The Holocene 16,2 (2006) pp. 277–286

The effect of climate variability on pollen productivity, AD 1975–2000, recorded in a *Sphagnum* peat hummock

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Received 9 May 2005; revised manuscript accepted 17 September 2005

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Abstract: Pollen accumulation rates and pollen percentages from a *Sphagnum* peat hummock in the Jura Mountains were used to determine past pollen deposition. Post-bomb calibrated radiocarbon dates allowed estimations of annual variability in pollen productivity AD 1975–2000. Percentages of abundant taxa were modified (downweighted) to reduce the influence of plant cover, mean pollen productivity, and interdependence of the variables. Significant correlations with seasonal climatic parameters (tested with simple linear regression) were found both for pollen accumulation rates and for modified pollen percentages. Winter temperature is an important factor for pollen productivity of several tree species. The climatic effect on the modified pollen assemblage is best explained by a wet/warm to cold/dry gradient, but seasonal influence is considerable (ordination by PCA, RDA). Modified pollen percentages showed similarities in annual fluctuations between sites in the Jura Mountains, the Western Alps and the Eastern Alps.

Key words: Annual resolution, climate, pollen productivity, *Sphagnum* hummock.

Introduction

It is commonly assumed that changes in fossil pollen records are caused by changes in the surrounding vegetation (von Post, 1916). But if changes in vegetation are caused by climatic fluctuations problems might occur. Pollen productivity will change together with the climate, making it hard to estimate the response in the vegetation pattern. Many palaeoecological investigations have given results that are problematic to explain entirely with shifts in the vegetation cover, eg, when there is no detectable time-lag between a shift in climate and pollen values (Ammann *et al.*, 2000), when a very rapid increase of pollen values of a taxon occurs over a large area (Tallantire, 2002), or when pollen is absent and macrofossils are present (Kullman, 1998). Estimates of relative pollen productivity have resulted in different values (eg, Andersen, 1970; Hjelle, 1998; Broström *et al.*, 2004). The methodology has not been the same in all investigations, but the most likely explanation is that there are regional differences in pollen productivity, likely caused by different climatic settings.

The need to better understand the influence of climate on pollen productivity has increased in the past decennia as more subtle and short-lived climatic shifts come under study (eg, Tinner and Lotter, 2001; Hausmann *et al.*, 2002). Under such circumstances the importance of pollen productivity increases compared with migrations, die-backs and colonization. New methods for quantitative landscape reconstruction are also developing in which correct estimation of pollen productivity is crucial (Prentice, 1985; Sugita, 1994).

One reason why the impact of climate on pollen productivity has earned relatively little attention is that it is difficult to investigate. To directly compare pollen productivity with climatic change, a site with stable and well-documented past vegetation is needed, and few, if any, such data sets exist, mainly because of large changes in landuse during the past few centuries (Nielsen and Odgaard, 2004). And even if our current climate is changing fast it is not fast enough for the time frame of modern research projects. The aim of many investigations is to predict climatic change and/or possible effects of such a change, and in that perspective it is not an option to wait until the change has occurred. An alternative is to study modern pollen productivity in different climatic regions. Different estimations of relative pollen productivity might be compared

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(Broström *et al.*, 2004), but currently these investigations are few. In regions with similar vegetation but with different climate, pollen traps can be used to measure actual differences in pollen influx (Hicks *et al.*, 2001), but such investigations are time-consuming and measurements can only be achieved for one or a few taxa at the time.

The method pursued in this investigation is to study annual variability in pollen productivity compared with climatic parameters. A climatic change can be described as a changed frequency of years with certain characteristics, eg, a mean warmer climate is equivalent to an increased number of years with warmer summers, mild winters, etc. It is thus possible to use the annual variability to assess the effect of climatic change on pollen productivity. An assumption is that the reaction of a taxon to specific weather conditions for a single year is similar to the reaction to the same condition over a sustained period of time.

The most exact results are achieved by studying the direct flowering of the plants (Litschauer, 2000) or by yearly measurements of pollen influx with pollen traps (Hicks, 2001; van der Knaap *et al.*, 2001). To get even reasonably long time series with these methods a considerable amount of work and planning is needed. An alternative is to use existing lake or peat deposits as natural archives of fluctuations in pollen productivity (van der Knaap and van Leeuwen, 2003).

In this investigation a *Sphagnum* peat hummock from the Jura Mountains is used as an environmental archive. Annually constrained pollen samples, pollen accumulation rates and modified pollen percentages will be used to achieve statistical relationships with measured climatic parameters (see van der Knaap and van Leeuwen, 2003), and similarities in annual pollen deposition with two sites in the Swiss and the Austrian Alps will be shown.

Methods

Site description and fieldwork

The peat section AH1 (Amburnex Hummock 1) was cut from a *Sphagnum* hummock in a small mire in Combe des Amburnex (Les Amburnex mire, 46°32′23″ N, 6°13′54″ E, 1370 m a.s.l.) in the Swiss Jura Mountains (Figure 1). The mire is partly covered by *Picea* and the hummock grows at the edge of the forested part. The hummock was growing below *Picea* branches, which seems to be the case for all *Sphagnum* hummocks in the area. The vegetation around the mire is a mosaic of pasture and forest. *Picea* is the most abundant tree, followed by *Abies*, *Fagus* and some *Acer*.

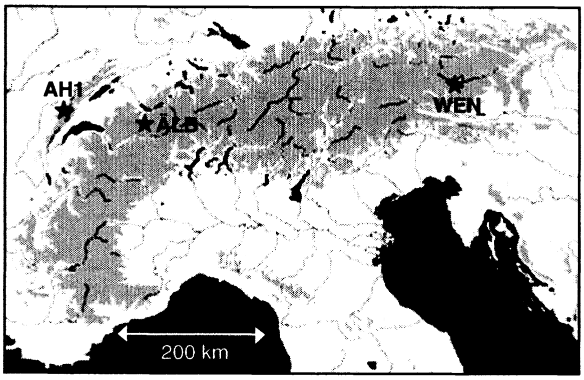

Figure 1 Overview map of localities: AH1, Les Amburnex Hummock 1 (southwest Swiss Jura Mountains); ÄLB, Älbi Flue mire (northwest Swiss Alps); WEN, Wengerkopf mire (Austrian Alps). Grey indicates areas above 1000 m altitude

Laboratory work

Subsampling was done with scissors, whereby the existing peat layering was followed. Pollen samples were prepared using the standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986). *Lycopodium* spores were added to establish pollen concentrations (Stockmarr, 1971). For identification of pollen Moore *et al.* (1991), Punt and Blackmore (1991) and the reference collection at the University of Bern were used. Nomenclature follows ALPADABA (Alpine Palynological Data-Base, housed in Bern, Switzerland).

Radiocarbon dating and depth–age relationship

Five *Sphagnum* samples were used for radiocarbon analysis with the AMS facility of Utrecht University (Table 1). The results of the ^{14}C analysis showed elevated activities expressed as fractions modern, and were accounted for by the effects of the atomic bomb activity in the atmosphere (Nydal and Lövseth, 1983). Using the computer program CALIBomb (Reimer *et al.*, 2004; data set: Levin and Kromer, 2004) 1σ-calendar ages were retrieved. From the calendar ages we derived the depth–age relationship of AH1 (Figure 2). Age determination of the pollen samples is based on linear interpolation between the calibrated ^{14}C-dates and the time of the hummock was collected (AD 2001.8). For AH1-6 an age of AD 1997 was used, ie, the first full year within the confidence interval (> AD 1996.2). A younger age would infer decreased peat accumulation rate between 10 and 17 cm depth, which is unlikely because of the upward decrease in compaction and decomposition.

Annual resolution

In order to compare pollen data with climatic data each pollen sample is assigned to a full year. The pollen data cover the period 1976 to 2001 with 29 samples. Samples assigned to the same year are averaged. The pollen years are not exactly equivalent to calendar years, as the sampling precision is too low and natural conditions make this impossible, so a smoothing of 2–3 years compared with annually separated pollen deposition can be assumed. The growth pattern of *Sphagnum* also affects the pollen signal. Field and laboratory observations suggest that *Sphagnum* (in central European mountain regions) grows rapidly in height early in the growing season primarily by expansion of biomass accumulated the previous year. Later in the season *Sphagnum* does not grow so much in height but forms a dense surface layer that can expand in the next year. The surface of a *Sphagnum* hummock thus remains more or less the same from summer until the following spring. Thus late-flowering taxa deposit their pollen on the same surface as early-flowering taxa of the following year, so the 'pollen deposition year' runs from summer to summer. Additional time-lag must therefore be allowed for late-flowering taxa. The uppermost pollen sample (collected in the autumn 2001) will thus theoretically contain pollen from the late-flowering season AD 2000 together with the entire flowering season 2001. Together with uncertainties in the depth–age relationship this sums up to a possible deviation of 1 year of a taxon-specific pollen signal, which must be accounted for in the analysis of the data.

Modification of pollen percentage values

The six most abundant taxa in the pollen record (*Fagus*, *Picea*, *Pinus*, *Quercus*, Gramineae and *Urtica*) have been down-weighted, as the high original percentage values disturb the climatic signal. The reduction factors have been calculated by dividing the mean pollen percentage value (AD 1976–2001) of *Betula* (the seventh most abundant pollen taxon) with the

Table 1 Radiocarbon analysis.

Sample	Depth (cm)	Lab code	δ^{13}C (‰)	Fraction modern pMC	1σ-calendar age	Mean
AH1-6	9.5	UtC-12572	−29.5	1.091±0.006	1996.2–2002.0	1999.1±2.0
AH1-16	17.7	UtC-11407	−28.7	1.173±0.005	1986.1–1990.2	1988.2±2.0
AH1-24	23.9	UtC-11408	−29.1	1.249±0.005	1980.7–1983.7	1982.2±1.0
AH1-30	28.4	UtC-11722	−29.4	1.462±0.006	1972.3–1972.8	1972.6±1.0
AH1-32	29.5	UtC-11409	−30.6	1.562±0.006	1968.2–1969.9	1969.1±1.0

mean pollen percentage value of the specific taxa. The original pollen percentage values of a taxon have then been multiplied with the reduction factor (Table 2) and subsequently new percentages have been calculated. With this modification the mean effective pollen sum decreases from 592 to 303. The mean pollen percentage value for the downweighted taxa after percentage recalculation is 6.1%. In the ideal case all taxa should be downweighted to the same value, because this would completely remove any differences between taxa in mean pollen productivity and plant cover. This has, however, the disadvantage that it would enhance the statistical error in taxa with low pollen counts. The removal of taxa with low pollen counts (eg, < 1% of the pollen sum) also has disadvantages, since it reduces the effective pollen sum and increases interdependence between the remaining taxa, and in addition the list of excluded taxa would depend on the taxonomic resolution of the investigation. The modification of the pollen percentages done here is a reduction of intertaxa differences in mean pollen productivity and vegetation cover, thus increasing the signal-to-noise ratio.

Comparison between sites

Two Alpine sites have been compared with AH1 (see Figure 1). ÄLB (Älbi Flue mire, 46°35′55″ N, 7°58′35″ E, 1850 m a.s.l.) is situated in the northern Alps of central Switzerland just below the forest limit (van der Knaap and van Leeuwen, 2003). The nearest trees (at 12 m distance) are *Pinus cembra*, but the general vegetation in the area is dominated by *Picea*. WEN (Wengerkopf, 47°10′40″ N, 13°52′40″, 1790 m a.s.l.) is situated in the Austrian Alps (Goslar *et al.*, 2005). *Pinus mugo* grows on the mire itself, while the surrounding forest is dominated by *Picea* with an admix of *Larix* and *Pinus cembra*.

The pollen records of ÄLB and WEN have been prepared in the same way as that of AH1 with reduction of the six most common taxa to the mean value of the seventh most common taxon (Table 2). In ÄLB the effective pollen sum decreased from 1226 to 383 and the mean modified pollen percentage of the downweighted taxa is 6.7%. In WEN the numbers are 703 to 306, and 7.2%. Taxa with a mean modified pollen percentage > 1% at all the sites have been used for comparison, and those with visible similarities among sites have been graphically displayed. Cyperaceae, *Potentilla* and *Vaccinium* are considered local plants and are therefore not included in the pollen sum or subject to downweighting.

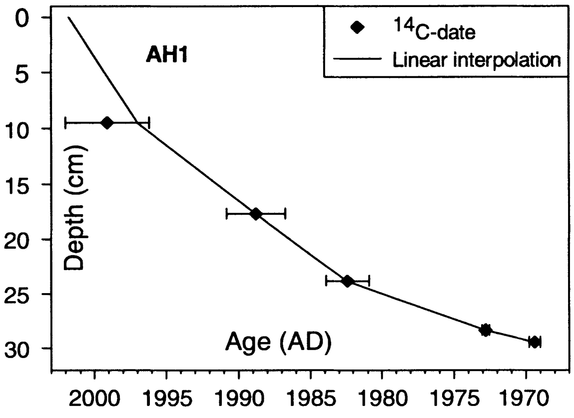

Figure 2 Depth-age relationship for AH1 (Les Amburnex Hummock 1, southwest Swiss Jura Mountains). Error bars show 1σ confidence interval. Linear interpolation used to infer the age of pollen samples is shown with line. Upper end of line is the surface (0 cm at AD 2001.8)

Climatic parameters and pollen–climate relationships

The climatic data are derived from the measurement station of Geneva (MeteoSchweiz; Begert *et al.*, 2005) *c.* 35 km south of the sampling site Amburnex (AH1). The main pollen source areas are the Jura Mountains (*Abies*, *Fagus*, *Picea*, herbs) and the Swiss plateau (deciduous trees, herbs). The absolute climatic measurements are primarily valid for the Swiss plateau, but both areas are likely affected by the same weather systems and can be expected to show similar annual variance in climatic parameters. Especially annual variations in temperature are representative for large areas (ie, Switzerland), while

Table 2 Reduction factors.

Sites and taxa	Reduction factor	Average percentage
Les Amburnex (AH1)		
Betula	1.00	3.1
Fagus	0.73	4.3
Gramineae	0.13	23.9
Picea	0.12	25.3
Pinus non-*cembra*	0.52	6.1
Quercus	0.81	3.9
Urtica	0.83	3.8
Älbi Flue (ÄLB)		
Alnus viridis	0.45	4.7
Betula	0.98	2.1
Gramineae	0.13	16.6
Picea	0.046	45.2
Pinus cembra	0.21	10.8
Pinus non-*cembra*	0.79	2.6
Urtica	1.00	2.1
Wengerkopf (WEN)		
Alnus glutinosa	1.00	3.1
Betula	0.61	5.1
Gramineae	0.42	7.5
Larix	0.35	8.8
Picea	0.097	32.2
Pinus cembra	0.28	11.0
Pinus non-*cembra*	0.30	10.5

Abundant taxa have been multiplied by a reduction factor to obtain a value similar to the seventh most abundant taxon. Average percentage refers to the average percentage value of the taxa AD 1976–2001 prior to modification.

annual precipitation anomalies might show larger spatial differences (Begert *et al.*, 2005).

Climatic parameters will not only affect the pollen productivity but also the pollen dispersal, primarily by prolonged rainfall, and wind direction and strength during the flowering season. Wind is not considered here, but as the wind pattern to some degree will vary together with temperature and precipitation it should be kept in mind.

Seasonal and annual temperature and precipitation were used as climatic parameters. Seasons are January/March (Winter), April/June (Spring), July/September (Summer), and October/December (Autumn). Results from pollen traps show that the pollen deposition of trees is affected by the weather conditions of the previous year (Hicks, 2001; van der Knaap *et al.*, 2001). Considering the uncertainties in the determination of the depth–age relationship and the characteristics of *Sphagnum* peat growth, both a 1-yr and a 2-yr time lag are used.

Statistics

Simple linear regression was used to test the correlation of single taxa with climatic parameters. Modified pollen percentages were used for further analyses of the assemblage because it is the more robust data set, and because the advantage of interdependence is limited in the methods used. Relationships within the modified pollen assemblage were tested with detrended correspondence analysis (DCA), which gave a short gradient length (0.95 SD), suggesting that a linear response model is appropriate (ter Braak and Prentice, 1988). Principal component analysis (PCA) and redundancy analysis (RDA) (ter Braak, 1987; ter Braak and Prentice, 1988) were applied to assess the internal relationships of the modified pollen assemblages and the relation between the modified pollen assemblages and climatic parameters. In PCA the grouping is done on the species composition, so the environmental variables do not affect the analysis. In RDA the ordination axes are linearly related to the climatic variables and thus show the impact of climate, but the choice of climatic variables affects the outcome. Both methods thus complement each other. *Sorbus*-type was removed from both PCA and RDA as the single strong peak would distort the analyses. The annual parameters of precipitation and temperatures were removed from the RDA to reduce autocorrelation between the climatic parameters. The statistical analyses were made with SYSTAT (Wilkinson, 1990) and CANOCO.

Results

Pollen diagrams

An unmodified pollen percentage diagram (Figure 3), a diagram of annually constrained pollen accumulation rates (Figure 4) and a diagram of annually constrained modified pollen percentages (Figure 5) are presented. Selected climatic parameters have been added for comparison. Cyperaceae, *Potentilla*-type and *Vaccinium* are not included in the pollen sum and have not been subjected to downweighting. These taxa occur on the mire itself and their pollen values are largely dependent on the plant distribution within the nearest few metres. *Picea* also occurs in the direct vicinity, but trees show less local influence on small distances (van der Knaap *et al.*, 2001), and it is included. In general as many species as feasible are included in the pollen sum (Wright and Harvey, 1963).

The unmodified pollen percentage diagram (Figure 3) does not show any clear trends, suggesting that no major changes in

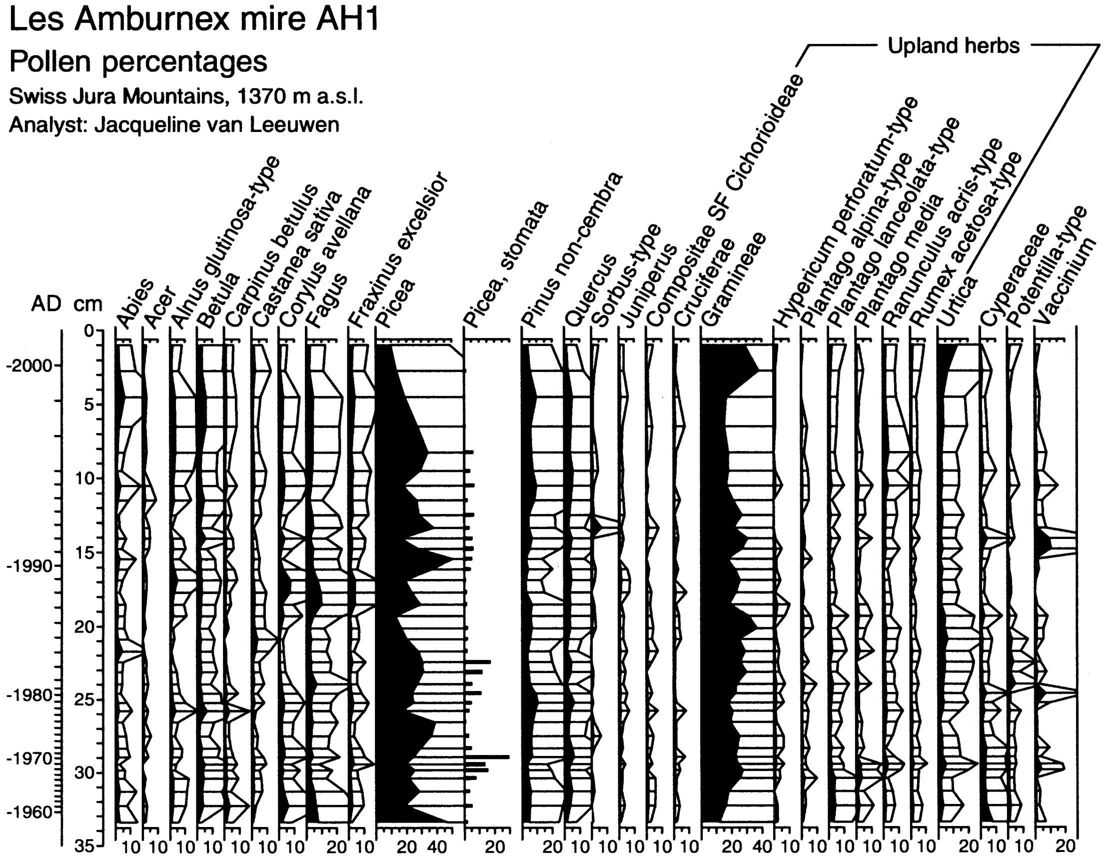

Figure 3 Pollen percentage diagram of Les Amburnex Hummock 1 (AH1). Percentages are based on the upland pollen sum. The scale (%) follows the black curve, and the white curve shows × 5 exaggeration. Bars in the white curve represent sample positions

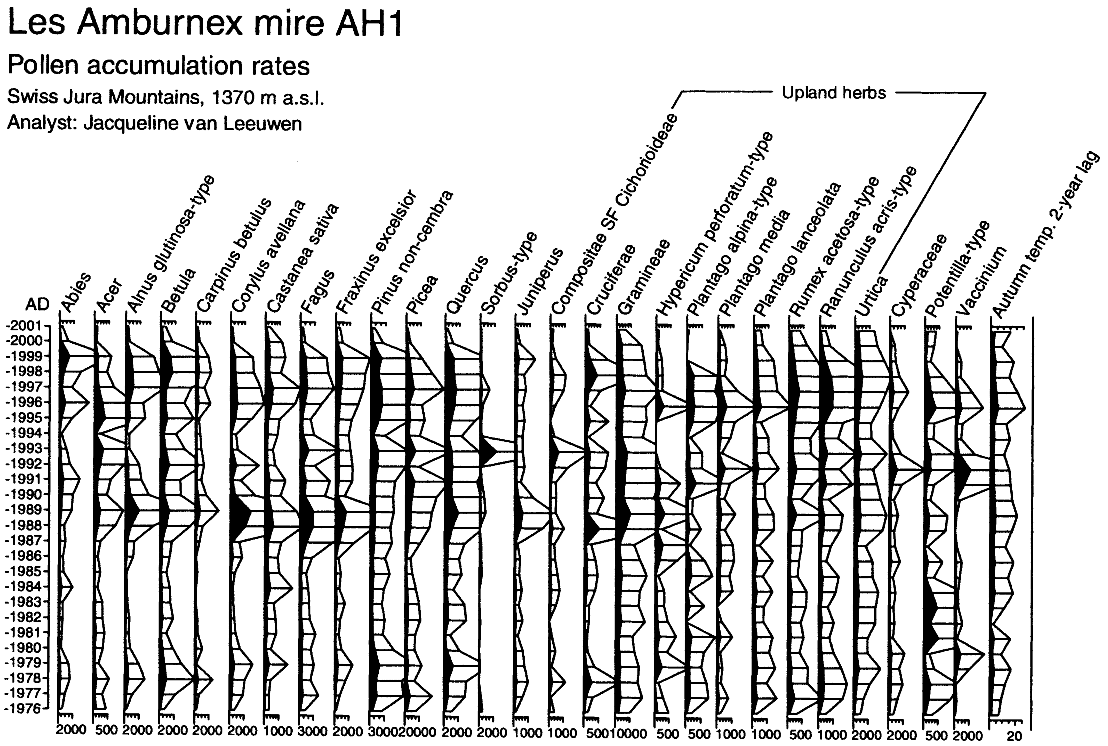

Figure 4 Pollen accumulation rates of Les Amburnex Hummock 1 (AH1). Autumn temperature has been added for comparison. Taxa with a mean modified percentage > 1% are included. The scale (grains/cm per yr) follows the black curve, and the white curve shows × 5 exaggeration. Bars in the white curve represent sample positions

the surrounding vegetation can be expected. The position of the hummock below *Picea* branches allows a ready supply of *Picea* needles. Undecomposed needles are sieved away during pollen preparation, so the frequencies of *Picea* stomata are probably more reflective of the needle decomposition rate than the deposition rate. Interestingly, increased values of *Picea*

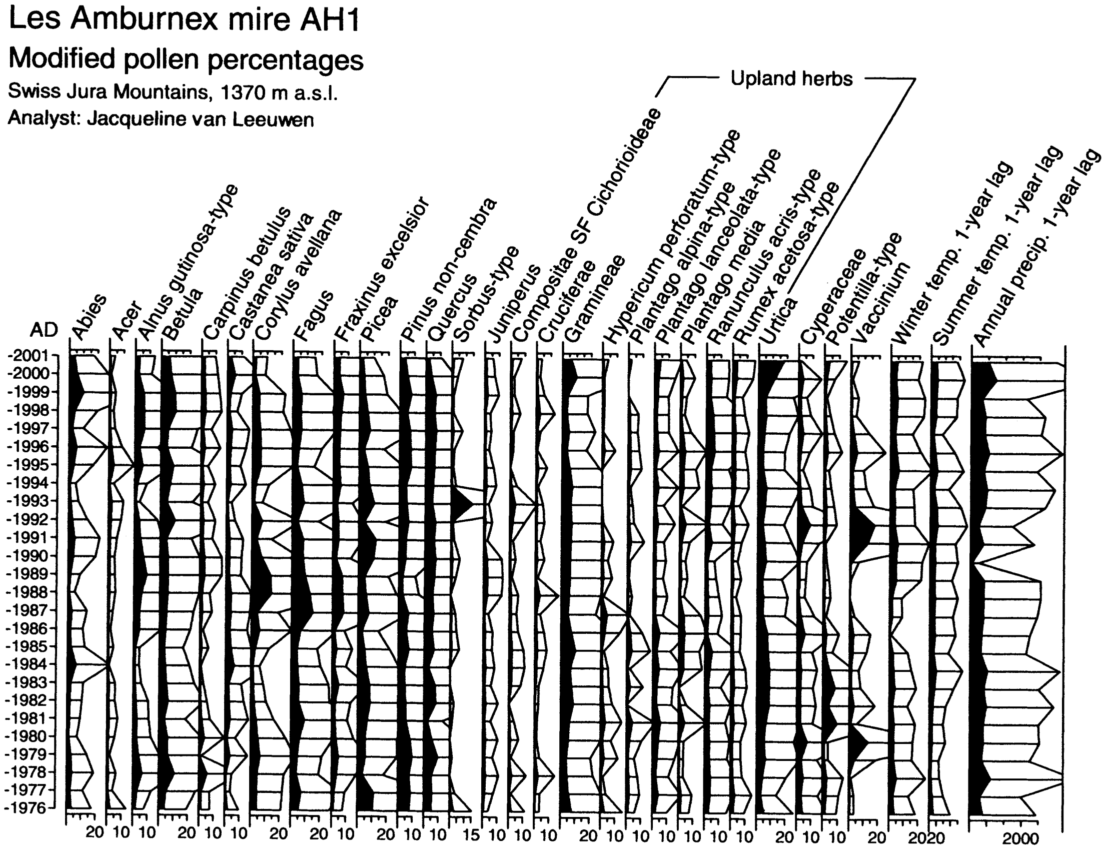

Figure 5 Modified pollen percentages of Les Amburnex Hummock 1 (AH1). The scale (%) follows the black curve, and the white curve shows × 5 exaggeration. Bars in the white curve represent sample positions. Climatic parameters have been added for comparison. The scale for summer temperature starts at 15°C, for annual precipitation at 500 mm/yr. Taxa with a mean percentage > 1% are included

stomata correspond to increased pollen values of *Vaccinium*, suggesting a common cause.

The diagram of pollen accumulation rates (Figure 4) shows low values for most taxa AD 1980–1987 and high values 1988–2000. Peaks occur 1978, 1988–1989 and 1996–1999.

The modified pollen percentage diagram (Figure 5) shows clear synchronous peaks and dips for some taxa. In 1978 there is a peak in *Alnus*, *Betula*, and Cruciferae, while *Fagus*, *Picea* and Gramineae dip. In 1987–1989 there is a peak in *Corylus*, *Fagus* and *Fraxinus*.

Comparison between sites

Several taxa show visual similarities (Figure 6) in annual fluctuations between the sites (*Betula*, *Corylus*, *Fagus*, *Fraxinus*, *Picea*, *Pinus*, *Quercus*, Cyperaceae and *Vaccinium*). Other taxa show little or no visual similarities (*Alnus glutinosa*, Gramineae, *Plantago lanceolata*-type, *Rumex acetosa*-type, *Urtica* and *Potentilla*-type). Simple linear regression analysis resulted in statistical significant correlation ($p \leq 0.05$) of *Corylus* for AH1–WEN, *Fagus* for AH1–ÄLB and *Fraxinus* for both AH1–ÄLB and AH1–WEN. *Potentilla*-type shows negative correlation for AH1–ÄLB, but this makes no ecological sense and is likely by chance. The strong correlation of *Vaccinium* for ÄLB–WEN ($P = 0.001$) might depend on the single-peak distribution of the *Vaccinium* pollen values.

Annual fluctuation in pollen deposition can be correlated between sites with different vegetation over a distance of 600 km. This suggests that climatic forcing of pollen production occurs on at least a regional scale. Trees correlate better than upland herbs.

Correlation of single taxa with climatic parameters

Annually constrained pollen accumulation rates and modified pollen percentages were tested with simple linear regression against seasonal and annual climatic parameters (Table 3). Only taxa with a mean modified percentage above 1 were tested. Pollen accumulation rates give independent measurements for each taxon but are sensitive to peat characteristics, age determination and laboratory work. Modified pollen percentages are more robust in the above senses, but the value of each taxon is relative to the pollen assemblage.

Pollen accumulation rates for many taxa give significant positive correlations with autumn temperature at a 2-yr time lag, and all other taxa respond positively. There is no ecological explanation to why all taxa should respond in the same way to autumn temperature, so the alternative explanation of short-term variations in peat growth is likely. Autumn temperature will therefore not be used to infer variance in pollen productivity from pollen accumulation rates. It should nevertheless be noted that if a climatic parameter affects several taxa in the same direction, this will be difficult to observe in the modified pollen percentages because of the interdependence of the taxa. With the exception of autumn temperatures, most of the correlations that are statistically significant in pollen accumulation rates are also significant for modified pollen percentages. The only exception is annual temperature, where significant positive correlations of *Acer*, *Plantago media*, *Ranunculus acris* and *Rumex acetosa* only occur in the pollen accumulation rate data set but not for the modified pollen percentages.

Modified pollen percentages give, in general, clearer statistical relationships with climate than pollen accumulation rates. Both pollen accumulation rates and modified pollen percentages indicate that winter temperature is an important factor for pollen productivity by several arboreal taxa (*Abies*, *Acer*, *Betula*, *Carpinus*, *Fagus* and possibly *Fraxinus*). See Table 3 for other interpretations of climate favourable for pollen productivity of individual taxa. Both pollen accumulation rates and modified pollen percentages have been considered in the interpretation.

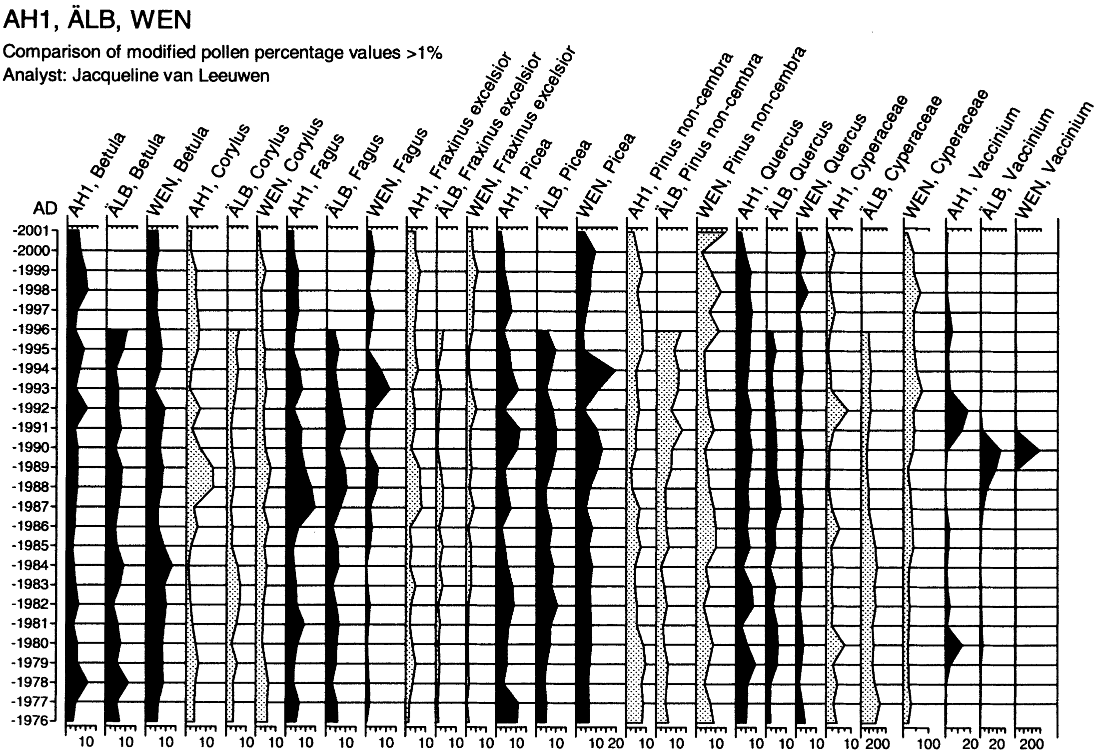

Figure 6 Comparison of modified pollen percentages between sites in Jura Mountains and Alps; see Figure 1 for sites. Taxa with modified pollen percentage values > 1% at all sites are used

Table 3 Statistically significant correlations (simple linear regression) between pollen accumulation rates or modified pollen percentages of single taxa and climatic parameters.

Taxa	Pollen accumulation rates										Modified pollen percentages										Interpretaion
	Temperature					Precipitation					Temperature					Precipitation					
	Win	Spr	Sum	Aut	Ann	Win	Spr	Sum	Aut	Ann	Win	Spr	Sum	Aut	Ann	Win	Spr	Sum	Aut	Ann	Favourable climate
Trees																					
Abies	+			(+)	(+)						+(+)	(+)			+(+)	(*n*)					Warm winter, year, spring?
Acer	+				+						+										Warm winter
Alnus				(+)										(+)							Warm autumn?
Betula	+										+	(+)									Warm winter, spring?
Carpinus	+			(+)							+										Warm winter
Castanea				(+*)													+				Wet spring?
Corylus				(+)										(+)					*n*		Warm autumn? dry autumn?
Fagus	(*n*)								(*n*)		(*n**)							(*n**)	(*n**)		Cold winter, dry autumn
Fraxinus				(+*)			(+)				(*n*)						(+*)				Cold winter? wet spring?
Picea														(*n*)		*n*				(*n*)	Cold autumn? dry?
Pinus				(+)									*n*								Cold summer?
Quercus				(+)																*n*	Dry?
Sorbus			(+)										(+)								Warm summer
Herbs																					
Cruciferae							+										+*				Wet spring
Gramineae														(*n*)							Cold autumn?
Hypericum		(*n*)		(+)		+*	*n*		(*n*)			(*n**)			*n**(*n*)	+(+)		(*n*)	*n*(*n*)		Cold spring, wet and dry
Plantago alpina												*n**									Cold spring?
P. lanceolata				(+)											*n*						Cold?
P. media				(+)	(+)																Warm?
R. acris				(+)	(+)															+	Warm? wet?
Rumex acetosa				(+)	(+)							+						+*(+)	+*		Warm? wet spring? summer?
Urtica				(+)																(+)	Wet?
Wetland																					
Cyperaceae												*n*			*n*						Cold spring? year?
Vaccinium	(+)																	*n* (*n*)			Warm winter? Dry?

+ = significant positive correlation ($p \leq 0.05$) at 1-yr time lag; *n* = significant negative correlation ($p \leq 0.05$) at 1-yr time lag; (+) and (*n*) as above but with 2-yr time lag. +* and n* mark highly significant correlations ($p \leq 0.01$). No significant correlation was found for *Juniperus*, Compositae Subfam. Cichorioideae, and *Potentilla*. Win, Winter (January/March); Spr, Spring (April/June); Sum, Summer (July/September); Aut, Autumn (October/December); Ann, Annual. Interpretation gives the clearest trends for the taxon. A question mark is added if the correlation only occurs in one of the data sets. Correlations of pollen accumulation rate with autumn temperature are not considered; see text for explanation.

Statistical analyses of the pollen assemblage and its relation to climatic parameters

The modified pollen assemblage (modified pollen percentages) has been analysed with ordination methods. In PCA the first two ordination axes explain 49% of the variance, for RDA this is 42%. The RDA ordination axes together are significant ($P = 0.004$). PCA and RDA show essentially the same pattern (Figure 7), suggesting that the applied climatic parameters explain the general pattern in the modified pollen assemblages. The first RDA axis is primarily related to summer temperature and autumn precipitation, the second RDA axis to winter, spring and autumn temperature together with summer and autumn precipitation. Some taxa are clearly grouped together: *Abies* and *Betula*; *Alnus*, *Corylus* and *Fraxinus*; Gramineae and Compositae Subfam. Cichorioideae; *Ranunculus acris*-type, *Rumex acetosa*, *Plantago lanceolata* and *Urtica*. It is likely that the taxa in a group react in a similar way to specific weather conditions.

Discussion and conclusions

Even a rather short timeseries of 26 years is sufficient to capture the relation of annual variation in climatic conditions with pollen productivity for many taxa, and the similarities in annual variation between sites far apart (600 km) suggests that pollen/climate relationships are valid on a regional scale. Still, differences in growing conditions likely affect the biotic responses to variations in climatic parameters. The results here are thus primarily valid for central European mid-altitude areas. For example, precipitation does not seem to affect pollen productivity in the northern boreal forests (Hicks, 2001), and pollen productivity of plants growing near their highest altitudinal limit is primarily affected by summer temperatures (van der Knaap and van Leeuwen, 2003). The pollen accumulation rates in the site studied here gave much better estimates of variations in pollen productivity than in earlier investigations (van der Knaap and van Leeuwen, 2003), where pollen

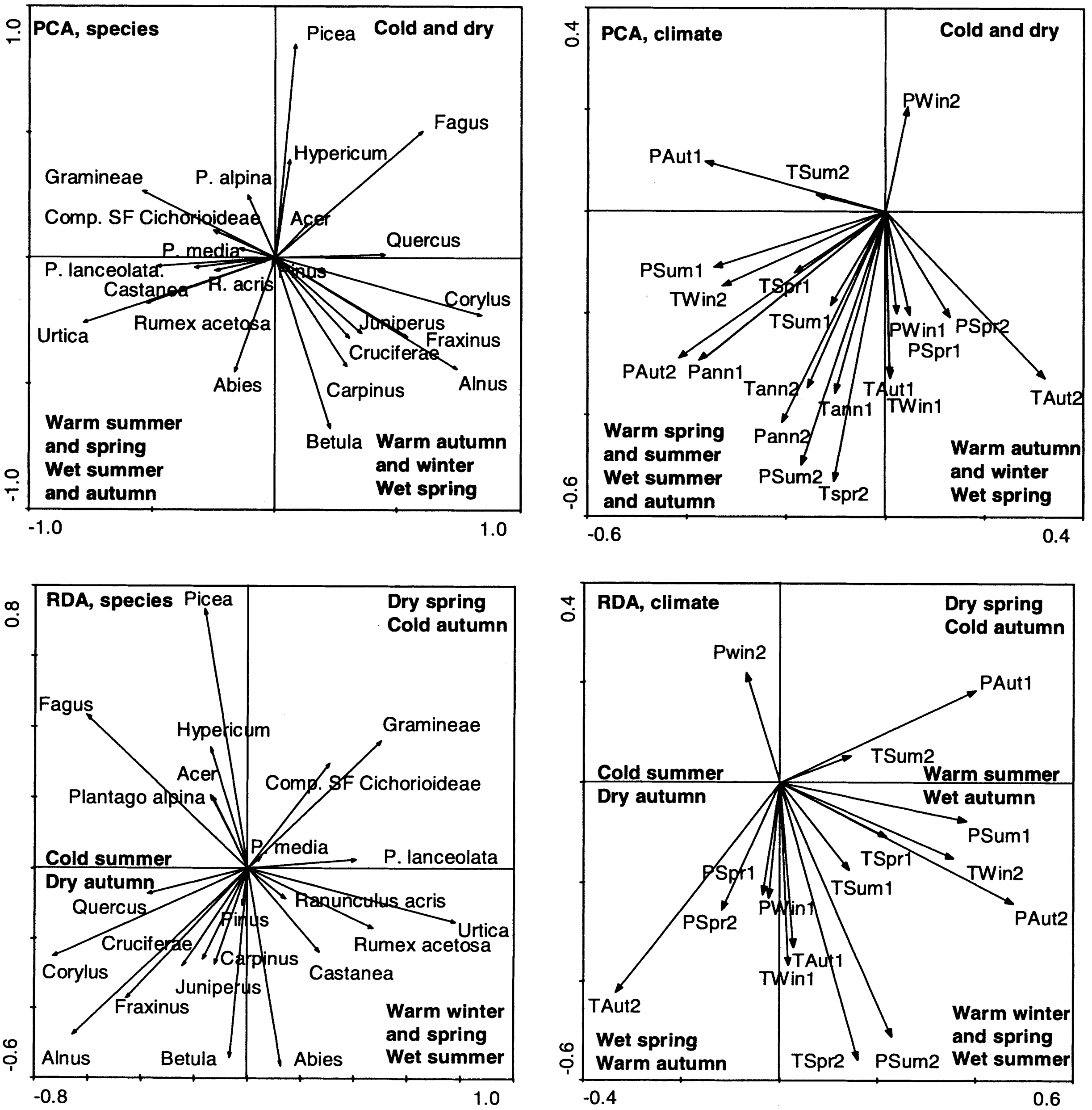

Figure 7 PCA and RDA scatter plots of modified pollen percentages (*Sorbus*-type excluded), and annual and seasonal temperature and precipitation with 1- and 2-yr time lag. Species and climatic parameters are displayed on separate plots. First ordination axis of PCA explains 30% of the variance, the first two 49%. First ordination axis of RDA explains 26% of the variance, the first two 42%. The general relationships between the climatic parameters and the modified pollen assemblage have been noted in the plots

accumulation rates (called there 'detrended pollen concentrations') were shown to be strongly affected by short-term variations in peat growth. This indicates that the sensitivity of peat growth to specific weather conditions varies between climatic settings.

The main results are shown in Table 3 and Figure 7, and the most important conclusions are discussed below.

(1) *Sphagnum* hummocks, or fast growing peat, can be dated with an accuracy of ±1 yr from 1960 onwards. This allows environmental parameters to be traced with annual resolution, but a 2–3 yr smoothing of the signal has to be allowed for.

(2) Downweighting of the most abundant pollen taxa reduces the effects of plant cover, mean pollen productivity, and interdependence of the pollen values. This increases the direct annual effect of climate on single taxa and allows comparison between sites with different surrounding vegetation.

(3) Pollen accumulation rates show climate-induced annual variations both in pollen productivity and in peat growth. Possible annual variation in peat growth can be expected if many taxa with different ecological requirements show a similar response to climatic parameters. Combined use of pollen accumulation rates and modified pollen percentages allows determination of the most important climatic parameters for the pollen productivity of a specific taxon.

(4) Similarities in annual pollen deposition can be seen in sites up to 600 km apart. Tree species show stronger similarities than herbaceous taxa, and lowland trees (*Corylus*, *Fagus* and *Fraxinus*) show the most similar pattern.

(5) The increased modified pollen percentages of *Fagus* and *Fraxinus* AD 1987–1994 that occurred in the Jura Mountains and the Alps can hardly be explained by anything other than climatic conditions. One explanation might be the rise in temperature in central Europe during the 1980s (Auer *et al.*, 2001). Several taxa show large variations in pollen deposition during the past 100 years (van der Knaap *et al.*, 2000), which is normally attributed to changes in vegetation cover or landuse. Considering the large changes in the landscape during the past century this is likely a correct assumption, but the results here suggests that it shall not be done uncritically.

(6) Winter temperature is important for the pollen productivity of many tree taxa. *Abies* and *Betula* respond positively to both winter and spring temperature; *Acer* and *Carpinus* respond positively to winter temperature; *Fagus* and possibly *Fraxinus* respond negatively to winter temperature; *Alnus* and *Corylus* respond positively to autumn temperature. The pollen productivity of many trees thus seems to be affected by climatic conditions outside the main growing season (summer). A possible explanation is that frost damage, failed hibernation or premature flowering are more critical than summer warmth. Careful studies of the physiology, phenology and ecology of specific taxa will be required to better understand the processes involved.

(7) Three major climatic gradients affect pollen productivity: summer and spring temperature (April–September) together winter and autumn precipitation (October–March); autumn and winter temperature (October–March) together with winter and spring precipitation (January–June); and temperature together with precipitation in general. The clearest climatic gradient in PCA and RDA is warm/wet to dry/cold, but the seasonal influence is considerable.

Acknowledgements

We thank Brigitta Ammann for encouragement and valuable comments, and Florencia Oberli for carrying out much of the laboratory work. Comments by Bas van Geel and an unknown referee were helpful to improve the manuscript. This paper is a contribution to the Swiss National Science Foundation (SNF) project NCCR Plant Survival; the European Union project PINE (Predicting Impact on Natural Ecotones, project EVK2-CT-2002-00136; and the NordForsk framework POLLANDCAL (Pollen/landscape calibration network). Additional support has been given by the Marie Curie Fellowship Association (MCFA) through the framework Cultural Landscapes of Europe (CULTLAND) at the University of Bergen.

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