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Masting by *Betula*-species; applying the resource budget model to north European data sets

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Abstract Masting, the intermittent production of large crops of flowers by a plant population, is a common feature among trees in boreal and temperate forests. The pollen of many broadleaved trees causes allergic diseases, which are major causes of increasing health-care costs in industrialised countries. As the prevalence and severity of allergic diseases are connected with the concentrations of airborne pollen, an universal model predicting the intensity of the coming flowering would be a valuable tool for pollen information services, and ultimately for allergic people and allergologists. We investigated whether a resource budget model created in Japan explains the fluctuations in the annual pollen sums of *Betula*-species in north European data sets (10–12 years at 4 sites, 20 years at 10 sites). Using the shorter data sets, the model explained 76–92% of the annual fluctuations at five study sites. Using the 20-year data set, the percentage for southern Finland was much lower, only 48%, compared with the 85% of the 12-year data set. The annual pollen sums have been higher during the 1990s than in the 1980s, which may explain the ineffectiveness of the model, while applied to the 20-year data set. Our results support the resource budget model: the masting of birch

species is regulated by weather factors together with the system of resource allocation among years. The model can serve pollen information service. However, only the 10 most recent years should be used to avoid interference from trends in changing vegetation and/or climate.

Keywords Allergic pollen · Birch · Masting · Resource allocation · Climate change

Introduction

Masting behaviour, the intermittent production of large crops of flowers or seeds by a plant population, is a common feature among many plant species in boreal and temperate zones (Herrera et al. 1998; Koenig and Knops 2000). The ecological implications of this phenomenon are manifold; besides the recruitment of the plant populations themselves, masting strongly affects the populations of animals using seeds as their major food (Curran and Leighton 2000; Janzen 1971). In addition, resource allocation to reproduction may affect plant growth and interactions between plants and their herbivores (Kaitaniemi et al. 1999; Selås et al. 2001; but see Klemola et al. 2003).

Besides its ecological impact, masting has important but less recognised health-related and economic implications. Symptoms of rhinitis and asthma due to aeroallergens such as tree pollen are major causes of morbidity, loss of productivity and increasing health-care costs in industrialised European countries (Aas et al. 1997; WHO 2003). The overall prevalence of seasonal rhinitis in Europe is approximately 15% and the current asthma prevalence 2.5–10%, with the highest figures among children and adolescents (WHO 2003; Ashe and Weiland 1998). The concentration of pollen grains greatly affects the prevalence and severity of symptoms of allergic diseases (Viander and Koivikko 1978). In years of abundant flowering, the counts of birch pollen grains m^{-3} of air exceed 5,000 over several days, while in low years even 100 grains m^{-3} of air is rarely exceeded. The most im-

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portant allergenic pollen in northern Europe is that of birch (*Betula*) (WHO 2003).

The flowering of birch, like many other economically important and common broadleaved trees with allergic pollen (e.g. *Alnus*, *Fraxinus*, *Quercus*), fluctuates greatly among years (Herrera et al. 1998; Koenig and Knops 2000). A model predicting the intensity of the prospective flowering would be a valuable tool for those responsible for pollen information services and ultimately for allergic individuals and allergologists, as well as for pharmacists and medical companies (Dahl and Strandhede 1996). Information on the expected pollen loads is also needed as input data for source-oriented dispersal models of allergenic pollen (Gálan and Cariñanos 2001). Other professional groups benefitting from such a model would be those working in forestry. The fluctuation of seed set of forest trees has consequences for forest regeneration and commercial seed production especially at northern latitudes and in alpine areas (Leikola et al. 1982; Pukkala 1987).

Many theories have been presented to explain the ultimate and proximate causes of masting (Kelly 1994; Koenig and Ashley 2003). The stress has been on evolutionary explanations. One commonly accepted theory is that of "economies of scale": large reproductive efforts are adaptive in terms of pollination efficiency, seed production and survival, which has favoured the evolution of occasional large efforts (Kelly 1994; Kelly et al. 2001). Also widely accepted is the idea that masting is an adaptive strategy against seed predation. According to the "predation satiation" theory, predators starve in low seed years and are swamped in high years (Kelly 1994).

A number of ideas have been proposed with regard to the proximate mechanisms regulating the extent of flowering. Weather conditions have been suggested to synchronize the masting behaviour of plant populations, even involving different plant species over large geographic areas (Dahl and Strandhede 1996; Kelly 1994). Schaubert et al. (2002) showed that the mast seeding of 17 species of ecologically varied New Zealand plant species is highly synchronized, and that this synchrony is related to summer temperatures during critical periods of floral bud formation and differentiation. They suggest that this could be due to hormonal regulation affecting floral initiation. On the other hand, Knapp et al. (2001) and Satake and Iwasa (2000, 2002) give evidence that pollen limitation and limited pollen dispersal could be behind highly variable but geographically synchronized seed set of wind-pollinated species.

Resource limitation and accumulation, and resource allocation between reproduction, vegetative growth and reserves have been suggested to affect the amount of flowering (Kaitaniemi et al. 1999; Kelly 1994). Isagi et al. (1997) presented a resource budget model which includes flowering costs in terms of seed weight, but in which the revenue of photosynthates is expected to be constant every year. Masaka and Maguchi (2001) developed the idea of a resource budget model further, taking into account annual fluctuations in weather conditions; through their

impact on photosynthesis, these fluctuations result in variation in resource accumulation. Their model, which included both weather variables and resource allocation systems during 2-years prior to the year in question, explained over 94% of observed annual fluctuation in the flowering of *Betula platyphylla* var. *japonica* in Hokkaido, Japan.

Assuming that the proximal causes are universal, we investigated whether the model of Masaka and Maguchi (2001) is able to explain the variation in annual birch pollen sums of six north European long-term (10–20 years) data sets. We also tested the sensitivity of the model to the time-span of the data set, and modelled one 20-year data set in 10-year overlapping segments, to determine whether the results were constant for all segments. A new weather variable was added to the model to increase the predictability. Our ultimate cause was to test whether the model can serve as a practical tool for pollen information services and forestry.

Materials and methods

Data sets

The reproductive investment of birch was determined using the annual sums of average daily birch pollen grain counts in m³ of air at six locations in Finland (Fig. 1, Table 1). The annual amount of pollen dispersed is shown to be proportional to the annual abundance of male flowers, which in turn is positively correlated with the annual female seed crop (Masaka and Maguchi 2001; Sarvas 1952, 1955). Pollen sampling took place at all sites with volumetric spore traps of the Hirst design (Hirst 1952) according to the standardized method for aerobiological sampling throughout Europe (British Aerobiology Federation 1995). Air samples were analysed by counting the pollen grains with a microscope from randomised fields.

Unlike the data used in the original study, our pollen data include pollen of two different birch species; silver birch (*Betula pendula* Roth) and downy birch (*B. pubescens* L.), both of which belong to the same taxonomic section (*Betula alba*) with *B. platyphylla*. In Utsjoki, the dominant tree is mountain birch (*B. pubescens* var. *cerepanovii*), a sub-species of downy birch. To study the synchrony of the flowering of the two birch species, data on the numbers of catkins in permanent plots of silver and downy birches in southwest Finland (4 *B. pendula* plots, 1 *B. pubescens* plot), central southern Finland (1 *B. pendula* plot, 1 *B. pubescens* plot), central Finland (2 *B. pendula* plots, 1 *B. pubescens* plot) and northern Finland (1 *B. pendula* plot, 1 *B. pubescens* plot) during 10 years (1992–2002) were provided by the Finnish Forest Research Institute (Fig. 1). Thirty to fifty selected trees per plot were observed during 1992–2002. The number of male catkins were estimated with binoculars in late autumn or winter, and the trees were classified into six groups according to the abundance of catkins (I, no catkins; II, 1–20; III, 21–200; IV, 201–1,000; V, 1,001–5,000; and VI, over 5,000 catkins per tree). Since the distribution of trees in each abundance class is expected to be even, catkin frequency may be calculated for each plot every year.

Meteorological data (daily mean temperature, sunshine hours, precipitation) for the pollen sampling sites (measured at the nearest airport) were provided by the Finnish Meteorological Institute. Although there is variation among years, the phenological schedule of such events as bud burst and flowering in south and central Finland is consistent with the schedule presented in Masaka and Maguchi (2001). The use of more accurate time periods for the calculation of weather variables might make the model more ef-

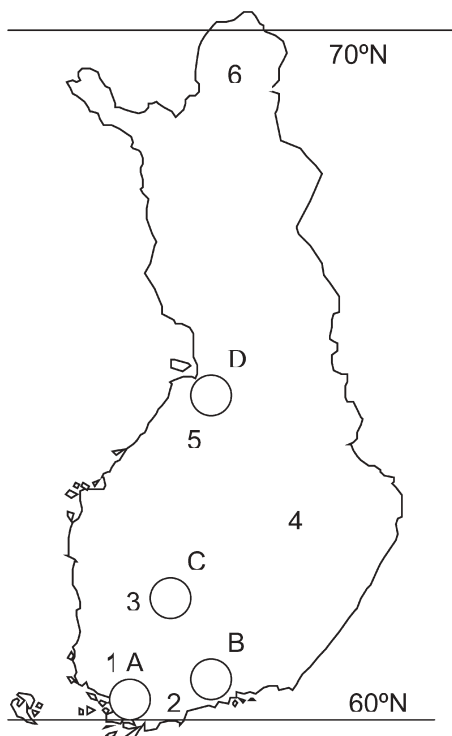


Fig. 1 Pollen sampling sites: 1 Turku; 2 Helsinki; 3 Kangasala; 4 Kuopio; 5 Oulu; and 6 Utsjoki. The locations of permanent plots where the amounts of male catkins were recorded (A) southwest Finland (4 *B. pendula* plots, 1 *B. pubescens* plot), (B) central southern Finland (1 *B. pendula* plot, 1 *B. pubescens* plot), (C) central Finland (2 *B. pendula* plots, 1 *B. pubescens* plot) and (D) northern Finland

fective in Oulu, but phenological data were available only for Utsjoki.

The starting dates of birch pollination have been recorded at the Kevo Subarctic Research Station, Utsjoki, over a 25 year period (Sulkioja and Valanne 1987). Kevo lies in the sub-arctic area, and the quantity of pollen produced by local birches is small. Pollen transported over long distances may in some years account for 50% of the annual pollen sum measured in northern Scandinavia (Hicks et al. 1994). We therefore calculated the annual pollen sum beginning from the date of the observed onset of birch flowering. Similarly, the weather variables (mean temperature and sum of sun hours) were calculated beginning from that date for 2 months onwards.

Analysis

The synchrony of flowering of *B. pendula* and *B. pubescens* was investigated by correlating (with the Pearson correlation) the numbers of catkins in permanent study plots of silver and downy

birch in four locations. The average numbers of catkins per plot were used. If there was more than one plot of one species in one locality, the average numbers of catkins per locality was used. The data were ln-transformed to normalise the distributions.

The equation applied to explain annual fluctuations in flowering was the following (Masaka and Maguchi 2001):

$$X_t = a_0X_{t-1}^{-1} + a_1TSX_{t-1}^{-1} + a_2X_{t-2}X_{t-1}^{-1}$$

where X_t is the amount of pollen dispersed in year t ; a_i ($i=0,1,2$) are regression coefficients; T , mean temperature (°C) between May and June in year $t-1$; S , sum of sunlight hours (h) between May and June in year $t-1$; X_{t-1} or X_{t-2} , amount of pollen dispersed (number of grains cm^{-2} in year $t-1$ or $t-2$). The most significant combinations of variables in the multiple regression analyses were identified using forward stepwise regression.

The amount of flowering and weather variables in the year $t-1$ are included because the inception of the male primordial for the following spring occurs just before bud burst, and male inflorescences begin to develop in early or mid summer (McDonald and Mothersill 1983; McDonald et al. 1984; Masaka and Maguchi 2001). It is assumed that the intensity of flower initiation is controlled by the amount of resource storage at bud burst. The induction of catkin development in early and mid summer is assumed to be controlled by the amount of resources produced through photosynthesis, together with resources allocated to seeding (Masaka and Maguchi 2001).

Preliminary analysis showed that the distribution of residuals in some data sets was not normal. Further, when used in its original form, the model explained only 60–75% of the observed fluctuations in annual pollen sums. To normalise the distributions and to enhance the predictivity of the model, a new variable R , amount of precipitation between 15 July and 15 September in year $t-1$ per X_{t-1}^{-1} , was added. The final model used in this study was

$$X_t = a_0X_{t-1}^{-1} + a_1TSX_{t-1}^{-1} + a_2X_{t-2}X_{t-1}^{-1} + RX_{t-1}^{-1}$$

The amount of precipitation is important for developing catkins, because during late summer anticyclones prevail in Finland and evaporation is high. Plants frequently experience drought stress, which may affect the amount of pollen through effects on catkin growth, mortality and predation (Larcher 2003).

Regression models were calculated for the 1991–2000 pollen data for Turku, Kuopio, Oulu and Utsjoki. For Kangasala, the period used in modelling was 1994–2002 and for Helsinki 1992–2001. Meteorological data from 1990 and pollen data from 1989 and 1990 were used to calculate values for variables for 1991 and 1992 in year $t-1$ (T and S), and in years $t-1$ and $t-2$ (annual pollen sums). For Kangasala, these values were calculated with meteorological and pollen data from 1992 to 1993, and for Helsinki from 1990 and 1991. The regression coefficients and the 2001 pollen data were used to calculate predicted pollen sums for 2001–2002 (for Kangasala these years were included in the model, for Helsinki 2001 was included).

The model was also tested with data sets of 1981–2000 for Turku and Kevo, to observe the sensitivity of the model to the time-span of the data set. The 20-year data from Turku was also analysed in 10-year overlapping segments, to determine whether the results were constant for all segments.

Table 1 Sampling sites and periods

Sampling site	Coordinates	Sampling height, meters above sea level	Period
Turku	60°32'N, 22°28'E	30	1981–2002
Helsinki	60°11'N, 24°54'E	40	1990–2002
Kangasala	61°30'N, 24°05'E	129	1992–2002
Kuopio	62°53'N, 27°38'E	100	1989–2002
Oulu	65°04'N, 25°31'E	25	1989–2002
Utsjoki	69°45'N, 27°01'E	107	1981–2002

Table 2 Final models for different locations using the 10–12-year data sets of forward stepwise multiple regression analysis of amount of pollen dispersed in year t (X_t) on pollen dispersed in year $t-1$, mean monthly temperature, sum of sunlight hours during May

Location	P	SS	R^2	Total F	Rejected variables
Turku	0.0009	7028480279	0.848	19.65	$R_{t-1} X_{t-1}^{-1}$
Helsinki	0.0059	12751821439	0.787	12.06	$X_{t-2} X_{t-1}^{-1}$
Kangasala	0.0018	10373444980	0.924	28.44	
Kuopio	0.0102	4281569403	0.763	9.07	
Oulu	0.0011	5192721399	0.837	18.07	X_{t-1}^{-1}
Kevo	0.0326	279429582	0.561	6.17	$R_{t-1} X_{t-1}^{-1}$

to June in year $t-1$ ($T_{t-1}S_{t-1}$) per X_{t-1}^{-1} , pollen dispersal in year $t-2$ (X_{t-2}) per X_{t-1}^{-1} and amount of precipitation between 15 July and 15 September in year $t-1$ (R_{t-1}) per X_{t-1}^{-1}

Table 3 Final models for Turku and Kevo using the 20-year data sets of forward stepwise multiple regression analysis of amount of pollen dispersed in year t (X_t). For more explanations see Table 2

Variables	P	SS	R^2	Total F	Rejected variables
Turku	0.0068	4876589609	0.477	6.17	$X_{t-2} X_{t-1}^{-1}$
Kevo	0.0005	430779822	0.612	13.60	$X_{t-2} X_{t-1}^{-1}, R_{t-1} X_{t-1}^{-1}$

Table 4 Adjusted R^2 -values for 20-year data set for Turku analysed in 10-year overlapping segments by forward stepwise multiple regression analysis of amount of pollen dispersed in year t (X_t)

82–91	83–92	84–93	85–94	86–95	87–96	88–97	89–98	90–99	91–00	92–01	93–02
0.93	0.89	0.86	0.86	0.46	0.46	0.49	0.49	0.88	0.83	0.91	0.87

Results

Correlation analysis

The numbers of catkins of silver and downy birch correlated statistically significantly in all study locations: the two sites in south Finland (SW Finland $r=0.73$, $p=0.007$, central southern Finland $r=0.80$, $P=0.002$), one site in central Finland $r=0.83$, $P=0.0007$, and one site in northern Finland $r=0.62$, $P=0.03$ (Fig. 1). Correlation analysis indicated that the fluctuations in flowering of the two species were in synchrony in different parts of Finland, and use of data originating from two birch species was thus appropriate.

Regression model

The model explained 76–92% of the annual fluctuations in pollen sums in Turku, Helsinki, Kangasala, Kuopio and Oulu when the 10–12-year data sets were used (Table 2). For Utsjoki the percentage was lower, only 56% (Table 2). When the 20-year data sets were used, the percentage for Utsjoki was approximately the same (61%), but for Turku it was considerably lower, only 48% (Table 3). When the Turku data set was analysed in segments, the adjusted R^2 -values remained fairly constant, between 0.83 and 0.93, with the exception of segments beginning from 1986 to 1989, during which time the values dropped to 0.46–0.49 (Table 4).

Coefficients from the regression models were used to calculate predicted annual pollen sums for 1992–2002.

The expected values generally matched or paralleled the actual values observed in Turku, Helsinki, Kangasala, Kuopio and Oulu, although for a few years there were also considerable differences, especially in Kuopio and Helsinki. The figures for Kangasala and Oulu are shown (Fig. 2a,b). When the coefficients calculated from 1991 to 2000 data were used to predict annual pollen sums for 1983–1990 in Turku, the predictions given by the model were greatly overestimated.

Discussion

Our results support the explanations and results of Masaka and Maguchi (2001): the masting behaviour of birch species seems to be regulated by weather factors together with the system of resource allocation among years. The tested resource budget model explained high percentages of the annual fluctuations in pollen sums at five sampling sites in Finland (Table 2). Only at the northernmost sampling site, Utsjoki, did the model explain the variation less well (Table 2).

The predicted values of pollen sums frequently fitted the observed ones closely or were parallel with them. Especially in Kangasala (Fig. 2a) and Oulu (Fig. 2b), but also in Turku, the predictions can be used as a practical forecasting tool. In Kuopio, there were marked differences between observed and predicted values for 3 years and in Helsinki for 2 years. In Helsinki and Kuopio, the distributions of residuals were not normal because of one outlying data point, that for 1998. Removing this outlier would have normalised the distributions, but we chose to

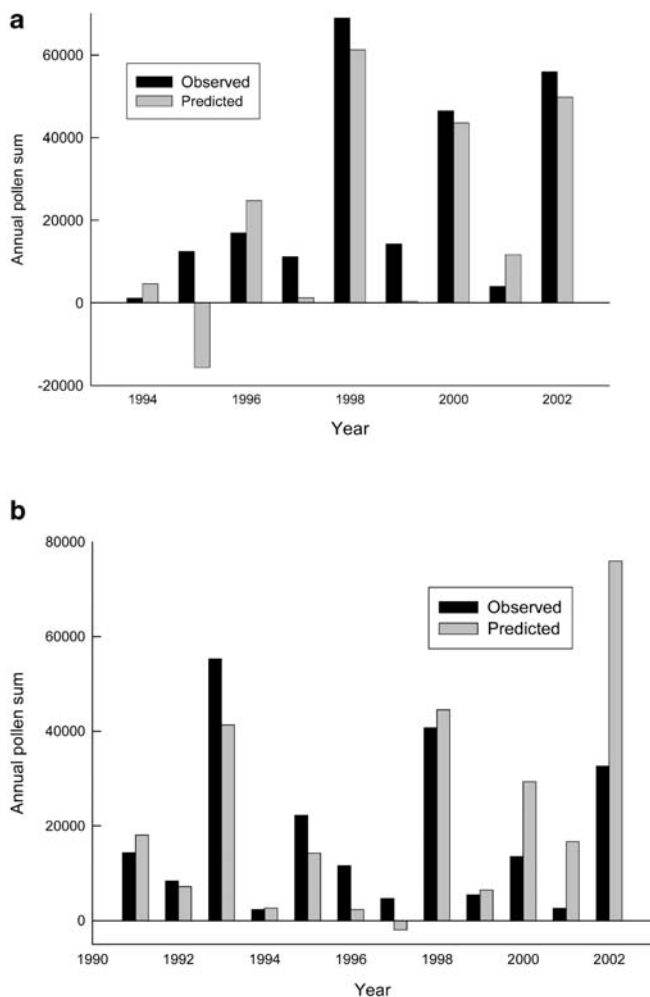


Fig. 2 Observed annual pollen sums (sums of daily averages) and predictions from regressions for **a** Kangasala (1994–2002) and **b** Oulu (1991–2002)

leave them; years of very high or very low pollen production are typical of birch, and are particularly relevant to the motivation of this research. With conifers it has been earlier noted that the possibility of predicting seed production on the basis of weather factors is particularly good with Scots pine (*Pinus sylvestris* L.), providing that the energy loss in trees caused by prolific flowering and seeding does not affect seed production during the following year. In Norway spruce (*Picea abies*), a good flowering year is usually followed by one or several poor flowering years (Leikola et al. 1982).

The northernmost sampling site, Utsjoki, was an intriguing exception. The model explained only 56% of the annual fluctuation in flowering (Table 2). Utsjoki is located in the sub-arctic zone, where climatic conditions are very harsh; the mean temperature for May and June between 1961 and 1990 was 3.2°C and 9.6°C, respectively. The duration of the growing season in Utsjoki is 115 days (days with mean $T > 5^{\circ}\text{C}$, mean value for 1951–1980), while in Oulu it is 148 days and in Helsinki 172 days (Finnish Meteorological Institute 2002). The annual pol-

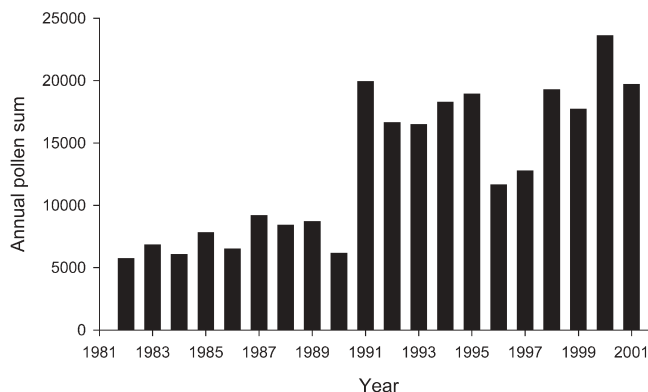


Fig. 3 Five-year moving average of annual pollen sums in Turku (1982–2001)

len sums are lowered by nearly an order of magnitude compared to southern Finland, and successive years with very low pollen production often occur (Finnish Aerobiology Unit 2002). Because of this, resource allocation to flowering may not be significant, and the model is not effective in extreme climatic conditions. Pukkala (1987) obtained similar results for Scots pine and Norway spruce: the prediction models of seed crops for Lapland and northern Finland were less reliable than the models for the rest of Finland.

Testing the model with both the 12-year and the 20-year data sets for Turku indicated that the time-span of the data set greatly affected the power of the model, the 12-year data set giving more effective predictions. In addition, when the Turku data were analysed in segments, the adjusted R^2 -values dropped sharply when the segments beginning from 1986 to 1989 were analysed (Table 4). The annual pollen sums have increased in Turku towards the end of the millennium (Fig. 3). Underlying the increasing pollen loads may be extraneous factors, such as changing vegetation and/or succession of birch forests or a trend towards a warmer climate. The trend of rising pollen loads in Turku goes inside with warm and early springs, and earlier onsets of birch pollen seasons (Emberlin et al. 2002; Menzel and Fabian 1999). In northern latitudes climate change may increase pollen production through increased basic production.

Our results suggest that the resource budget model is not suitable for long data sets if there is some long-term trend in environmental conditions affecting the amount of flowering. For the purpose of forecasting the coming season of allergenic pollen and seed set, only the 10 most recent years should be used.

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