

A double-threshold temperature sum model for predicting the flowering duration and relative intensity of *Betula pendula* and *B. pubescens*

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ABSTRACT

The accurate prediction of the flowering period and the amount of released pollen of wind-pollinated trees is important for predicting the aerobiological pollen amounts and for estimating the intensity of background pollination of orchard seed production. Current phenological models, such as the commonly used temperature sum (thermal time) model, are efficient for predicting the timing of point events, e.g. the onset of flowering or leaf unfolding. However, the flowering period of boreal trees, including *Betula pendula* and *B. pubescens*, may last up to 5 weeks with widely varying flowering intensity. Therefore, the ability to predict the duration of the whole flowering period and the intensity of pollination is very important.

In this paper, we present a new phenological model that predicts the whole flowering period and daily (normalized) variation of flowering intensity. The model is based on similar principles as the temperature sum model. The model was calibrated against pollen data recorded with pollen traps placed in several locations in Southern and Central Finland. Our new model predicted accurately the variation in the intensity throughout the flowering period. Moreover, it was able to predict the start and end of the pollination season with accuracy comparable to that achieved with an ordinary temperature sum model for point events. Due to limited amount of test data, the data-dependency of the model had to be tested with a bootstrapping approach. With this method, the model fit and parameter values showed to be independent of the parameter fitting data. The model can be used to predict the whole flowering period of wind-pollinated boreal trees for many different purposes, such as aerobiological forecasts of allergenic pollen, or generation of input data for models of long-range pollen transport.

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1. Introduction

Silver birch (*Betula pendula* Roth.) and downy birch (*Betula pubescens* L.) are common forest trees with distribution covering most of Eurasia, excluding the northernmost and southernmost areas (Atkinson, 1992; Hämet-Ahti et al., 1998). They are monoecious, wind-pollinated trees. Successful flowering and production of viable seeds requires large concentrations of airborne pollen. Thus, an exponential positive relationship exists between the amount of pollen production and the pollination efficiency and seed viability (Sarvas, 1952). Moreover, there is a strong evolutionary pressure towards simultaneous flowering and a positive correlation

between the annual amounts of male and female birch catkins (Masaka and Maguchi, 2001). The female flowers usually become receptive one day before the male flowers of the same tree start pollinating (Sarvas, 1952, 1955); therefore, cut-crossing (i.e. fertilization with pollen from a different individual) is strongly preferred (Hagman, 1971).

In Northern Europe, the main pollination seasons of *B. pendula* and *B. pubescens* begin in late April to late May and in the sub-arctic area during the first half of June (Jäger and D'Amato, 2001). The length of the birch pollen season in Finland, our study area, may vary from two to five weeks (Luomajoki, 1999). The beginning of the flowering period depends mostly on the prevailing meteorological conditions, especially on the cumulative air temperature. Flower buds are developed during the previous summer and fall for the winter into a state of inhibited growth, i.e. dormancy (Sarvas, 1974). The buds need to be released from dormancy before bud development can proceed in the spring. However, factorial

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modeling studies indicate that additional cues, related to changes in the light environment of the plants, are required to initiate the bud development in the spring (Linkosalo and Lechowicz, 2006). After the initiation, the bud development is driven by ambient air temperature (Sarvas, 1972; Linkosalo and Lechowicz, 2006).

The release of mature pollen is largely a passive process dependent on gravity, anther splitting when dry, and agitation of the source plant by air currents (Solomon, 2002). Consequently, once the flowering has started, other factors in addition to the temperature affect the actual pollen release, too. For example, rainy weather can postpone the beginning or inhibit the already started pollen release, even if the required temperature sum has been accumulated. Windiness, on the other hand, has been shown to positively correlate with airborne pollen concentrations (Pernel et al., 2005).

Many phenological events, such as leaf bud burst, can be considered point events, in other words, they take place in a discrete moment of time. This does not apply to flowering of wind-pollinated trees whose flowering period may last up to 5 weeks on a stand level (Luomajoki, 1999). There is some variation in the ripening of catkins within a single tree, as is in the onset of flowering between individuals of the same population. This variation adds to the overall length of the flowering period.

Many applications of pollen release models require data covering the whole extent of the flowering period, as well as daily variation in the flowering intensity. For example, determining the pollen release of surrounding stands is important for estimating the significance of background pollination for seed orchard plantations (Parantainen and Pulkkinen, 2003). Aeroallergic pollen forecasts are another obvious application. In addition, the long-range transport models, developed to predict the occurrence of the pollen airborne transport episodes, require the whole temporal distribution and intensity of flowering events as input data for the predictions (Skjøth et al., 2008; Sofiev et al., 2006).

Most spring phenological models can only predict a specific point event in time. Incidentally, comparisons of several models of spring phenology suggest that simple temperature sum (thermal time) type models, with a fixed starting date for temperature sum accumulation, predict the observed onset of flowering with the highest accuracy (Linkosalo et al., 2006, 2008). However, such models cannot be used to predict the whole flowering period of wind-pollinated trees. In this study, we developed a new model, which is based on the same principles as the temperature sum model but can be used to describe the whole period of flowering from its onset to the end, and especially daily variations of the flowering intensity. The aim of this paper is to describe this new phenological model and to test it with historical flowering data.

2. Materials and methods

The pollen data used in this study was collected by the Finnish Forest Research Institute during 1963–1973 from several locations in Finland. Luomajoki (1999) describes the data in detail. There are 45 records for flowering of *B. pendula* and 84 for *B. pubescens*; each record corresponds to a specific location and year. The data was collected with 1–3 self-recording pollen samplers (Sarvas, 1968) per site, and the daily observations were the average values of the data from all the samplers at that site. The locations of the study sites are presented in Table 1 and Fig. 1.

Luomajoki (1999) had omitted altogether 13 observations from the original data, due to obvious long-range transport episodes detected based on measurements of substantial pollen concentrations before the local start of flowering. For technical reasons related to the model implementation, we also omitted the cases where the flowering extended past 1 July. Finally, we omitted the

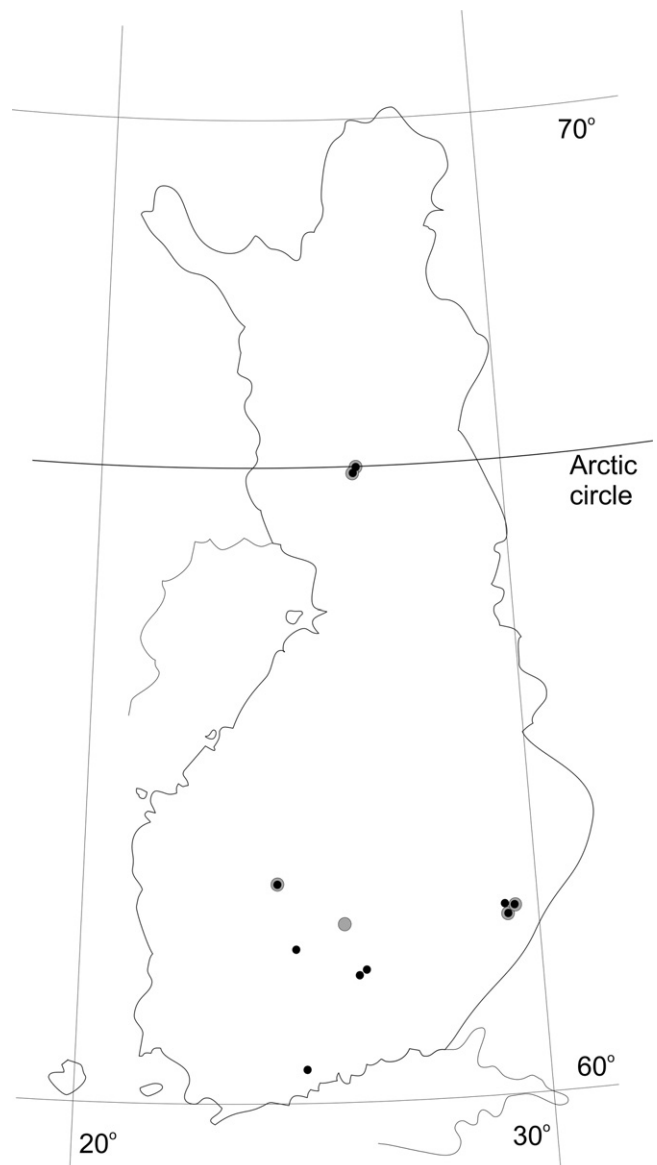


Fig. 1. The phenological observation sites on the map of Finland. Grey circles refer to *Betula pendula* observation sites and the black ones for *B. pubescens*.

northernmost site in the sub-arctic area (Utsjoki) as it represents different climate conditions and vegetation zone as the rest of the data.

The original data, consisting of the daily numbers of caught pollen grains, showed a great annual variation of overall pollen grain numbers. We normalized the absolute numbers of pollen grain counts in order to focus on the temporal development of the flowering and pollen release, disregarding the year-to-year variation in the flowering intensity and total amount of pollen released. For each day, the ratio of the cumulative pollen count until that day was divided by the total pollen count recorded at the site during that particular year; this procedure yields a daily figure starting from zero, before the flowering has started, and ending at unity, once the flowering has finished. We chose this approach, as the current models for flowering intensity, especially those derived from data of airborne pollen, seem to be rather data-dependent (Ranta et al., 2005; Jato et al., 2007).

The corresponding temperature data were extracted from those operational weather stations of the Finnish Meteorological Institute (FMI) most adjacent to the pollen recording sites. Three

Table 1
The observation sites for the phenological data and the corresponding temperature measurements.

Site #	Phenological data					Temperature data			
	Location	Lat (degree, hour N)	Lon (degree, hour E)	Elevation	Age in 1970	Site name	Lat (degree, hour N)	Lon (degree, hour E)	Elevation
<i>B. pendula</i>									
70	Punkaharju LXIII	61°48'	20°19'	88	32	Punkaharju Laukansaari	61°48'	29°20'	83
71	punkaharju LIV	61°49'	29°18'	90	59	Punkaharju Laukansaari	61°48'	29°20'	83
72	Vilppula V	62°04'	24°29'	150	38	Juupajoki Hyytiälä	61°50'	24°17'	153
73	Rovaniemi XXI	66°21'	26°45'	114	113	Rovaniemen Milk Apukka	66°34'	26°00'	106
74	Rovaniemi XXVIII	66°21'	26°41'	251	44	Rovaniemen Milk Apukka	66°34'	26°00'	106
94	Hartola 571	61°45'	25°54'	173	63	Leivonmäki Savenaho	61°52'	26°05'	146
<i>B. pubescens</i>									
75	Tuusula 12	60°22'	25°02'	45	52	Tuusula Hyrylä	60°25'	25°02'	45
76	Padasjoki VIII	61°24'	25°03'	106	42	Lammi Biologinen Asema	61°03'	25°03'	125
77	Punkaharju XIV	61°48'	29°20'	85	43	Punkaharju Laukansaari	61°48'	29°20'	83
78	Punkaharju L	61°48'	29°20'	90	70	Punkaharju Laukansaari	61°48'	29°20'	83
79	Punkaharju LX	61°48'	29°20'	83	38	Punkaharju Laukansaari	61°48'	29°20'	83
80	Vilppula 153	62°03'	24°30'	120	68	Juupajoki Hyytiälä	61°50'	24°17'	153
81	Rovaniemi XVII	66°21'	26°38'	170	123	Rovaniemen Milk Apukka	66°34'	26°00'	106
82	Rovaniemi XX	66°21'	26°45'	108	118	Rovaniemen Milk Apukka	66°34'	26°00'	106
96	Heinola 568	61°10'	26°04'	82	52	Heinola Plaani	61°12'	26°02'	100
97	Heinola 569	61°11'	26°00'	87	53	Heinola Plaani	61°12'	26°02'	100

temperature recordings per day were used, at 6:00 a.m., 12:00, and 6:00 p.m. local time. The minimum of these three temperature values was used as the fourth measurement, the daily minimum (Table 1). Thus each temperature measurement was considered to represent a time period of 6 h. Due to the non-linear temperature response of the temperature sum accumulation, we used the 4 daily temperature measurements instead of daily mean temperature for a somewhat better response of the model to the observational data.

The model predicts the relative, cumulative amount of pollen release on a daily basis, as follows. $S(t)$, the stage of ontogenetic (bud) development on time t , depends on a cumulative temperature sum calculated since a fixed date during spring, t_0 :

$$S(t) = \int_{t_0}^t r(i)di \cong \sum_{i=t_0}^t (r(i) \cdot \Delta t), \tag{1}$$

where $r(i)$ is the rate of ontogenetic development, Δt is the time step of temperature measurements (6 h in the current case), t_0 is the starting day of the temperature sum accumulation.

The rate of ontogenetic development, $r(i)$, depends on the ambient air temperature. The rate of development used here has been empirically measured and tabulated by Sarvas (1972) (Fig. 2). The units of temperature sum accumulations are in relative units, quite similar to the degree days in an ordinary temperature sum model. The temperature sum units were named as ‘period units’ (PU) by Sarvas, to highlight the non-linear relation between the accumulated heat and the temperature. We used these tabulated values for the rate of development in our pollen release model.

In an ordinary temperature sum model, the phenological event is predicted to take place once the stage of bud development $S(t)$ exceeds a pre-set threshold value S_{CRIT} . The current pollen release model utilizes two critical thresholds. The model predicts that pollen emission starts when the stage of development reaches the first threshold, S_1 , and ends when the second threshold, S_2 , is reached. The focus of the model is not in the flowering starting and ending dates, but in the day-to-day variation of the intensity of pollen release throughout the whole flowering period. The cumulative pollen release $R(t)$ on a day t depends on the temperature sum $S(t)$ achieved by that day. The pollen release accumulates as a

linear function of the stage of development:

$$R(t) = \begin{cases} 0, & S(t) < S_1 \\ \frac{S(t) - S_1}{S_2 - S_1}, & S_1 \leq S(t) \leq S_2 \\ 1, & S(t) > S_2 \end{cases} \tag{2}$$

The pollen release model defined by Eqs. (1) and (2) contains three parameters (S_1 , S_2 , and t_0), which must be identified by fitting the predictions of the model to the measured data. The fitting measure used in the current work is the Root Mean Square Error (RMSE) between the observed $[O(i, j)]$ and predicted $[R(i, j)]$ ratios of daily pollen release over the years and sites,

$$RMSE = \sqrt{\frac{1}{N} \sum_1^N (O(i, j) - R(i, j))^2} \tag{3}$$

where N is the total number of records (product of the number of stations i and the number of years j), separately for both the species of *Betula* addressed here.

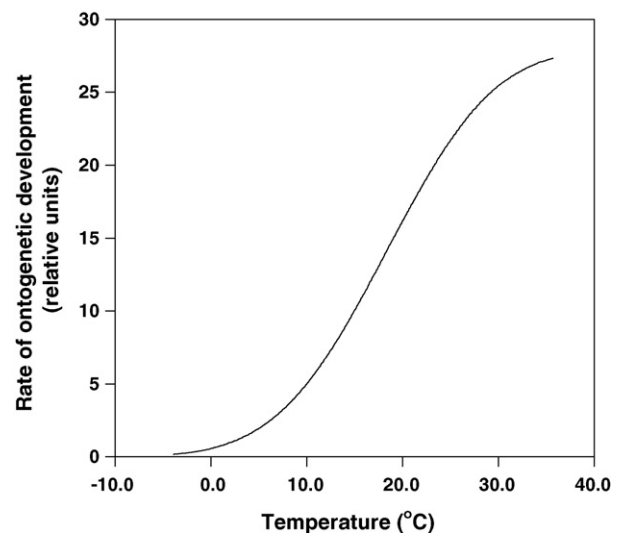


Fig. 2. The rate of bud development as a function of temperature, as determined and tabulated by Sarvas (1972). This function is based on empirical measurements for birch, aspen, and willow in the boreal vegetation zone.

Table 2
The model RMSE values and corresponding parameter values.

	RMSE	Starting date	S_1 (PU)	S_2 (PU)	Flowering period (PU)
<i>B. pendula</i>	0.82	4 March (fitted)	92.9	146.4	53.5
	1.09	26 April (fixed)	49.7	121.5	71.8
<i>B. pubescens</i>	0.58	26 April (fitted)	70.5	147.2	76.7
	0.69	4 March (fixed)	108.8	187.5	78.7

We used a bootstrapping method (Efron, 1979; Efron and Tibshirani, 1993; Hakkinen, 1999) to evaluate the dependency of the model on the specifics of the observational data used for its identification. As the available data set was rather limited, we used this method rather than splitting the data sets into two parts. In the bootstrapping method, one observation is omitted from the dataset, the model is refitted to the rest of the data, after which the omitted observation is predicted with the refitted model. The process is then repeated for another observation. Resulting distributions of the prediction errors and estimated parameter values indicate the extent to which the model parameters depend on the data specifics. Small variations indicate that the model is robust.

3. Results

The RMSE values for fitting the two-threshold model to the phenological data were 0.82 and 0.58 for *B. pendula* and *B. pubescens*, respectively. The corresponding model parameter values are presented in Table 2. The predicted and measured values of cumulative pollen release are plotted in Fig. 3. The mean values of the predicted pollen release over the sites and years fit the observed data. The standard deviation, given as the bars in the figure, illustrates the variation of pollen release on the particular Julian day over years and sites. Comparison of these differences in the variation of observed and predicted cumulative pollen release values suggests that the model for *B. pubescens* fits the observed data better, but this may be due to almost twice the number of data points available for this species (Fig. 3). For both species, the models underestimate the length of the flowering period by up to a few days. In particular, the end of flowering is predicted to be earlier than the observed date. This is evident from the standard deviation of the daily observed and predicted values of the accumulated pollen count (Fig. 3).

The values of the starting date parameter for temperature sum accumulation, resulting from the model fitting, 4 March for *B. pendula* and 26 April for *B. pubescens*, were considerably different. Therefore, the models were also tested with the starting date that was optimal for other species (stated as ‘fixed’ values in Table 2). The resulting RMSE values were 19–33% larger than those resulting from the optimal starting date parameters. The different starting dates reflected in different values of the thresholds were expected because the starting date and threshold parameters are known to be inter-dependent in temperature sum models. The resulting cumulative pollen release, the estimated dates of the start and end of the flowering period or the length of the flowering period did not, however, change much with the changing start of accumulation.

The average starting and ending dates for the flowering of *B. pendula* in the observed data were 17 May and 1 June. The corresponding dates for *B. pubescens* were 16 May and 5 June. Thus, the observed flowering periods were 15 and 19 days, respectively. We estimated the starting and ending days from the model as the days on which the thresholds S_1 and S_2 were met. The starting days fit the observed data well, with standard deviation of -1.5 and -1.2 days for *B. pendula* and *B. pubescens*, respectively. For the end of the flowering period, the deviations were larger: 3.1 and 5.1 days. In both cases the model tends to slightly underestimate the length of the flowering period (Table 3). The RMSEs of the starting and ending dates were 3 and 5 days, which correspond well to

the values achieved when a standard temperature sum model (for a phenological point event) is fitted to the data (Table 3). Therefore, the suggested model can be considered as an extension of the temperature sum-approach: it predicts more features of the flowering season and produces the same scores for previously available parameters. Importantly, the accuracy of the prediction of the starting dates is not obvious, as the two-threshold model is fitted to cumulative pollen count data. Accordingly, the model does not emphasize the starting and ending dates, but any day during the flowering period is given an equal weight in the fitting of the model.

The model contains three governing parameters. However, the values of these parameters are not independent: the values of the two-threshold parameters, S_1 and S_2 , are dependent on the starting

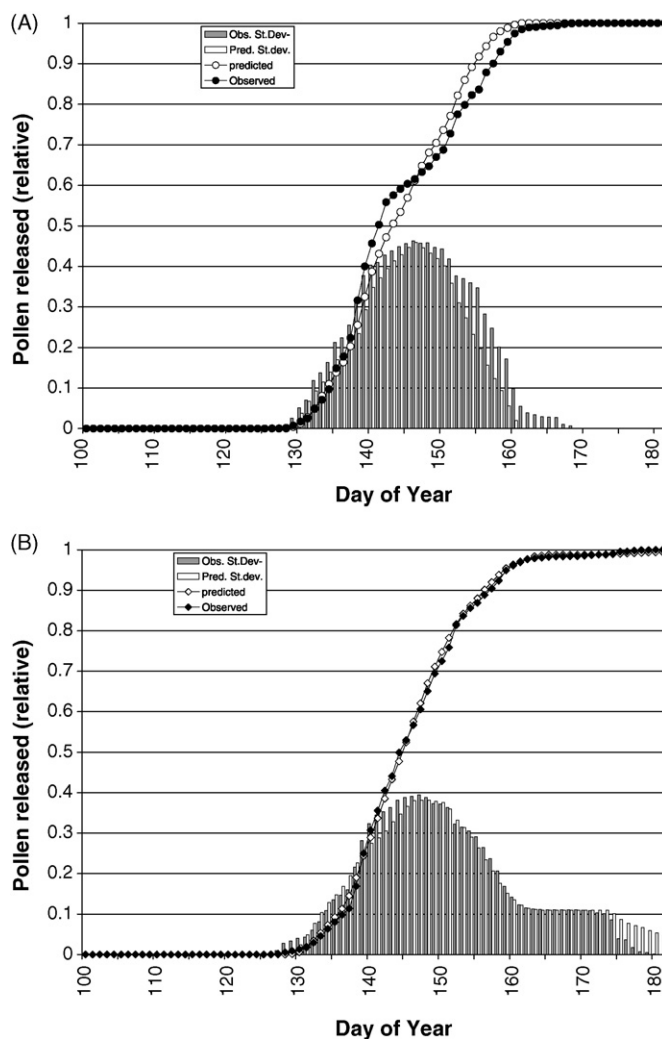


Fig. 3. The average accumulation of pollen release over the years (for the whole data set). The line with black marks refers to the observed values and the one with the white marks to the predicted values. The bars show the standard deviation of the accumulated pollen release per given day over the sites and the years, grey and white for observed and predicted release, respectively. (A) For *B. pendula* and (B) for *B. pubescens*.

Table 3

The starting and ending dates of flowering, as derived from the normalized flowering data. The standard deviation of prediction errors is calculated as the difference of observations and predictions for the first and last (for starting and ending dates, respectively) days of the flowering period, when the cumulative pollen counts are larger than zero and less than unity, respectively.

	<i>B. pendula</i>			<i>B. pubescens</i>		
	Observed	Predicted		Observed	Predicted	
Starting date of temperature sum accumulation (t_0)		4 March (fitted)	26 April (fixed)		4 March (fixed)	26 April (fitted)
Starting date of flowering	17 May	19 May [−1.5]	16 May [0.9]	17 May	14 May [2.0]	18 May [−1.2]
St. dev. Prediction error (days)		3.0	4.6		4.3	4.3
Ending date of flowering	1 June	29 May [3.1]	30 May [2.0]	5 June	25 May [10.8]	31 May [5.1]
St. dev. Prediction error (days)		4.8	4.1		4.1	3.1
Period of flowering (days)	15.1	10.5	14.0	19.2	11.7	13.5

date t_0 (Fig. 4). As one can see from Fig. 4, the RMSE values increase steeply when the starting date is too late in the spring and more shallowly when the starting date is too early. In between these two extremes, the RMSE value shows only weak dependence on t_0 (with correspondingly adjusted flowering thresholds). The two species, however, show somewhat different features. For the *B. pendula* data, RMSE values are low for t_0 selected throughout most of the early spring. Unexpectedly, there is a rather deep and narrow minimum in the corresponding *B. pubescens* data around the latter half of April. It is unclear whether the RMSE minimum in the *B. pubescens* data actually reflects a feature of the phenology of the plant or if it is an artifact. Such behavior has not been detected in the previous studies concerning phenological point events (Linkosalo et al., 2000; Linkosalo et al., 2008). As expected, the difference between the threshold parameters S_1 and S_2 remains constant throughout all data sets.

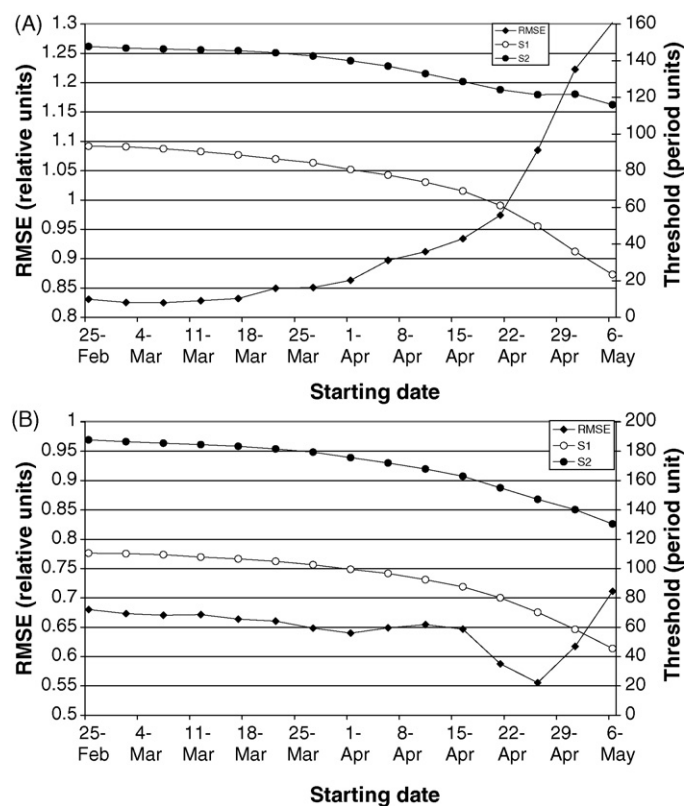


Fig. 4. RMSE values and corresponding flowering thresholds when fitting the model to observed phenological data. (A) For *B. pendula* and (B) for *B. pubescens*. Black diamonds refer to the RMSE value of the model and the white and black circles to the temperature sum thresholds S_1 and S_2 , respectively.

For both the species, the bootstrap analysis showed that neither the RMSE values nor the optimal parameter values vary significantly. This suggests that the models were robust with regard to the features of the data. The variation was smaller especially for the *B. pubescens*, which is probably due to the larger amount of observations in that data set (results not shown).

Neither dataset shows a trend in model residuals (defined as the difference of the measured and predicted values) along the latitude; therefore the use of the model with the same parameter values for the whole observation area is justified. In the *B. pubescens* data, there is a trend of residual over the years, which is statistically significant in a 2-way ANOVA. This trend, however, is not seen in the *B. pendula* data (ANOVA results not shown).

4. Discussion

The results indicate that the proposed model is suitable for simulating the whole flowering period and daily (normalized) pollen release of *B. pendula* and *B. pubescens* in Finland, and it produces useful figures for the variation of flowering intensity in addition to the length of the flowering period. The model is probably valid in the whole of the boreal zone; however, the parameter values should possibly be revised using measurements in various countries. The model structure is general and not in any way specific to birch species. The basic dependency of bud development on temperature in the current model is similar to that in a temperature sum type model; therefore the validity areas of the new model and temperature sum model are the same. The temperature sum type model has been shown to apply to several species (Linkosalo, 2000). Therefore, we expect the new model to be also valid for several other tree species once the parameter values have been readjusted.

Even though our pollen release model is aimed at covering the variation in daily pollen release throughout the flowering period, it was also able to predict the starting dates with accuracy similar to that of a point-event temperature sum model. The bias of the predicted ending dates was somewhat larger as the model predictions of the flowering period ended quite abruptly, while the observed pollen counts tended to linger on. There are three potential explanations for this. For one, the weather conditions, other than the temperature used in our model as the driver of the pollen ripening, may sometimes inhibit the release of ripened pollen from the catkins until the weather is again favorable. Secondly, a resuspension of previously released pollen back to the air can contribute to the air concentrations. Finally, birch pollen is fairly light (characteristic density is of the order of 800 kg m^{-3}) and may therefore be carried by the wind for extended time periods and distances (Sofiev et al., 2006). This introduces another feature affecting the length of the flowering period: long-range transport. The pollen present at some place and time may have originated from a far away location, and on some occasions, these events have been shown to start the pollen periods several weeks before the start of the local flowering

(Ranta et al., 2006; Siljamo et al., 2008; Skjøth et al., 2007; Sofiev et al., 2006). Similar episodes at the end of the flowering period are also possible, but they are harder to detect due to the gradually fading nature of the pollination. For these reasons, the completion of the pollen season may extend beyond the modeled end of the season, which explains why the uncertainty of the model predictions is larger at the end of the flowering period.

Previous studies using the standard temperature sum model have indicated that the two-threshold parameters, the starting date of temperature sum accumulation and the temperature sum threshold for the phenological event, are correlated so that the precise estimation of the two is quite difficult. In contrast, a wide variation of the parameter value couples the results with similar accuracy of the model fit to the parameter estimation data. For instance, when modeling the leaf bud burst date of *Betula* in Finland, Linkosalo et al. (2000) found that the starting date parameter could vary from early March to mid-April with almost constant RMSE of model fitting, provided that the temperature sum threshold was adjusted accordingly. In this study, the flowering of *B. pendula* showed a similar behavior. Curiously, *B. pubescens* behaved differently, with a pronounced global minimum of RMSE values in the parameter space (Fig. 4). This model behavior was quite unexpected, especially as the minimum RMSE occurs with a rather late starting date of the temperature sum accumulation. We suggest that this phenomenon may be an outcome of some curious anomaly in the data rather than dissimilar behavior in the flowering pattern of the two species. However, the model did not show much dependency on the data set, and therefore it is unclear what feature in the data could cause the odd local minimum with the *B. pubescens* data.

The accuracy of daily pollen release amount predictions could be further improved by considering the influence of meteorological parameters, such as humidity, rain, and wind velocity during the flowering. However, the mechanism of the release of ripe pollen has not been determined in detail, which makes their involvement quite uncertain. For instance, do the unfavorable weather conditions prevent pollen from ripening or is pollen ripened but the release restrained with the restrained pollen releasing immediately when conditions improve? This would considerably affect the daily pattern of the amount of pollen released after a period of unfavorable weather conditions.

Thus far, our new pollen release model only predicts the relative variation in released pollen amounts *within* a year, but does not consider the variation in the flowering intensity *between* years. This is the result of the normalization of the daily pollen counts to the annual level. We selected this approach because of the fact that the models for predicting the annual intensity of flowering tend to be quite data-dependent. There is a high chance that a model fitted to one data set would not apply to another one. A good example of this is the introduction of a new independent parameter to a regression model by Ranta et al. (2005), modifying the model presented by Masaka and Maguchi (2001). These fluctuations in flowering intensity are possibly caused by regional stochasticity on stand level (Lyles et al., 2009). We therefore thought that the incorporation of the intensity of the flowering in the model would have degraded the accuracy of the estimation of the timing of the flowering. However, the structure of our model allows for combining it easily with a model of flowering intensity, if such a model is developed, simply by multiplying the normalized pollen release predictions by an estimate of the total annual release of pollen.

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