes predicts good seed crops when the observed seed crop is poor (Fig. 2). This does not happen with Models 2 and 3. Model 2 seems to be the best one for predicting rather good and good seed years reliably. On the basis of these comparisons, Model 1 or Model 2 should be used for pine and Model 2 for spruce.

Evaluation of Models 1 and 2 was continued with visual comparisons in many stands, some of which are shown in Figs. 3 and 4. Fig. 3 shows that Models 1 and 2 for spruce give rather similar predictions; the largest errors such as overestimation in 1990

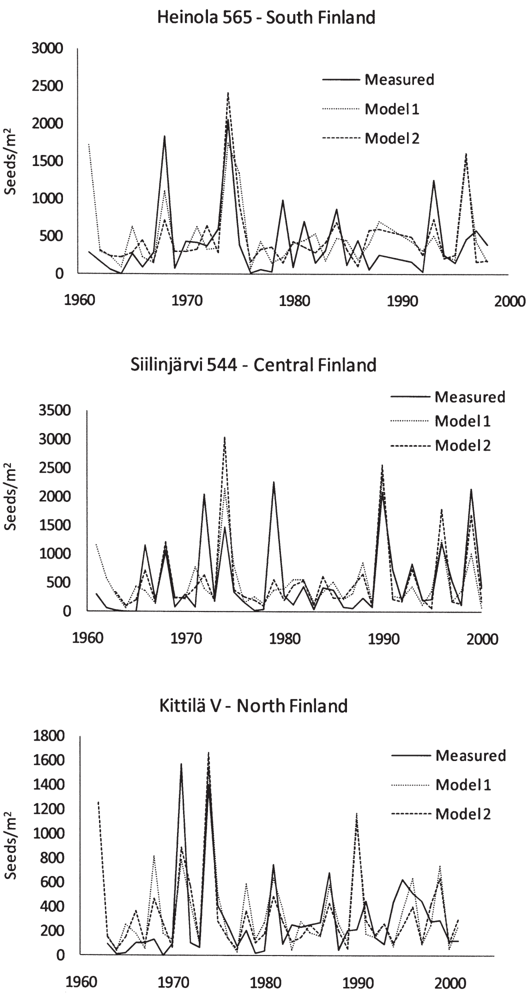

Fig. 3. Measured and predicted seed crop in three spruce stands representing Southern (UTM y coordinate 6780 km), Central (6987 km) and Northern (7552 km) Finland. The *x* axis indicates the year of seed fall (one year later than flowering year).

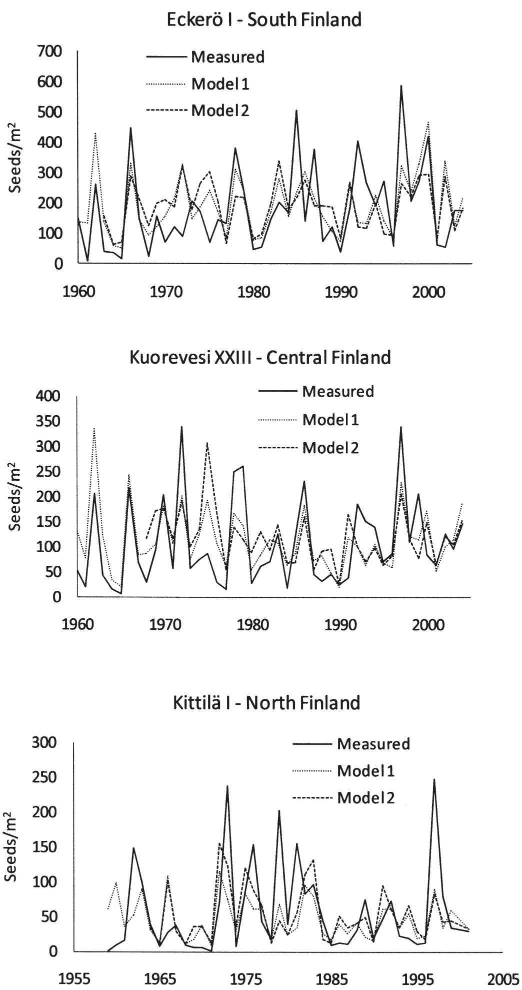

Fig. 4. Measured and predicted seed crop in three pine stands representing Southern (UTM y coordinate 6698 km), Central (6882 km) and Northern (7552 km) Finland. The *x* axis indicates the year of seed fall (two years later than flowering year, and one year later than seed maturing year)

(flowering year 1989) in North Finland and in 1996 in South Finland are also similar with both models. Both models also predict that 1990 was not a peak seed year in the Heinola 565 stand although it was a peak year in most stands of Southern and Central Finland, i.e. both models gave similarly localized predictions. Both models missed the good seed year of 1979 in South Finland. In pine (Fig. 4) it seems that the largest errors are bigger for Model 2 than for Model 1, such as the overestimation of seed crop in Eckerö and Kuorevesi in 1975.

An important feature of a seed production model is its overall accuracy in regional prediction. If the prediction for a region agrees with the measured mean seed crop of stands in that region, it can be concluded that the model gives

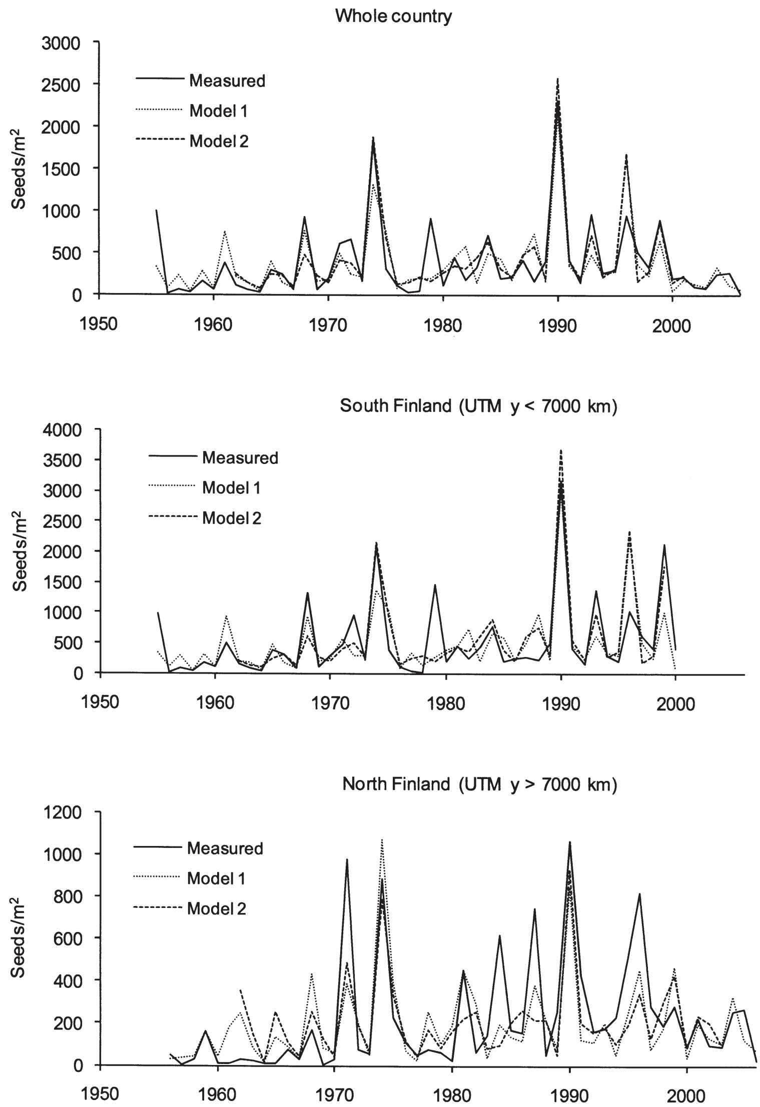

Fig. 5. Comparison of the means of measured and predicted spruce seed crops in South and North Finland, and in whole country. The *x* axis indicates the year of seed fall.

good advice for the timing of natural regeneration. Regional comparisons are provided in Figures 5 and 6. The predicted mean crops of a large region agree well with the measured crops of stands within the same region. For example, the predictions for the good spruce seed crop of 1975 and 1990 are strikingly accurate, as are the predictions for several poor seed years. In regional prediction, there seems to be not much difference between Model 1 and Model 2

In regional prediction for pine (Fig. 6), the predictions for the peak years are less accurate than for spruce. Models 1 and 2 perform similarly in Southern Finland or across the whole country. Both models predict poor seed years rather well (for example 1965 and 1990) but the predictions for good years are more approximate. However, the peaks and troughs of the measurements and

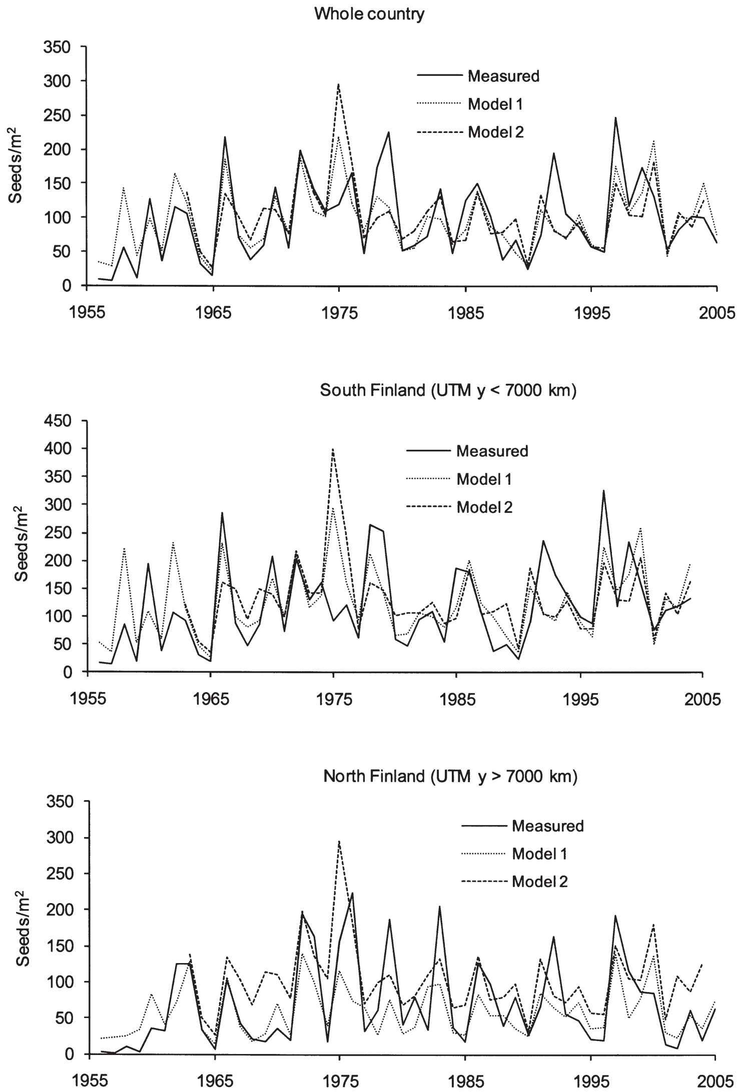

Fig. 6. Comparison of the means of measured and predicted pine seed crops in South and North Finland, and in whole country. The *x* axis indicates the year of seed fall.

predictions often coincide. In North Finland, Model 2 gives higher predictions than Model 1. Model 1 predicts poor seed crops more accurately than Model 2, but Model 2 sometimes predicts good crops more accurately.

On the basis of the visual stand level and regional comparisons, Models 1 and 2 for spruce are equally good. Because the probability analyses of Fig. 2 show better performance for Model 2, it is recommended for practical use. In pine, the visual comparisons indicate that Model 1 is better than Model 2 because Model 1 is more robust in regional seed crop prediction settings.

5 Discussion

The study presented improved models for predicting the seed crops of pine and spruce stands in Finland. The models are easy to use, and the same model can be used anywhere in the country. The R^2 of the seed crop models are of the same magnitude as those developed by Pukkala (1987) but the new models are probably more robust, as they are based on a spatially and temporally more extensive data set. New findings following those of Pukkala (1987a) are that September mean temperature and summer rainfall influence pine flowering and the consequent seed crop, in addition to the May–August temperatures used in the earlier modelling. The interesting result that a cool June is correlated with the amount of pine flowering the following year in Southern Finland is similar to what was found by Pukkala (1987a). The general conclusion that conifers flower abundantly after a warm summer and two years after a cool summer corroborated previous research findings (Lester 1967, Brøndbo 1970, Eis 1973, Bastide and Vredenburch 1979, Pukkala 1987a, Nikkanen and Ruotsalainen 2000).

The most important stand parameters influencing the seed crop are the age, density, height and size of living crown. In the study of Karlsson (2000), the number of cones per tree correlated positively with diameter at breast height. For example, the seed production of mature conifer stands is directly linked to stand density. Koski and Tallqvist (1978) have calculated that an increase from 200 to 500 stems/ha means that the seed production capacity of spruce will increase threefold. On the other hand, excessive reduction of the crown size due to high stem density may significantly decrease the size of the seed crop of pine and birch (Hokkanen 2000).

The degree of explained variance is not particularly high for the models presented in this study. This means that the prediction of individual seed crops in individual stands is not particularly accurate. This is partially explained by sampling errors in seed crop measurement. The seed crops were measured with 2–15 litter funnels of 0.5 m^2 per stand (usually 10 funnels), which gives maximally a 7.5-m^2 sampling area (Koski and Tallqvist 1978). The sampling errors are typically 20% (standard error of mean) which means that if the measured crop is 1000 seeds/m^2, the true crop is between 600 and 1400 seeds with 95% probability.

Other known reasons for decreased model accuracy are temporally changing stand-specific factors such as stand structure, diseases, and wind throw. In addition, the closest weather station is sometimes far from the subject stand. Consequently, daily weather conditions within the stands are not known exactly.

The effect of random errors is decreased when means of measurements and predictions for several stands are compared. Comparison of stand means instead of individual stands results in a greatly improved prediction accuracy (Figs. 3 and 4 vs. Figs. 5 and 6). Moreover, rather than predicting correctly the amount of seed rain (given the context in which the models are to be used) a key criterion of a good model would be one that reliably predicts those years in which good or poor seed crops can be expected. The models perform well in this kind of prediction. For example, when Model 2 for spruce predicts seed crops more than 1000 seeds/m^2, the probability to have at least 400 seeds/m^2 is 0.8, and the probability to obtain at least 1000 seeds/m^2 is 0.67 (Fig. 2). When any of the models predicts a poor seed year, the probability of obtaining good seed crops is very low. When the models predict good seed years, the probability of obtaining very little seed is also low. For regional prediction this type of result would be even much better than Fig. 2 suggests. Therefore, it can be concluded that the models developed in this study can reliably predict whether a particular year is a good seed year or whether it is a poor seed year.

Unfortunately, reliable prediction of seed crop does not guarantee successful natural regeneration. The seed crop forecasts based on our models are obtained for spruce about 1.5 years and for pine as much as 2.5 years before seed fall. During this long time period from flower bud development to seed fall several sensitive stages such as flowering, pollination and the ripening of seeds, are affecting the eventual quantity and quality of the seed crop. For instance, the pollination of female flowers can be unsuccessful. In North Finland the summer preceding seed fall may be too short for the seeds to mature, which means that the quality of even an abundant crop may be poor. According to Hilli et al. (2008) a combination of more than 100 pine seeds/m^2 and an expected germination potential of over 50% was observed only once during 1986–2004 in North Finland. Moreover, many kinds of pests and diseases may destroy the seed (this is particular problem with spruce seeds) and the soil may be too dry during the time of seed germination. While there is always a risk of failure in natural regeneration, our models are a significant tool towards mitigating this risk. However, it is recommended that some kind of cone count is performed annually in addition to the use of our models.

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