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Author(s): Linkosalo, Tapio; Le Tortorec, Eric; Prank, Marje; Pessi, Anna-Mari; Saarto, Annika

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Alder pollen in Finland ripens after a short exposure to warm days in early spring, showing biennial variation in the onset of pollen ripening

Tapio Linkosalo^{1,2}, Eric Le Tortorec^{1,3}, Marje Prank^{4,5}, Anna-Mari Pessi¹, Annika Saarto¹

¹University of Turku, Aerobiology Unit

²Natural Resources Research Institute Finland

³University of Jyväskylä

⁴Finnish Meteorological Institute

⁵Cornell University, Ithaca, NY, USA

Abstract

We developed a temperature sum model to predict the daily pollen release of alder, based on pollen data collected with pollen traps at seven locations in Finland over the years 2000 to 2014. We estimated the model parameters by minimizing the sum of squared errors (SSE) of the model, with weights that put more weight on binary recognition of daily presence or absence of pollen. The model results suggest that alder pollen ripens after a couple of warm days in February, while the whole pollen release period typically takes up to 4 weeks. We tested the model residuals against air humidity, precipitation and wind speed, but adding these meteorological features did not improve the model prediction capacity.

Our model was able to predict the onset of pollen season with similar accuracy as models describing only the start of the pollen release period (average prediction error 8.3, median 5.0 days), while for the end of the pollen release period the accuracy of our predictions was not as good. We split the pollen data into odd and even years, and fitted our model separately to each half. Difference in the parameter values suggests a biennial behavior in the onset of pollen ripening, with almost two weeks of difference in the modeled starting date of the pollen development. Monte Carlo resampling of the observation data confirmed that the difference is not just a random anomaly in the data.

Introduction

In Finland, alder (*Alnus* sp.) is together with the far less common hazel (*Corylus* sp.) the starter of the allergenic pollen season. It belongs to the *Betulaceae* family including also birch (*Betula* sp.), which is the most important genus for pollen allergies in Finland. The major allergen of alder (AIn g 1) resembles the major allergen of birch (Bet v 1) both structurally and immunochemically (Matthiessen et al. 1991, Pehkonen and Rantio-Lehtimäki 1995), and allergic cross reactivity is common. The temporal sequence of alder and birch flowering lengthens the period of allergenic exposure for those sensitive to *Betulaceae* pollen. Moreover, exposure to high alder pollen counts may increase the sensitiveness to pollen later on during the season (Emberlin et al. 1997). In their study concerning alder and birch, Jantunen et al. (2012) found a fair correlation between allergy symptoms and pollen counts, but further concluded that the risk of developing symptoms is influenced by the progression of the *Betulaceae*

1 pollen season. Therefore, more accurate predictions of the onset of alder pollen release, by means of
2 modeling, would help the allergy sufferers to manage their symptoms.

3 A number of phenological models have been produced to predict the onset of alder flowering. Some of
4 these are simple temperature sum models, starting the temperature sum accumulation from a fixed day
5 in spring (Linkosalo 2000, Linkosalo et al. 2006). Also more complex models including a chilling submodel
6 have been proposed (Andersen 1991, Jato et al. 2000, Rodríguez-Rajo et al. 2006, 2009, González-
7 Parrado et al. 2006). However, Linkosalo (2000) found that the temperature sum model without the
8 chilling submodel performs better for predicting the start of alder flowering in Finland, and Linkosalo et
9 al. (2008) showed that this applies at least to later-flowering species also when using independent data
10 for model evaluation.

11 The pollen release period of birch was predicted using temperature sum as the driving environmental
12 variable of pollen release in a previous paper (Linkosalo et al. 2010). With the application to provide
13 input for the long range transport model, another version of the model was produced, using also air
14 humidity and wind speed as controls of the pollen release (Sofiev et al. 2013). The latter model is in use
15 of a prediction system for birch long-range pollen transport events (Siljamo et al. 2013). For this study,
16 we used similar model structures than in the two papers mentioned above.

17 The aim of this study was to develop and test a pollen release model for alder. Our model uses only
18 temperature sum as control of the pollen release period. Further we tested if additional environmental
19 variables would improve the prediction potential of the model. We split the data to odd and even years
20 and fitted the model separately to each half. Difference in optimal model parameter values revealed a
21 biennial behaviour in the onset of pollen ripening. We utilised Monte Carlo resampling from a large
22 matrix of parameter values combinations to enhance the calculation efficiency of the Monte Carlo
23 resampling.

24 **Materials and methods**

25 There are two common species of alder in Finland, namely Black Alder (*Alnus glutinosa* (L.) Lam.) and
26 Grey Alder (*Alnus incana* (L.) Moench.). Using historical time series of onset of flowering, Linkosalo
27 (2000) found that in Finland Black Alder starts flowering on average 6 days before Grey Alder. However
28 in the pollen trap data, it is not possible to distinguish between the pollen of the two species.

29 We used alder pollen data counts measured at seven pollen measurement sites (table 1, Fig. 1). The
30 sampling followed the Burkard-spore trap procedure described by Hirst (1952). In Turku, where the
31 flowering starts first of all observations sites, the pollen data is collected throughout the year. On the
32 other sites the collection is started once pollen is observed in the Turku site, and carried on until the
33 pollen season has clearly ended.

34 The traps were located on open rooftops. The alder pollen grains were identified and counted on bi-
35 hourly basis, taking 2 randomized samples per each strip representing a 2 hour time period (Mäkinen
36 1981). The resulting variable was average pollen grain concentration /m³. We studied the pollen counts
37 on a daily basis, and daily data were summed up from the bi-hourly samples for each day.

1 The meteorological data were obtained from the Finnish Meteorological Institute
 2 (<https://en.ilmatieteenlaitos.fi/open-data>). The weather stations were located on average 8 kilometers
 3 from the corresponding pollen trap. Tri-hourly data from meteorological stations closest to the pollen
 4 traps were used and daily averages (or in the case of precipitation, daily sum) were calculated for the
 5 analyses.

6 Boreal wind-pollinated trees typically show quite large inter-annual variation in the amount of pollen
 7 release, and alder is no exception. There are some attempts to model the pollen amounts based on
 8 weather conditions and pollen intensity of previous years (Masaka and Magushi 2001, Ranta et al.
 9 2008), but these models lack prediction power on independent data (Ranta et al. 2008). Therefore we
 10 decided to normalize the pollen amounts for each year, and focus our modeling on the timing of the
 11 pollen release only. For this purpose, the total accumulated pollen amount for each year and site was
 12 calculated, and daily pollen observations were divided with this annual total. Similarly, the pollen model
 13 predicts the daily pollen amounts as fractions of annual total. As the pollen count captures with Burkard
 14 traps is normalized, we used it as proxy for the released pollen, which was then predicted with the
 15 model.

16 The pollen model predicts the ripening of the pollen to depend on a temperature sum, TS , accumulated
 17 from a fixed starting date, t_0 , in spring. Temperature sum is accumulated from the fraction of daily
 18 temperature, T , above a critical temperature threshold, T_{crit} . The cumulative amount of ripened pollen,
 19 P , is modeled to increase as a linear function between two temperature sum thresholds TS_{min} and TS_{max} ,
 20 as was modeled for birch by Linkosalo et al. (2010).

$$21 \quad TS(t) = \sum_{x=t_0}^t \max(T(x) - T_{crit}, 0) \quad (1)$$

$$22 \quad P(t) = \begin{cases} 0, & TS < TS_{min} \\ \frac{TS(t) - TS_{min}}{TS_{max} - TS_{min}}, & TS_{min} \leq TS(t) < TS_{max} \\ 1, & TS \geq TS_{max} \end{cases} \quad (2)$$

23 Our model assumes that the pollen is released as it ripens. The model has 4 parameters, the starting
 24 date t_0 , critical temperature threshold T_{crit} , and the two temperature sum thresholds TS_{min} and TS_{max} .

25 We estimated the model parameters by minimizing the sum of squared errors (SSE) between the model
 26 predictions and measured data. To emphasize the model accuracy in predicting the start and end of the
 27 pollen season, we modified the calculation of SSE with a weight function W , that was 1 in the case both
 28 observed (O) and predicted (P) pollen counts were positive, but had a value of 10 if either predicted or
 29 observed pollen count was zero:

$$30 \quad W(t) = \begin{cases} 1, & P(t) > 0 \text{ and } O(t) > 0 \\ 10, & P(t) = 0 \text{ or } O(t) = 0 \end{cases} \quad (3)$$

$$31 \quad Q(t) = P(t) - O(t) \quad (4)$$

$$32 \quad SSE = \sum(Q(t)^2 * W) \quad (5)$$

1 Parameter estimation of phenological models tends to be a challenge to optimization algorithms, and
2 take a multitude of model evaluations. To reduce the calculation time, to be able to find the parameter
3 set that minimizes the model prediction error, and to be sure that we have reached a global minimum of
4 the SSE, we calculated the model in a large matrix of parameter values, covering the potential range of
5 parameters, and at the same time fine enough to correspond to sufficient accuracy of parameter values.
6 In phenological models, both observations and temperature data come with a time-step of one day, so
7 this was obvious value for the starting day parameter, t_0 . On a typical spring day, the temperature is
8 several degrees above the temperature threshold used in the model, so we concluded that a step of one
9 degree-day will be sufficient for the two temperature-sum thresholds, TS_{min} and TS_{max} . Finally we chose a
10 step of 0.1 °C for the temperature threshold T_{crit} . After calculating the model predictions in the matrix,
11 finding the optimal parameter combination was simply finding the minimum SSE value in the matrix.

12 To evaluate the data dependency of our model parameters, we did a Monte Carlo –resampling of pollen
13 observations, in which each combination of year and sampling site acted as one data point. We picked
14 49 random data points from each subset of observations with resampling, and repeated this 900 times.
15 We then picked the model prediction deviations for the random data points for the whole parameter
16 matrix, summed up the SSE values for all parameters combinations, and found the parameter values
17 that minimized the SSE value for that specific subset on observations. Thus the model parameter
18 estimation for each Monte Carlo sample was done by tallying the model predictions errors for all
19 observations drawn into that sample, over the whole parameter value matrix, and then selecting the
20 parameter combination that resulted in the smallest sum of squared prediction errors. The models and
21 scripts managing the parameter-related data were written in R, and the calculations were done on a
22 Unix mainframe calculation server, using at most 25 parallel cores.

23 We classified the days into 4 classes depending on if the observed and model predicted pollen release
24 were positive or zero. We further classified the days where observations were positive but predictions
25 were zero, or the other way round, to three classes, before, during and after the predicted pollen
26 release period.

27 Preliminary results indicated that the model parameters would have different values for the odd and
28 even years, so we split the pollen data to two subsets and fitted the model to both subsets
29 independently.

30 Results

31 We first fitted the model to all the observed data. Adding the weights as in eq. 3 to 5 improved the
32 prediction accuracy of the starting date of pollen release considerably. Minimizing the SSE without the
33 weights would sum the squared difference of the modeled and observed pollen count for each day.
34 Adding the weights emphasize the binary recognition of presence of pollen, and improved the model
35 considerably. The resulting model gave rather good estimates for the start of the pollen release period,
36 average deviation was -8.3 days (table 2), which is of the same magnitude as with temperature sum
37 models predicting observed onset of flowering (Linkosalo 2000). Negative values indicate that the
38 observed date precedes the predicted. The median prediction error is -5.0 days, indicating that the

1 distribution of the errors is skewed. The mean error for Turku is considerably large and negative, which
2 is probably due to long range transported pollen present in the Turku observations. In Turku the pollen
3 data is collected continuously throughout the year, while on the other sites the collection is only started
4 when the presence of pollen is observed in the Turku site.

5 Similar analysis for the end of the pollen season show much larger deviation of the predicted end of the
6 season from the observed one (table 3). Typically the prediction error of the model is positive, so there
7 are pollen observations after the last predicted pollen release date. The penalty coefficient in the SSE
8 calculation (eq. 3 to 5) tends to set the end of the predicted pollen release period for the first
9 occurrence of consecutive multiple days without observed pollen. We therefore conclude that the
10 observed airborne pollen during the days after the model has predicted the pollen release period to end
11 are likely to be cases of long-range transported pollen from more Northerly locations. The model-
12 predicted pollen season is on average 24.2 days, and the length is consistent throughout the sites on the
13 same year (table 4).

14 On counting the binary pollen event days, the model caught correctly 1860 "event" days, but missed 724
15 days and falsely predicted the pollen release to take place on 1472 days (Table 5a). However, of the
16 1472 "false alarms", a majority, 872 cases occurred during the modeled pollen release period, that is
17 between the predicted starting and ending dates of the pollen season (Table 5b). Therefore it is likely
18 that these dates are such that the air was washed from pollen due to local precipitation or some similar
19 event. In a similar fashion, majority of the "misses" were after the modeled pollen season had ended, so
20 these are likely to be cases of long-range transport events (Table 5b).

21 We split the data to two halves, odd and even years, and used Monte Carlo resampling to produce 900
22 different subsamples of each half of the data. We fitted the model separately to each subsample of the
23 data by finding a set of parameter values that minimize the SSE. We then calculated distributions of the
24 model parameters for each half and over the Monte Carlo samples. The model parameter values for
25 either half of the data were remarkably stable, there were very few Monte Carlo samples where any of
26 the parameter values differed from those values for the majority (fig 2). The optimal parameter values
27 for each half of the data were, however, different (table 6). Especially the starting day parameter value
28 differed considerably for the two data sets, by 11 days (day-of-year 44 vs. 55, for odd and even years).
29 When splitting the data to early and late years, the parameter values for the two subsets were similar
30 (Table 6).

31 The result suggests that alder shows a biennial behavior of the timing of onset of pollen development in
32 spring. When comparing the model parameters, they mostly deviated in the value of the starting date of
33 temperature sum accumulation. There was also a slight difference in the temperature sum threshold for
34 the start of the pollen season, but taking into account the low value of critical temperature, the
35 difference should not make much difference in the timing of the onset of flowering. The other two
36 model parameters had practically similar values for both halves of the data (Table 6).

37 The model was able to reproduce the pollen release days with rather good accuracy, but did not do so
38 well in reproducing the day-to-day variation of the pollen release. Fig. 3 shows an XY plot of the

1 observed vs. predicted pollen release. The figure indicates a rather poor correlation between the two,
2 and also shows how the magnitude of the observed pollen release is threefold to that of modeled.
3 When we compare only the points where both observed and modeled pollen release are positive, there
4 is very little correlation between the two. The model seems to perform better in binary prediction of
5 timing the pollen release than predicting the intensity of the pollen release.

6 The residuals of the model did not show correlation with environmental features such as temperature,
7 air humidity, precipitation or wind speed (results not shown). However, a previous model for birch
8 pollen release used air humidity and wind speed as controls of the release of ripe pollen from the
9 catkins (Soviev et al. 2013). Therefore we also fitted another model version to the observed data, with
10 humidity, expressed as water vapour pressure deficit (VPD), controlling the pollen release. Adding the
11 VPD to the model did not increase the variance explained (results not shown).

12 Model parameter values for the model are given in table 6. It should be noted that the temperature sum
13 threshold for the start of the pollen season is quite low, only 2 to 10 degree days. Combined with the
14 low threshold of effective temperature, $-1.5\text{ }^{\circ}\text{C}$ this means that our model predicts the Alder flowering
15 to start after just a few warm days in the spring, following the onset of temperature sum accumulation
16 on 10th of February.

17 Discussion

18 In this paper we developed a pollen release period model for alder. The model follows the structure that
19 Linkosalo et al. (2010) suggested for birch, where only the accumulating temperature sum controls the
20 pollen release. Additional meteorological features such as air humidity have been used as control of the
21 release of ripe pollen in other models, such as the current version of the birch pollen release model used
22 in the SILAM atmospheric transport model (Sofiev et al. 2013), which proposes that the ripened pollen is
23 stored in the catkins and then released when conditions are favorable. The model structure is also quite
24 similar to the approach is described in Zink et al. (2013) for COSMO-ART model. The birch model in
25 SILAM uses both humidity and wind speed as drivers of the pollen release. When we related the
26 residuals of our temperature sum based model against meteorological features, we found that the
27 correlations were minimal. However for a comparison with the birch pollen model used in SILAM, we
28 still developed a model where air humidity impacts pollen release. This model did not fit observed data
29 any better (as indicated by the model SSE values). We conclude that temperature sum is the main driver
30 of Alder pollen release.

31 The model proved quite accurate on predicting the onset of the pollen release period, the results were
32 of similar precision as models aiming only to predict the start of the pollen season (e.g. Linkosalo 2000,
33 Linkosalo et al. 2006). However, the predictions of the end of the pollen release period seemed less
34 accurate, with typical prediction error of 30 days or even more. We assume that the error in the latter is
35 actually caused by outlying observations of long-range transported pollen in the data, as the model-
36 predicted results for the end of the pollen release and the length of pollen release period are consistent
37 and in good agreement between years and observation sites. We do not know of any consistent and

1 objective means of recognizing the outliers in the pollen trap data, and therefore did not use any outlier-
2 cleaning.

3 Fitting a model to a single data set always poses a risk that the model reflects some specific features of
4 the data set, and cannot therefore be generalized. Thus the use of independent data is proposed.
5 Lacking sufficient amounts of data to use part of it as independent test data, we did a Monte Carlo
6 resampling of the observations to induce variation in the observation data, and studied how this
7 variation impacts the optimal model parameter values. We also split the data to odd and even years to
8 compare if we observe different model behavior on these halves. This test with splitting the data
9 revealed an interesting observation that the Alder shows a biennial pattern in the onset of pollen
10 development, presented in the model as the accumulation of temperature sum, as the value of the
11 starting day parameter is one and half weeks earlier on odd years compared to even years. Our dataset
12 is too short to give conclusive results on the phenomenon or to speculate what environmental features
13 could be driving the difference. Yet when we repeated the calculation splitting the data to two
14 consecutive sections, the feature of model parameters depending on data was totally dissipated,
15 suggesting that indeed there is a difference in the timing of development of Alder pollen between odd
16 and even years. We did not find similar results in earlier publications. Emberlin et al. (2007) found the
17 Alder pollen release *intensity* to have a slight biennial pattern in the UK, but not the timing. Skjoth et al.
18 (2015) claim the biennial variation in the pollen release timing only occurs in Birch, not in Alder. Biennial
19 variation in pollen release intensity and hence acorn production has been observed e.g. in oak (Díaz-
20 Fernández et al. 2004, Otárola et al. 2013) on more Northerly growing sites where annual seed
21 production would be hard for the limited growth resources, but this does not explain why onset of
22 pollen development should show a biennial pattern.

23 Our pollen release model resulted with considerably smaller day-to-day variation of released pollen
24 amounts than was observed in the data, the maximum daily values in observed pollen amounts were
25 four times larger than the model predicted (fig 3). It remains unclear what is the cause for this larger
26 variation in the data, whether it is some environmental feature that could not be captured in a model,
27 or if it is some imminent random feature produced in a trap-collected pollen data. In some stations the
28 main pollen source areas are not evenly located around the trap. In Turku and Vaasa for instance, there
29 is only a short distance to the sea in the southern or western direction, whereas in other directions the
30 forest cover is wider. In these conditions the wind direction may have a major impact on the trapped
31 pollen counts even if the actual pollen release intensity does not change. Also, wind speed is known to
32 affect trapping efficiency. A study on clubmoss spores (which are about the same size as alder pollen
33 grains) showed that a change in wind speed from 1.5 to 9 m/s resulted in approximately 30 % increase in
34 trapping efficiency (Lacey and Venette 1995).

35
36 Even though our model was not able to promptly capture the variation in pollen amounts, it did a good
37 work on capturing the timing of pollen release period. The model fitting emphasized the amount of daily
38 pollen catch, and yet the prediction accuracy of the start of the pollen season was comparable to the
39 results from models aiming only to predict the very start of the season. We conclude that the presented
40 temperature-sum based model works well in predicting the onset of the pollen release period of Alder

1 for Finland. Added features of the air humidity provide no improvement in the accuracy of pollen
2 release. The end of the pollen period is most likely also predicted with similar accuracy, but outliers in
3 the pollen data indicate larger deviation of the model prediction from measured data. The modeled
4 figures of the day-to-day variation in the daily pollen counts are not very predictive, but for the
5 aerobiological forecasting the binary data for presence or absence of airborne pollen is more important
6 anyway. Thus the model can be used to predict the Alder flowering to give in advance a warning of the
7 becoming pollen season. If the model is to be used to provide input for long range transport models,
8 then the parameters probably need to be estimated against a dataset covering a larger geographical
9 (more southerly) area. The biennial behavior of Alder flowering also needs to be further addressed.

10 A number of previous studies of phenological modeling have shown that estimating the model
11 parameters with SSE (or RMSE) minimization, using optimization algorithms, is computer time-
12 consuming. Even worse, the results may vary depending on the data and starting point of the
13 optimization. Our method of calculating the model SSE in a large matrix of parameter values, and using
14 Monte Carlo sampling to produce distributions of the model parameters should provide more robust
15 and reliable results for model parameters. For one thing, calculating the model in parameter matrix
16 ensures that the whole parameter space is covered when looking for the optimum. Further, the
17 parameter distributions give information on how sensitive the model parameters are. And finally
18 calculating the model deviations for each observation into a matrix, and then doing the Monte Carlo
19 simulations by sampling these model prediction deviations, turned out to be more computer-time
20 efficient than the traditional method of using an optimization algorithm repeatedly for each Monte
21 Carlo sample.

1

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3

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1 Table 1: The sites, coordinates and years, where alder pollen was collected with Burkard-type pollen
2 traps.

Site	Years	Latitude	Longitude
Kangasala	2000-2007	61°30'N	24°05' E
Kuopio	2000-2014	62°54'N	27°38' E
Oulu	2000-2012	65°04'N	25°31' E
Rovaniemi	2002-2014	66°33'N	25°44' E
Tampere	2008-2014	61°30'N	23°49' E
Turku	2000-2014	60°32'N	22°28' E
Vaasa	2000-2014	63°06'N	21°37' E

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Table 2. Deviations (days) in the start of the alder pollen season between the observation and prediction with the temperature sum model. The observed season is started with the first pollen captured, with long-range transport excluded (see text for details). Negative sign indicates first observation before model predicted season starts

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	Average
Kangasala	-10.0	-4.0	-35.0	-5.0	-11.0	-2.0	-9.0	-2.0								-9.8
Kuopio	-3.0	-17.0	-9.0	-5.0	-11.0	-1.0	-9.0	5.0	-20.0	-19.0	-9.0	-12.0	-9.0	-5.0	-2.0	-8.4
Oulu	0.0	-3.0	-1.0	0.0	0.0	-1.0	7.0	2.0	-9.0	-2.0	-9.0	10.0	-2.0			-0.6
Rovaniemi			-9.0	7.0	-5.0	-10.0	-5.0	17.0	0.0	17.0	5.0	3.0	-6.0	2.0	-3.0	1.0
Tampere									-7.0	-12.0	-7.0	-13.0	4.0	0.0	4.0	-4.4
Turku	-22.0	-65.0	-44.0	-12.0	-14.0	-1.0	-7.0	-7.0	-26.0	-37.0	-16.0	-24.0	-72.0	-64.0	-23.0	-28.9
Vaasa	-1.0	-5.0	-9.0	0.0	5.0	-1.0	-8.0	0.0	-7.0	-17.0	-9.0	-2.0	5.0	0.0	-1.0	-3.3
Average	-7.2	-18.8	-17.8	-2.5	-6.0	-2.7	-5.2	2.5	-11.5	-11.7	-7.5	-6.3	-13.3	-13.4	-5.0	-8.3

Table 3. Deviations (days) in the end of the alder pollen season between the observation and prediction with the temperature sum model. Observed pollen season may contain long-range transported episodes (see text for details). Negative sign indicates model predictions after the end of observed pollen season.

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	Average
Kangasala	79	39	134	75	125	81	85	64								85.3
Kuopio	38	4	79	10	58	108	143	67	58	59	83	49	83	57	118	67.6
Oulu	25	6	131	99	56	43	104	54	79	26	39	30	16			54.5
Rovaniemi			7	-11	51	-4	17	52	4	0	64	43	14	5	12	19.5
Tampere									29	67	72	43	30	117	55	59.0
Turku	22	1	14	15	25	24	39	26	227	66	198	49	43	31	98	58.5
Vaasa	67	53	134	23	98	79	39	26	55	43	93	59	38	119	82	67.2
Average	46.2	20.6	83.2	35.2	68.8	55.2	71.2	48.2	75.3	43.5	91.5	45.5	37.3	65.8	73.0	57.6

Table 4. The length of the alder pollen season (days), modeled with the temperature sum model.

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	Average
Kangasala	21	21	24	28	21	21	14	27								22.1
Kuopio	23	20	28	35	21	24	15	27	26	11	24	19	20	16	40	23.3
Oulu	21	24	28	40	21	29	16	31	29	15	27	24	24			25.3
Rovaniemi			19	31	21	32	14	35	14	14	30	18	20	21	42	23.9
Tampere									22	20	22	17	33	16	35	23.6
Turku	29	22	24	28	21	15	14	20	41	22	22	20	29	17	30	23.6
Vaasa	25	24	27	31	22	25	14	30	38	22	25	20	38	16	36	26.2
Average	23.8	22.2	25	32.2	21.2	24.3	14.5	28.3	28.3	17.3	25	19.7	27.3	17.2	36.6	24.16

Table 5a. Classification of the binary flowering data. The number of cases where both observation and prediction are zero is not given, as the value is arbitrary, depending on the length of the observation period before and after flowering season.

	Observation > 0	Observation = 0
Model > 0	"hit" 1860	"false alarm" 1472
Model = 0	"miss" 724	"rest of the year"

Table 5b. Classification of the "false alarms" and "misses"

	False alarm	Miss
Total	1472	724
Before predicted flowering	553	59
During predicted flowering	872	100
After predicted flowering	47	565

Table 6. Model parameter values for the model without air humidity coefficient, and number of days of different “events”.

		all	Odd	even	early	Late
Starting date of temperature sum accumulation	Day of the year	46.4	43.93	55.24	46.6	45.5
Critical temperature	°C	-1.30	-1.23	-1.47	-1.39	-1.30
Minimum threshold for pollen ripening	Degree-day	2.32	2.04	10.0	9.7	2.11
Maximum threshold for pollen ripening	Degree-day	187.3	187.8	185.7	185.4	188.2
Model SSE, fitted to all years	(relative)	11.72	17.3	7.01	7.75	15.2

Figure captions

Fig 1. The locations of the pollen measuring sites.

Fig 2. The distribution of the starting day parameter values in the Monte Carlo –resampling, for odd and even years. Average starting date is 43.9 and 55.2 (day-of-year) for odd and even years.

Fig 3. XY-plot of the observed (X-axis) vs. predicted (Y-axis) pollen amounts for the pollen model. Red dots show points where either observed or predicted pollen count is positive, and blue dots require the both to be positive. The number on observations where either one is zero pulls the red regression line to run next to the origin of the graph. For the points where both observed and predicted pollen count is positive, the model poorly reproduces the day-to-day variation in pollen counts.