

Predicting the intensity of the birch pollen season

Åslög Dahl*, Sven-Olov Strandhede

Department of Systematic Botany, Carl Skottsbergs gata 22B, S-413 19 Gothenburg, Sweden

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Abstract

We present a model for the prediction of the magnitude of *Betula* flowering and pollen dispersal which may be used in the management of birch pollinosis and in the planning of clinical trials. The pollen sum during the flowering season is regressed on the temperature sum from May 1st to July 20th during the initiation year, the pollen sum of the initiation year, and the temperature sum during the main pollen season in the flowering year. We suggest that the fluctuating flowering pattern in *Betula alba*-species is primarily determined by the availability of assimilation products during inflorescence initiation and development during the spring one year before anthesis. When inflorescences, which are initiated during the previous year, elongate in the beginning of anthesis, they act as strong sinks to stored carbohydrates, and thus compete with developing leaves and shoots. The result is an initially reduced photosynthetic capacity in years with intense flowering, and a limited potential for the initiation of new inflorescences for the following year. The ambient temperature during catkin initiation affects assimilation efficiency and is a determinant of about equal importance to flowering intensity as is the magnitude of the flowering in the initiation year. The amount of pollen dispersed is also dependent on the weather during anthesis, which is not possible to predict until about one month in advance. The two other independent variables are available during the previous summer, making it possible to give a sufficiently valid prediction to allergologists about the magnitude of the next birch pollen season, according to its botanical determinants. We suggest that the varying reproductive output in *Betula alba* should not be described as true masting. A more parsimonious explanation to the flowering pattern is that an individual continually maximizes reproductive effort, according to what is possible, but that reproduction is often constrained by the environment.

Keywords: *Betula* L.; Mast flowering; Prediction model; Pollen season; Pollinosis; Aerobiology

1. Introduction

Pollen counts show that there is great variation among years in the flowering of *Betula* in southern Scandinavia (Fig. 1). A method of predicting the magnitude of the next flowering season would be of great value as a planning instrument to allergologists and pharmacologists. Periodic and synchronous flowering, resulting in alternate bearing, is well known in fruit cultivation, and is also reported from studies of several natural populations of deciduous and coniferous trees (Toumey and Korstian, 1937; Baldwin, 1942; Sharp and

Sprague, 1967; Sork et al., 1993; Koenig et al., 1994). In a few species, the distribution of reproductive output among years is bimodal, with or without overlap between the tails, e.g. in some monocarps, such as bamboos, and in a number of oaks (Kelly, 1994). In others, e.g. *Betula alba*, reproductive output varies more continually among years. The hypotheses to explain the oscillating behaviour have been in two categories: those that explain the variation of reproductive output as a feature favoured by natural selection, and those that claim that the variation merely mirrors varying resources in the environment.

In the first category of hypotheses, varying reproductive effort is claimed to be due to the presence of an inherent ability to 'switch' allocation from vegetative

* Corresponding author. Tel.: +46 31 7732664; +46 31 7732667; fax: +46 31 7732677; e-mail: aslog.dahl@systbot.gu.se.

growth to reproduction (Norton and Kelly, 1988; Sork et al., 1993; Kelly, 1994), or to the ability to accumulate resources over years to be used in a large reproductive effort (Smith et al., 1990). Only when the presence of such mechanisms is at hand, the term 'masting', which formerly has been assigned to variation in reproductive output in general, should be used (Kelly, 1994). Fitness is then supposed to be enhanced by exaggerated or emphasized variation in reproductive output in certain years. Selection would favour those individuals that accentuated their response to variable weather conditions. In wind-pollinated species, such as *Betula alba*, masting may be advantageous because of a proportional increase in fertilization and seed set due to high pollen concentrations during years of intense flowering (Nilsson and Wästljung, 1987; Norton and Kelly, 1988; Smith et al., 1990). The predator satiation hypothesis (Silvertown, 1980; Ims, 1990) predicts that individuals should mast synchronously, since this maximizes the probability of swamping predators in mast years. The presumed evolutionary advantage of both theories is dependent on synchronous behaviour among conspecifics, which Silvertown (1980) suggested may be induced by similar reactions to some weather cue. Other theories have been advanced, but with less experimental support (Kelly, 1994) or less potential relevance to the present investigation.

Authors forwarding hypotheses belonging to the second category do not describe variation in flowering and seed output in evolutionary terms, but claim that it is a simple consequence of variation in climate conditions (Toumey and Korstian, 1937; Baldwin, 1942; Baker, 1950; Sharp and Sprague, 1967; Lavee, 1989). Lavee (1989) suggested that a year with favourable climate would trigger a rich fruit set, and give a simple oscillation effect which starts by an occasional small difference in yield and then amplifies annually, eventually synchronizing the fruiting habit for an orchard, a region or even a country. If variation is just a passive response to environment, and there is no inherent switching mechanism in the tree, or no resource accumulation over years, it is, by definition, not a question of true masting (Kelly, 1994).

We suggest that variation itself is not necessarily the result or the target of selection. A more parsimonious explanation to variable reproductive output is that an individual may continually maximize reproductive effort, according to what is possible, but that reproduction is often constrained by the environment. Hence, adaptation to the environment is not, and can never be, optimal. Before postulating that varying reproductive output per se in a certain species has adaptive significance, it is important to evaluate the extent of environmental influence, and also to investigate the nature of the inherent characteristics that influence the observed variation among years.

Birches are among the most common deciduous tree species in southern Scandinavia, and birch pollen is one of the major hay fever provokers in the area. The development of models to predict the magnitude of the coming pollen season is thus of great interest in the planning of treatment of hay fever patients and of the planning of clinical trials. In this investigation, we determine the importance of climate and of reproductive effort in dictating the flowering pattern in the Swedish species of the *Betula alba*-complex, by the use of multiple regression.

2. Materials and methods

2.1. Study species

Three species of *Betula* occur in southern Scandinavia, *B. nana*, a rare, low shrub of no importance with regard to regional pollen dispersal, and the two trees *B. pendula* and *B. pubescens*, both belonging to the circum-polar *B. alba*-complex. They differ in chromosome numbers and, although non-chromosomal sterility barriers exist between the species, they sometimes form triploid hybrids (Furrow, 1990 and references therein).

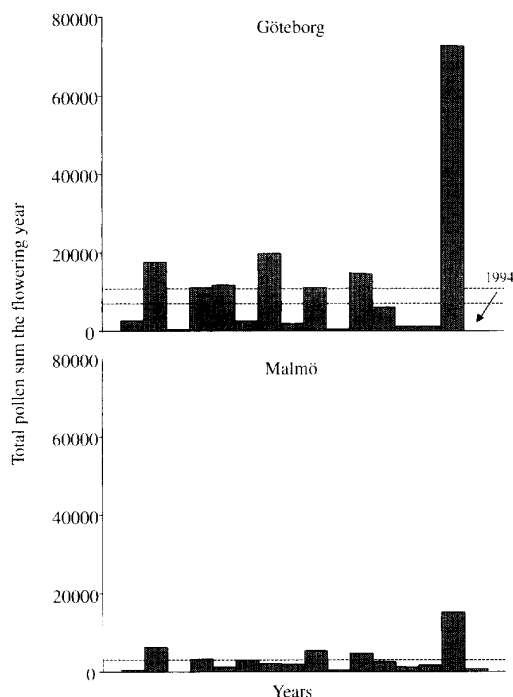


Fig. 1. Total annual sums (pollen m⁻³) of *Betula* pollen from the years 1979–1994 in Gothenburg and Malmö. The horizontal bars indicate the average of all seasons; the lower horizontal bar in the Gothenburg figure indicates the average when the extreme year of 1993 is excluded.

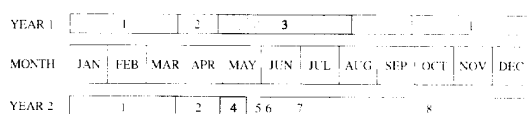


Fig. 2. Phenology of development and of reproductive events in *Betula alba*: 1, Winter dormancy; 2, Heat accumulation; 3, Initiation and growth of male catkins until the formation of microspores; 4, Elongation of male catkins and flowering; 5, Pollen tube growth and megagametophyte differentiation; 6, Fertilization; 7, Seed maturation; 8, Seed dispersal. (Data from Caesar and Macdonald, 1983a,b, 1984; Macdonald and Mothersill, 1983; Macdonald et al., 1984; Andersen, 1991; Dahl and Fredrikson, in press).

B. pubescens is more common in moist habitats. Birches produce large quantities of small, winged, wind-dispersed nuts, and are efficient colonists of disturbed ground.

Betula alba-species are sympodial, monoecious trees. The organogenesis and growth of buds, shoots and inflorescences of *B. papyrifera*, closely related to *B. pubescens*, have been thoroughly investigated (Caesar and Macdonald, 1983a,b, 1984; Macdonald and Mothersill, 1983; Macdonald et al., 1984). The growth pattern of *B. papyrifera* is characteristic of the entire species-complex of *B. alba* and thus also of the species of interest in the present study. Initiation of male inflorescences takes place just before bud burst one year before flowering, whereas the initiation of female ones is slightly later (Caesar and Macdonald, 1983a,b; Fig. 2). At the end of June or in the beginning of July, the male catkins are visible to the naked eye, and at the onset of winter rest in autumn, they are fully developed but are still short and dense. They are naked and exposed during the winter. The pollen grains survive the winter as microspores (Dunbar and Rowley, 1984). The onset of the male gametophyte development takes place during early spring, and in southern Sweden, the pollen is shed in late April and May. In the following text, we will refer to the two different years as 'the initiation year' and 'the flowering year', respectively.

2.2. The effect of fruits upon initiation of male catkins

In the beginning of August 1992, 30–50 arbitrarily chosen long shoots from each of 14 trees of *Betula pendula* were cut, in order to test the effect of the presence of fruit upon the development of male catkins (Table 1). The shoots were cut at the easily detected line of demarcation to the wood formed during the previous year. The presence and the number of initiated male catkins and mature fruit catkins were counted in each one, and the male catkins were dried at 70°C and weighed.

2.3. Heat accumulation

The amount of energy available to a tree during a certain period can be estimated by the Growing Degree Hour (GDH) function (Richardson and Anderson, 1986). The hourly temperatures used for the calculations were estimated by the method of Linvill (1990), from 24-h daily maximum and minimum temperatures from each of the cities where the pollen traps were situated (Swedish Meteorological and Hydrological Institute, 1978–1994). The GDH function was found to be applicable, e.g. on the relationship between temperature and different vital processes in many temperate fruit trees (Richardson and Anderson, 1986). It was also tested for heat accumulation from the end of winter rest to flowering in *Betula* (Andersen, 1991). According to this algorithm, GDH accumulation (i.e. the processes governing growth and development) is regarded as optimal at 25°C and decreases to zero at 2°C and 36°C, respectively. We found empirically that the most accurate predictions of flowering intensity were made when we calculated temperature sums from May 1st to July 20th, during the initiation year, i.e. during the entire period of catkin development, and from a period of 2 weeks during the flowering year, starting with the first day of the main pollen period. As is the custom in Scandinavia, the main pollen period is defined as beginning at the day when the sum of registered airborne pollen grains per cubic meter air reaches 5% of the total amount that year.

2.4. Pollen counts

Pollen counts have been measured in Gothenburg and Malmö since 1975, with Burkard Seven-Day Recording Volumetric Spore Traps. The city of Malmö (55°33'N, 13°0'E) and the area of Gothenburg (57°44'N, 11°48'E) have a suboceanic temperate climate. The difference in the total amounts of birch pollen between the two areas is at least partly due to the fact that Malmö lies in an area dominated by agricultural land, whereas Gothenburg is mainly surrounded by woods (except for the sea about 20 km W of the pollen registration site). The year 1979 was chosen as the starting point to the present study. The number of pollen grains was expressed as the sum of average number per cubic meter of air for 24-h periods during the anthesis in a certain year. The number of long distance transported pollen grains known to be registered before the start of the local flowering period (Hjelmroos, 1991) was excluded from the data. The counts represent pollen from both *Betula pubescens* and *B. pendula*.

Table 1

Two-way factorial ANOVA table on the effect of adjacent infructescences on male catkin weight in *Betula pendula*

	DF	SS	MS	F-value
Fructiferous and non-fructiferous shoots	1	0.00022	0.00022	0.259 ns
Trees	2	0.071	0.035	41.835***
Fructiferous and non-fructiferous shoots* Trees	2	0.001	0.00037	0.442 ns
Residual	108	0.091	0.001	

Comparisons were made among catkins developing in fructiferous and non-fructiferous 1-year-old shoots and among different trees. The analysis was performed on square root transformed data.

*** $P < 0.001$; ns, non-significant.

Table 2

The result of a multiple regression of the total annual sum of registered airborne *Betula* pollen in Gothenburg during 1979–1994 regressed on three different variables: (1) heat accumulation (GDH) from 1 May–20 July and (2) total pollen sum during the inception year, when the male catkins are initiated, and (3) heat accumulation (GDH) during the main pollen season in the flowering year

	Adjusted R^2	B-coefficient	F-value, regression ANOVA	t-value
Sqrt of total pollen sum (dependent during the flowering year vs. all three independents)	0.835		24.559***	
Dependent vs. heat accumulation during 1 May–20 July the inception year		0.660		5.692***
Dependent vs. sqrt of pollen sum during the inception year		–0.461		–3.830***
Dependent vs. heat accumulation during the main pollen season in the flowering year		0.013		3.068*

The pollen sums were square root transformed.

* $P < 0.05$.

*** $P < 0.001$.

2.5. Statistical analyses

Using multiple regression, the total amount of birch pollen registered during one flowering season (the dependent variable) was regressed on the temperature sum from May 1st to July 20th during the initiation year, the pollen sum of the initiation year, and the heat accumulation during the main pollen season of the flowering year (the independent variables). In Tables 2 and 3, the F - and P -values in the uppermost row give the result of an ANOVA for the regression equation. The B-coefficients represent the independent contributions of each independent variable to the prediction of the dependent variable, and the t -values and their adjacent P -values show the statistical significance of these contributions. The results of multiple regression analyses with the exclusion of the third independent variable, i.e. the temperature sum during the main pollen season in the flowering year, are given in Tables 4 and 5.

In all statistical tests performed, P -values < 0.05 were considered to be statistically significant.

3. Results

We did not find any negative relationship between the proportions of initiated male catkins (for next

year's flowering) and of infructescences in the samples from the 11 *Betula pendula* trees (Fig. 3) nor any significant difference in August between the weight of catkins initiated adjacent to fruits and the weight of catkins of non-fruited shoots (Table 1).

The regression model explained 83.5% of the variance in annual *Betula* pollen sums in Gothenburg ($P < 0.0001$), and in Malmö, 78.5% ($P = 0.005$). All three independent variables had significant effects on the pollen sum (Tables 2 and 3), although their relative importance varied. The two temperature sums made positive contributions, whereas the pollen output the initiation year had a negative effect (Tables 2 and 3, Fig. 4). A scatter diagram of the real pollen sums plotted against values fitted to the regression equation shows good concordance (Fig. 5). When the data from the extreme pollen year 1993 were excluded, the regression model explained 61.2% in Gothenburg ($P = 0.0087$). In that case, the effect of the heat accumulation during the main pollen season was non-significant (Fig. 5).

When the effect of the temperature accumulation during the main pollen season in the flowering year was excluded, the model explained 72% ($P < 0.0002$) of the variance in Gothenburg and 53.1% ($P = 0.0041$) in Malmö (Tables 4 and 5). In both these cases, the relative contribution of heat accumulation during catkin initiation and development was slightly larger

Table 3

The result of a multiple regression of the total annual sum of registered airborne *Betula* pollen in Malmö during 1979–1994 regressed on three different variables: (1) heat accumulation (GDH) from 1 May–20 July and (2) total pollen sum during the preceding year, when the male catkins are initiated, and (3) heat accumulation (GDH) during the main pollen season in the flowering year

	Adjusted R^2	B-coefficient	F-value, regression ANOVA	t-value
Sqrt of total pollen sum during the flowering year vs. all three independents	0.785		0.134***	
Dependent vs. heat accumulation during 1 May–20 July the inception year		0.395		2.777*
Dependent vs. sqrt of pollen sum during the inception year		–0.702		–4.836**
Dependent vs. heat accumulation during the main pollen season in the flowering year		0.400		2.770*

The pollen sums were square root transformed.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 4

The result of a multiple regression of the total annual sum of registered airborne *Betula* pollen in Gothenburg during 1979–1994 regressed on two different variables: (1) heat accumulation (GDH) from 1 May–20 July and (2) total pollen sum during the preceding year, when the male catkins are initiated

	Adjusted R^2	B-coefficient	F-value, regression ANOVA	t-value
Sqrt of total pollen sum (dependent) during the flowering year vs. both independents	0.719		18.889***	
Dependent vs. heat accumulation during 1 May–20 July the inception year		0.679		4.494***
Dependent vs. sqrt of pollen sum during the inception year		–0.360		–2.385*

The pollen sums were square root transformed.

* $P < 0.05$.

*** $P < 0.001$.

than that of the annual pollen sum during the initiation year.

4. Discussion

Reproductive output may be limited by the amount of available assimilation products, and a competition among different functions is plausible. The presence of fruit is often suggested to be the dominant factor governing among-year variation in flowering. The bearing year of an apple tree can be changed if the crop is removed early enough (Davis, 1957). The developing fruits may act as 'sinks' for resources (Binnie and Clifford, 1981; Chapman and Sajadi, 1981; Sage, 1986). The strength of a sink appears to be determined by its metabolic activity, which in turn is related to the production of phytohormones. The phytohormones produced by the developing fruits may also actively inhibit the induction or differentiation of new flowers (Lee, 1988 and references therein).

We claim that the fluctuations in the magnitude of flowering in *Betula* are not due to competition or antagonism among catkins and fruits. Catkin initiation

is already in an advanced stage when fruit development begins (Fig. 2). In the North American *Betula papyrifera*, initiation of the new male catkins is shown to occur immediately after winter dormancy, even prior to bud burst in the spring (Macdonald et al., 1984). In southern Sweden, birch usually comes into leaf around the turn of April to May, whereas fertilization takes place in June (Dahl and Fredrikson, in press). After initiation, the new terminal male inflorescence develops rapidly and concurrently with the extension of shoot internodes, and it is visible to the naked eye towards the end of June or, in cold summers, in the middle of July in southern Sweden. Hence, the absence in our results of a relationship between number and weight of initiated catkins and the presence of maturing fruits in long shoots is to be expected.

The presence of inflorescences, formed during the previous year, obviously executes a constraint upon foliage development and thus upon the overall photosynthetic capacity of the tree during the flowering year. Leaf areas are generally smaller and leaves more narrow in reproductive shoots compared to those of vegetative ones. Furthermore, the number of flushing long shoots is lower in flowering, compared to nonflowering,

Table 5

The result of a multiple regression of the total annual sum of registered airborne *Betula* pollen in Malmö during 1979–1994 regressed on two different variables: (1) heat accumulation (GDH) from 1 May–20 July and (2) total pollen sum during the preceding year, when the male catkins are initiated

	Adjusted R^2	B-coefficient	F-value, regression ANOVA	t-value
Sqrt of total pollen sum (dependent) during the flowering year vs. both independents	0.531		8.914**	
Dependent vs. heat accumulation during 1 May–20 July the inception year		0.540		2.928*
Dependent vs. sqrt of pollen sum during the inception year		–0.488		–2.645*

The pollen sums were square root transformed.

* $P < 0.05$.

** $P < 0.01$.

1-year-old long shoots (as also reported for *B. papyrifera* by Caesar and Macdonald (1984)), and thus also the possible sites for late leaves are fewer. The magnitude of the limitation depends on the number of inflorescences. In the extreme year of 1993, the contrast between the sparse, dwarfed leaves and the abundant male catkins in flower was striking in birches in west Sweden (Fig. 6). Many trees appeared to be almost dying. A similar situation was reported by Gross (1972). According to him, the flowering and fruit-set of *Betula alleghaniensis* and *B. papyrifera* were so intense in 1967 that foliage was often dwarfed, and even entirely missing in the heavily seeded portions of the crown. Terminal growth and bud production were inversely related to the amount of flowering.

When the inflorescences initiated during the previous year elongate prior to anthesis, they probably act as strong sinks to stored photosynthates (Caesar and Macdonald, 1984). Considerable amounts of assimilates are necessary for internode expansion (Kozłowski, 1963). Hence, there are less carbohydrates available for leaf area expansion and shoot elongation (Fig. 7). The result will be a further shortage of assimilation prod-

ucts, which negatively affects the development of the new catkin primordia. The following year there will be only few catkins in flower, and their combined demands on the available resources are small. More assimilates will be available to leaves and to initiation of new catkins. The resulting pattern will be one of oscillation among years with regard to flowering intensity (Fig. 7).

The limitations to reproductive effort are also of morphological nature, due to the growth pattern of birches: the long shoot carrying terminal male inflores-

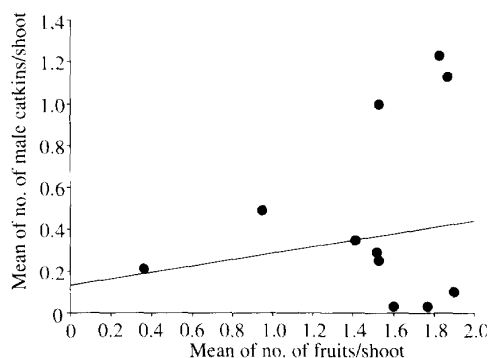


Fig. 3. The mean number of newly initiated catkins per 1-year-old shoot from 11 trees of *Betula pendula* in Gothenburg versus the mean number of infructescences in the same shoots. ($r = 0.319$, $P = 0.7497$, ns, Spearman Rank Correlation Test).

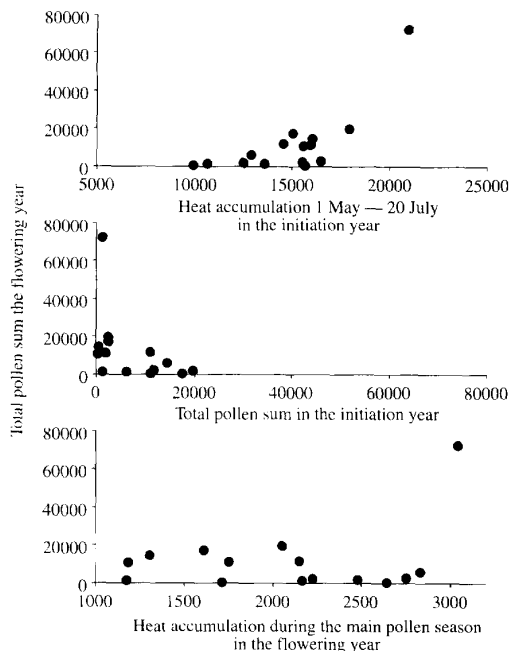


Fig. 4. The relationship of annual sums of registered airborne *Betula* pollen in Gothenburg during the period 1979–1994 and (a) heat accumulation (GDH) from 1 May–20 July and (b) total pollen sum during the preceding year, when the male catkins are initiated, and (c) heat accumulation (GDH) during the main pollen season in the flowering year.

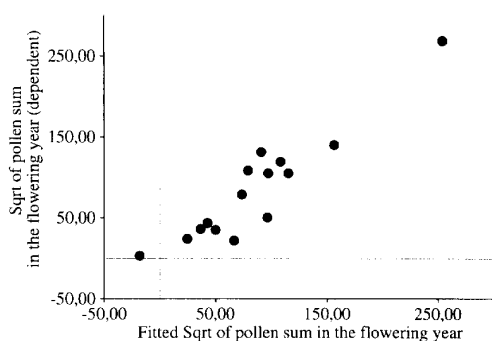


Fig. 5. The result of a multiple regression of the annual sum of registered airborne *Betula* pollen in Gothenburg during the period 1979–1994 and (1) heat accumulation (GDH) from 1 May–20 July and (2) total pollen sum during the preceding year, when the male catkins are initiated, and (3) heat accumulation (GDH) during the main pollen season in the flowering year. True values ('dependent') are plotted against values fitted to the regression equation. The analysis was performed on square root transformed data.

cences has determinate growth. As a consequence, the number of potential sites for initiation of new shoots, in which new inflorescences might be initiated, are restricted, as is also observed by Caesar and Macdonald (1983a, 1984) and Macdonald et al. (1984).

The amplitude of the oscillation is to a large degree determined by the influence of weather upon the amount of carbohydrates, since temperature and the amount of available light have an effect on assimilation efficiency. According to our results, weather during the initiation and growth of new inflorescences is at least as important as a determinant of the magnitude of reproductive effort as is the magnitude of flowering during the initiation year. Warm weather during catkin initiation does not, however, compensate for an extreme flowering the same year (e.g. 1980–1981), but a year with a moderately rich flowering (e.g. 1982) may be followed by another one (1983), if late spring and early summer are sunny and warm enough (Fig. 1). It may be suspected that the result of the statistical analysis is mainly due to the extreme pollen sum of 1993 in Gothenburg. However, the regression ANOVA is still statistically significant when 1993 is excluded, and the true values ('dependent') and those fitted to the regression equation (Fig. 5) are still in good concordance. Already in 1992, we were able to use the model to predict that the pollen sum in 1993 would be of an extraordinary magnitude. The exceptionally heavy flowering in the year of 1993 in Gothenburg (with a 24-h maximum of 13 510 pollen grains/m³ and a total sum of 72 606 pollen grains/m³) was due to the combined effect of an insignificant flowering and a very warm spring in 1992. The spring and summer of 1993 were cold and rainy in southern Sweden, and in the following year 1994, the amounts of birch pollen were almost negligible there.

Kelly (1994) discussed different explanations to variation in reproductive output and suggested that the term 'masting' should be used only to denote the presence of a mechanism that diverts resources from vegetative growth to reproduction, or when resources are accumulated over several years to be used in a large reproductive effort. The two hypotheses which have been suggested as favouring such mechanisms and which have the most experimental support (Kelly, 1994) are 'the predator satiation hypothesis' and 'the wind pollination hypothesis'. Norton and Kelly (1988) suggested that predator satiation should select strongly against reproduction in successive years, since the high predator levels following the first year would lead to heavy seed losses in the following year. Hence, the predator satiation hypothesis is not applicable to *Betula alba*, since variation in reproductive output is continuous and a year of moderately rich flowering may follow upon another (Fig. 1). But Smith et al. (1990) present a model that demonstrates under what circumstances the masting behaviour may increase the effectiveness of wind pollination. The model is based upon a number of assumptions, of which at least three hold true for *Betula*-species: they grow in habitats with low species diversity, their male and female reproductive effort vary in concert (Sarvas, 1952; personal observation) and their ovules are situated in expensive strobili which develop before fertilization. Also, pollination success clearly is related to pollen concentration (Sarvas, 1952; personal observation). Under these circumstances, it is favourable to develop a strategy that maximizes pollen concentration since the gain that may follow the expenditure is likely to increase proportionally to the effort. It is implied in the model of Smith et al. (1990) that saving resources for sparse, but intense, events is more efficient than to swamp them uniformly over years, to get only middling results.

But saving resources may also be a risk, since for any individual, life-length is unpredictable. In a species for which life-expectancy in general is relatively short, such as is the case for *Betula alba*-species, and which belongs to early successional stages, every spring may be the last one for a particular tree. In a comparison among gymnosperm and angiosperm trees belonging to different orders and families, Waller (1979) found that slow to mature, long-lived and large-seeded trees, as well as trees of late succession, most often were engaged in masting. There are other hazards with intermittent reproduction for a wind-pollinated tree: when the tree finally spends its resources, weather may spoil the possibilities for efficient pollen dispersal. The damage is greater if there is a long delay until the next opportunity; and even more so to a short-lived tree.

We do not believe that the flowering pattern in *Betula alba*-species should be defined as true masting according to the definition of Kelly (1994). Favourable



Fig. 6. *Betula alba* in SW Sweden. (a) a branch of the tree almost without catkins but with well-developed foliage; and (b) a branch of the tree with abundant flowering and dwarfed foliage.

weather has been described as a cue to trigger intensified reproduction in masting species. In *Betula*, the response to climate appears to be a passive one, and not to be an actual switch that governs resources from vegetative growth to reproduction. We believe that vital processes simply are slower at low temperatures, probably due to slow enzymatic activities. A possible way to continue the exploration of causes for varying reproductive effort would be to study populations of the same species subject to different climatic regimes, or to see what happens if there is a sequence of favourable years. Even if the presence of inflorescences appears to impede the development of a foliage, there is so far no evidence that the strength of this action is disproportionately increased in certain years. The number of

inflorescences appears to be the important factor, as indicated by the linear relationship in the regression analyses.

Sork et al. (1993) claim that an inverse relationship between seed crop size and prior seed production, and the presence of endogenous and unique rhythms of flowering and seeding in different species, would be strong evidence supporting the hypothesis that varying reproductive effort is an evolved character. We do not believe that this is an obvious inference either from the mere presence of such a correlation, or from theoretical models on the presumptive advantages of masting. It is important to distinguish the forces responsible for the origin of character states from those responsible for their maintenance in contemporary populations: all properties in a species must not necessarily be the consequence of extant selection pressures, and all must not necessarily be optimal during the present circumstances. Fertilization efficiency is increased by more efficient cross pollination at high pollen concentrations in *Betula* (Sarvas, 1952; Nilsson and Wästljung, 1987; Norton and Kelly, 1988; Smith et al., 1990). But we do believe that the differences in reproductive success among years are the consequences, rather than the ultimate causes of the flowering pattern. We suggest that each birch tree constantly maximizes reproductive effort, according to its capacity, but is impeded by unfavourable weather in certain years. There is no contradiction between this theory and the apparent advantage of high pollen concentrations to fertilization.

The third independent factor in the regression, the temperature during the main pollen season, reflects the efficiency of pollen dispersal and thus also the probability of pollinosis. We have used heat accumulation in the model, since low temperatures in spring are often associated with high humidity and rainy weather in NW Europe. In 1991, for example we expected a moderate pollen output, but because of the chilly and rainy weather, the pollen sum registered in Gothenburg was

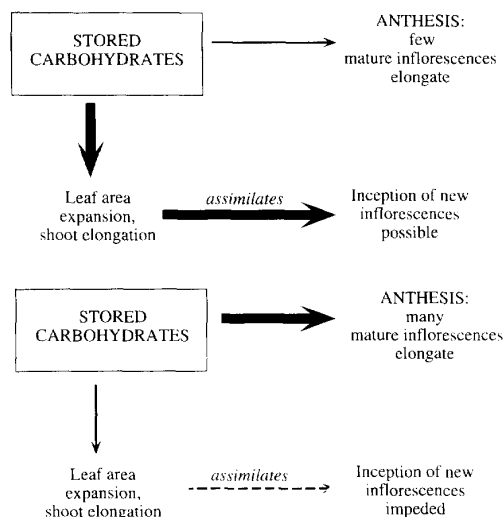


Fig. 7. The postulated relationship between allocation of carbohydrates during the period of inflorescence initiation in the *Betula alba*-complex, and the magnitude of flowering during the following year.

much lower than anticipated. Only 1135 GDH were accumulated during the main pollen season, as compared to the mean of 2070 GDH.

It is not possible to predict the temperature realized during the main pollen season more than about one month in advance. The two other independent variables are available during the previous summer, and they are sufficient to give a maximum value for the magnitude of the coming birch pollen season (Tables 2–5). It is generally not necessary to be more accurate than to tell if the airborne pollen amounts will be 'around average', 'less than average', 'more than average', or 'much over average'. It is also possible to make an iterative test with different amounts of accumulated GDH:s (e.g. the minimum value, the average value and the maximum value from the 16 registered main pollen seasons) to get a range of possible values.

A difficulty in the prediction of the reproductive output of a wind-pollinated species in a certain region is the fact that part of the registered pollen may be derived from sources far from the local populations (Tyldesley, 1973a,b; Hjelmroos, 1991). It is not unusual that pollen, derived from southwestern Russia, the Baltic States or Poland, are registered in Stockholm or Umeå in east Sweden. In Stockholm, much higher pollen sums were registered in the years 1978 and 1983 than could be expected from the accumulated temperature sums from the previous summers. The region of Gothenburg, situated on the Swedish west-coast, however, is less affected by pollen produced SE of Scandinavia. The number of pollen registered in Gothenburg, and the timing of their occurrence, are more in accordance with what could be expected from what is produced by the local trees of the region. The lower predictive accuracy of our model when applied to the values from Malmö may be due to a larger influence of allochthonous pollen in this region as compared to the situation in Gothenburg.

5. Conclusions

We suggest that the intensity of the pollen season is dependent on the amounts of assimilates, and on the potential number of sites, available for catkin initiation during the previous year, as well as on the weather during pollen dispersal. We claim that the variation in flowering intensity in *Betula alba*-species is not due to the presence of an inherent mechanism favoured by natural selection, because of exaggerated reproductive output in certain years, and hence should not be defined as true masting.

For practical use, the temperature sum and the total amount of airborne pollen registered during the period of catkin initiation is sufficient for prediction of next year's pollen sum as independent variables in a multiple

regression model. About a month before the onset of anthesis, the precision of the prediction may be increased by predicting the weather during pollen dispersal.

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References

- Andersen, T.B. (1991) A model to predict the beginning of the pollen season. *Grana* 30, 269–275.
- Baker, F.S. (1950) *Principles of Silviculture*. McGraw-Hill, New York, p. 1.
- Baldwin, H.L. (1942) *Forest Tree Seed of the North Temperate Region*. Chronica Botanica, Waltham, MA.
- Binnie, R.C. and Clifford, P.E. (1981) Flower and pod production in *Phaseolus vulgaris*. *J. Agric. Sci. Cambridge* 97, 397–402.
- Caesar, J.C. and Macdonald, A.D. (1983a) Shoot development in *Betula papyrifera*. II. Comparison of vegetative and reproductive short-shoot growth. *Can. J. Bot.* 61, 3066–3071.
- Caesar, J.C. and Macdonald, A.D. (1983b) Shoot development in *Betula papyrifera*. IV. Comparisons between growth characteristics and expression of vegetative long and short shoots. *Can. J. Bot.* 62, 446–453.
- Caesar, J.C. and Macdonald, A.D. (1984) Shoot development in *Betula papyrifera*. V. Effect of male inflorescence formation and flowering on long shoot development. *Can. J. Bot.* 62, 1708–1713.
- Chapman, G.P. and Sajadi, A.S. (1981) Exogenous growth substances and internal competition in *Vicia faba* L. *Z. Pflanzenphysiol.* 104, 265–273.
- Dahl, A.E. and Fredrikson, M. (in press) The timetable for development of maternal tissues sets the stage for male genomic selection in *Betula pendula*. *Am. J. Bot.*, in press.
- Davis, L.D. (1957) Flowering and alternate bearing. *Proc. Am. Soc. Hort. Sci.* 70, 545–556.
- Dunbar, A. and Rowley, J.R. (1984) *Betula* pollen development before and after dormancy: exine and intine. *Pollen Spores* 17, 429–486.
- Furlow, J.J. (1990) The genera of Betulaceae in the southeastern United States. *J. Arnold. Arboretum* 71, 1–67.
- Gross, H.L. (1972) Crown deterioration and reduced growth associated with excessive seed production by birch. *Can. J. Bot.* 50, 2431–2437.
- Hjelmroos, M. (1991) Evidence of long-distance transport of *Betula* pollen. *Grana* 30, 215–228.

- Ims, R.A. (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am. Nat.* 136, 485–498.
- Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends Ecol. Evol.* 8, 122–123.
- Koenig, W.D., Mumme, R.L., Carmen, W.J. and Stanback, M.T. (1994) Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 73, 99–109.
- Kozlowski, T.T. (1963) Growth characteristics of forest trees. *J. For.* 61, 655–662.
- Lavee, S. (1989) Involvement of plant growth regulators and endogenous growth substances in the control of alternate bearing. *Acta Hort.* 239, 311–323.
- Lee, T.D. (1988) Patterns of fruit and seed production. In: J. Lovett Doust and L. Lovett Doust (Eds.), *Plant Reproductive Ecology. Patterns and Strategies*. Oxford University Press, London, pp. 179–202.
- Linville, D.E. (1990) Calculating chilling hours and chill units from daily maximum and minimum temperature observations. *Hortic. Sci.* 25(1), 14–16.
- Macdonald, A.D. and Mothersill, D.H. (1983) Shoot development in *Betula papyrifera*. I. Short-shoot organogenesis. *Can. J. Bot.* 61, 3049–3065.
- Macdonald, A.D., Mothersill, D.H. and Caesar, J.C. (1984) Shoot development in *Betula papyrifera*. III. Long shoot organogenesis. *Can. J. Bot.* 62, 437–445.
- Nilsson, S.G. and Wästljung, U. (1987) Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* 68, 260–265.
- Norton, D.A. and Kelly, D. (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economics of scale. *Funct. Ecol.* 2, 399–408.
- Richardson, E.A. and Anderson, J.L. (1986) The omnidata biophenometer (TA45-P): A chill unit and growing degree hour accumulator. *Acta Hort.* 184, 95–99.
- Sage, T. (1986) Relationship of carbon availability to abscission in reproductive tissues of *Phaseolus vulgaris*. In: A.R. Cooke (Ed.), *Proceedings of the 13th Annual Meeting of the Plant Growth Regulator Society*.
- Sarvas, R. (1952) On the flowering of birch and the quality of seed crop. *Commun. Inst. For. Fenn.* 40, 1–35.
- Sharp, W.M. and Sprague, V.G. (1967) Flowering and fruiting in the white oaks: pistillate flowering, acorn development, weather, and yields. *Ecology* 48, 243–251.
- Silvertown, J.W. (1980) The evolutionary ecology of mast seeding in trees. *Bot. J. Linn. Soc.* 14, 235–250.
- Smith, C.C., Hamrick, J.L. and Kramer, C.L. (1990) The advantage of mast years for wind pollination. *Am. Nat.* 136, 154–166.
- Sork, V.L., Bramble, J. and Sexton, O. (1993) Ecology of mast-fruiting in three species of Missouri oaks, *Quercus alba*, *Quercus rubra*, and *Quercus velutina* (Fagaceae). *Ecology* 74, 528–541.
- Swedish Meteorological and Hydrological Institute (1978–1994) Väder och vatten. Norrköping.
- Toumey, J.W. and Korstian, C.F. (1937) *Foundations of Silviculture upon an Ecological Basis*. Wiley, New York.
- Tyldesley, J.B. (1973a) Long-range transmission of tree pollen to Shetland. I. Sampling and trajectory. *New Phytol.* 72, 175–181.
- Tyldesley, J.B. (1973b) Long-range transmission of tree pollen to Shetland. II. Calculation of pollen deposition. *New Phytol.* 72, 183–190.
- Waller, D.M. (1979) Models of mast fruiting in trees. *J. Theor. Biol.* 80, 223–232.