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Past Pollen Production Reconstructed from Needle Production in *Pinus sylvestris* at the Northern Timberline: a Tool for Evaluating Palaeoclimate Reconstructions

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Annual needle production (PROD) of Scots pine (*Pinus sylvestris* L.) and pine pollen accumulation rates (PAR) are compared along a 5-site transect from the Arctic Circle to the northern timberline. PROD is calculated using the Needle Trace Method (NTM). PAR is monitored by two series of pollen traps, located in the centres of mires and within forests, respectively. There is a strong year-to-year agreement in PAR and PROD between the sites for the common 19-year period for which both proxies are available. Mean July temperature of the previous year (T_{JUL-1}) correlates statistically significantly with PROD at all five sites and with PAR in the four northernmost sites. There is also a significant relationship between T_{JUN-1} and PROD at all sites, and T_{JUN} and PAR at the two northernmost sites. PROD and PAR correlate most strongly in the three near tree line sites, where PROD explains up to 51% of the variation in PAR. On the basis of the calibration between PROD, PAR and T_{JUL-1}, PROD and T_{JUL-1} are used to reconstruct past PAR. That such a reconstruction is realistic is supported by its agreement with the pollen record for 1982–2000 and with records of male flowering for the period 1956–1973. The use of PROD in reconstructing past PAR can help in interpreting the fossil pollen signal in terms of climate rather than vegetation change and in evaluating the high-resolution dating of peat profiles and calculations of the rate of peat accumulation.

Keywords age-depth chronology, annual resolution, needle trace method, NTM, pollen accumulation rate, Scots pine, temperature reconstruction, tree line

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1 Introduction

Scots pine (*Pinus sylvestris* L.) is a species with a very wide distribution in the northern hemisphere, being found from northern Norway in the north to Spain and Greece in the south and from Scotland in the west to far eastern Russia and Mongolia in the east, and occurring on a wide range of soil types (Sarvas 1964). It is also a species for which long dendrochronological records exist (Eronen et al. 2002, Grudd et al. 2002). Tree-ring width records from pine have been increasingly used as proxies for climate (Briffa et al. 1990, Helama et al. 2005), providing an annual record of temperature variation for the past. Recent studies, however, suggest that other growth factors recorded in the same trees may, in fact, provide a better climate record than tree-ring width does. Latewood density (Briffa et al. 1998), stable carbon isotopes (Gagen et al. 2007) and height increment (Jalkanen and Tuovinen 2001) are such proxies. Similarly combinations of two or more proxies may provide a more reliable record than any proxy individually (McCarroll et al. 2003). One combination of growth factors, which has not received much attention to date, is needle production and pollen production.

Primordia of both short shoots with needles and male flowers with pollen form in the same bud, initiating in the summer of one year but only expanding and growing in the early summer of the following year. These two very visible indicators of the well-being and growth of the tree appear together on the same shoots (Fig. 1). Both the number of needles and the quantity of pollen produced vary from year to year, in response to climate, sometimes dramatically (Sarvas 1962, Koski and Tallqvist 1978, Autio and Hicks 2004, Pensa et al. 2005).

Annual records of needle production in Scots pine can be obtained through the Needle Trace Method, NTM (Kurkela and Jalkanen 1990), and work has already demonstrated that the annual needle production correlates with July temperature of the previous year (Jalkanen and Tuovinen 2001, Salminen and Jalkanen 2004). Long continuous records of pollen accumulation from peat profiles at the same high temporal (near-annual) resolution as the needle-production records are now being produced (van der Knaap et al. 2003, Hicks et al. 2004, Barnekow et al. 2007, Räsänen et al. 2007). It is also becoming apparent that, at this annual resolution, pollen accumulation rate (PAR) reflects both local and regional pollen production. That annual pollen accumulation is also potentially a temperature record has been demonstrated through recent monitoring studies (Hicks 1999, Autio and Hicks 2004), and pollen dispersal models (Sugita 1994) support the hypothesis that this is a regional, as much as a local, signal. Pollen accumulation is a mean indicator of pollen production for a whole forest, not just one or two individual trees and, as such, is potentially a strong temperature proxy.

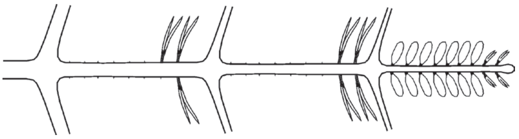

Fig. 1. A schematic presentation of a *Pinus sylvestris* branch with short shoots (needles) in the top and male flowers in the base and middle of the same annual long shoot. Previous-year shoot has no organs in the site where male flowers were located. Some shedding of short shoots has happened in the third-year annual shoot.

The aim of this article is to demonstrate firstly to what extent the quantity of these two growth products; needle production and pollen production are related both to temperature and to each other, and secondly whether one record can be used to predict or confirm the other. It is hypothesised that if a common signal, for instance July temperature, is determining both needle production and pollen deposition, the former, which is much easier to produce than the latter, may be used to evaluate the accuracy of high-resolution pollen-accumulation chronologies from peat profile. By comparing the predicted long-term high resolution pollen-accumulation chronology with the actual pollen-accumulation record it will be possible to evaluate the extent to which the fossil pollen signal reflects temperature variation rather than changes in forest density/composition/biomass and, at the same time, assess the validity of the age-depth chronologies of the peat deposits containing the record.

2 Material and Methods

2.1 Needle-Production Analysis

Ten Scots pine trees from each of the five sites along the transect (Rovaniemi (F1), Sodankylä (F2), Laanila (F3), Kaamanen (F4) and Kevo (F5)) from the Arctic Circle to the northern tree line of pine in northernmost Finland (Fig. 2, Table 1) were felled in September 1996 for needle-production analyses. The Kevo site is located north of the continuous pine timberline, while the other sites are inside the area of continuous pine forest, i.e. the northern boreal zone. To extend the chronologies five additional pines per site were sampled in Rovaniemi and Laanila in September 2000. Annual samples were prepared and treated according to NTM standardized protocol (Aalto and Jalkanen 1998, Jalkanen et al. 2000). Needle production (see Jalkanen et al. 2002, referred to hereafter as PROD) is determined as the number of short shoots produced annually in a long shoot, and it is calculated based on measured shoot length and needle density (Jalkanen et al. 1998). PROD has been recorded from the main stem (rather than from branches), which has been shown to have many advantages (Jalkanen et al. 2000).

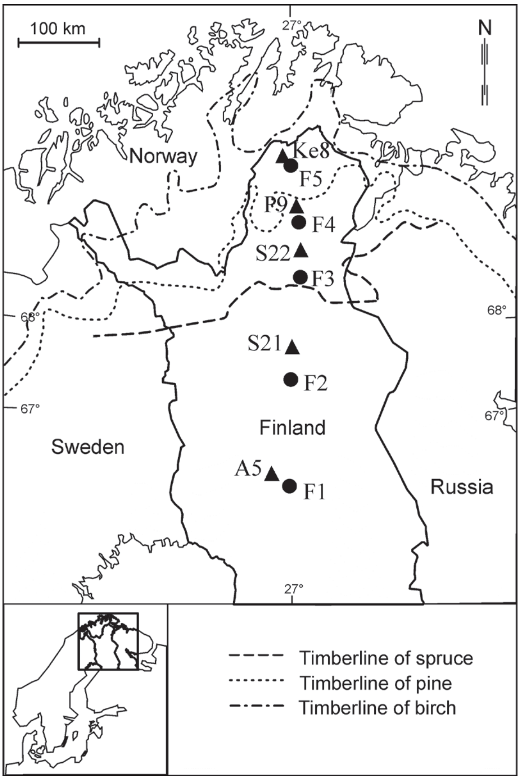

Fig. 2. Location of the experimental sites. Abbreviations for the NTM and short-term pollen monitoring sites: F1 = Rovaniemi, F2 = Sodankylä, F3 = Laanila, F4 = Kaamanen, and F5 = Kevo, and for the long-term pollen monitoring sites: A5 = Apukka, S21 = Petkula, S22 = Ukonjärvi, P9 = Palomaa, and Ke8 = Kevo.

2.2 Pollen-Accumulation Analysis

Annual pollen-accumulation was monitored by means of modified Tauber traps following the standard procedure of the Pollen Monitoring Programme (PMP, Hicks et al. 1996, 1999). Two transect series of traps were used from the Arctic Circle to the northern timberline. In the first set (Apukka (A5), Petkula (S21), Ukonjärvi (S22), Palomaa (P9) and Kevo (Ke8) (Fig. 2, Table 1), each trap was situated in the centre of a small mire (c. 200 m in diameter), which formed an opening in the regional forest. In the second set for the short-term pollen monitoring (code numbers F2, F3, F4 and F5 respectively), each trap was placed within the same forest (no sample for F1) from which the trees for the needle-production analyses were felled (Fig. 2). Results are available for twenty years, 1982–2001 (inclusive) for the mire set but only for the 5-year period of 1997–2001 for the 'within forest' set. This article uses the longer series but results from the shorter series are included to indicate annual variation in both the mire and the 'within forest' situation.

The whole range of pollen taxa collected in each trap was identified but only the results for the *Pinus* diploxylon pollen type are presented here (by default Scots pine because the only other diploxylon *Pinus* species, the introduced *Pinus contorta* (Dougl.) Loud., has a very limited distribution, occurring just in the southernmost part of the monitoring transect). The amount of pollen accumulated was calculated relative to added marker grains (Stockmarr 1971, Maher 1981) and expressed as grains $cm^{-2}\,year^{-1}$ (referred to hereafter as pollen accumulation rate, PAR;

for error ranges on these calculations, see Hicks 2001). In this study it is not the absolute quantity of pollen in any single year, but the variation in pollen abundance between years, especially the timing of years of very high or very low pollen production, which is of interest.

2.3 Data Analysis

The longest PROD chronologies date back to 1948. The common period for the two proxies (PROD and PAR) is 19 years long, 1982–2000. The relationship between PROD on the one hand and PAR on the other, and the mean monthly temperatures was analysed for the two previous biological years, i.e. from October to September. Mean monthly temperatures (T_{MONTH}, $T_{MONTH-1}$, $T_{MONTH-2}$) were chosen as the main group of predictors because temperature, rather than precipitation, has shown to be important for both PROD (Jalkanen and Tuovinen 2001), height increment (Salminen and Jalkanen 2004) and PAR (McCarroll et al. 2003, Autio and Hicks 2004) in timberline situations.

Prior cross-correlation analysis, PROD series were de-trended and also pre-whitened if a white noise test indicated statistically significant autocorrelation. In the two-phase de-trending a linear regression was fit to individual series and thereafter a 21–26-year (50% of the series length) cubic spline was applied to remove higher frequency variation in the series. If necessary, the series were pre-whitened using the autocorrelation-modelling feature of program ARSTAN. This selects the appropriate model based on the minimum Akaike information criterion. The mean indexed PROD for each year (PROD chronology) was calculated from the residual values using the bi-weight robust mean method (Cook et al. 1990). Measured PAR series passed both white noise and unit-root tests and were used without transformations to produce PAR chronologies.

PROD and PAR chronologies were cross-correlated with mean monthly temperatures. Time-series regression analysis was applied when reconstructing the past PAR. Either PROD chronology or temperature were used as independent variables. The parameters of the models were solved using AUTOREG procedure of SAS

Table 1. Description of the sampling sites along the latitudinal transect in northern Finland. Climate data are average values of the normal period of 1961–1990.

Site code	Location	Latitude	Longitude	Altitude (m)	Annual precipitation (mm)	Average July temperature (°C)	Thermal sum (d.d)	Average annual temperature (°C)	Forest site	No. of trees/ha	Stand age (yrs)	Average height (m)	Average diameter (cm)
F1	Rovaniemi	66°22´	26°43´	150	540	14.6	880	−0.1	Dryish	1800	45	8.3	10.2
A5	Apukka	66°35´	25°35´	95									
F2	Sodankylä	67°22´	26°38´	180	500	13.8	770	−1.1	Dry	1950	65	9.4	10.1
S21	Petkula	67°43´	26°46´	202									
F3	Laanila	68°30´	27°30´	220	460	13.1	670	−1.6	Dryish	1200	45	6.9	9.4
S22	Ukonjärvi	68°44´	27°26´	136									
F4	Kaamanen	69°07´	27°15´	155	430	13.0	670	−1.5	Dry	1450	50	7.8	9.1
P9	Palomaa	69°17´	27°12´	215									
F5	Kevo	69°40´	27°05´	110	410	12.7	630	−1.9	Dryish	1700	65	7.5	10.2
Ke8	Kevo	69°45´	27°00´	152									

statistical software (SAS User's Guide 2001). Each stand was analysed separately. On the basis of a graphical pre-examination, the dependence between PAR and PROD was non-linear. Recorded PAR (the dependent variable) was, therefore, centered and log-transformed prior to the analysis. As a result, the reconstruction model followed a simple exponential form:

$$Y_t = \overline{Y} \cdot e^{\alpha + \beta \cdot X_t} \tag{1}$$

where Y_t is the recorded PAR of year t, $\overline{Y}$ is the mean PAR of the stand, X_t is an independent variable (current-year PROD or the average temperature of the previous July), and α and β are parameters.

Meteorological data from the nearest climate stations were used as follows: Apukka for F1 and A5, Sodankylä for F2 and S21, Ivalo airport for F3, S22, F4 and P9, and Kevo for F5 and Ke8. Meteorological data of the years 1961–2000 and 1980–2001 were used for PROD and PAR, respectively.

3 Results

3.1 Chronologies for PROD and PAR

There was a good year-to-year agreement in raw and residual PROD among the five sites in 1948–2000, with the highest correlation coefficients (r>0.7) being between neighbouring sites. During the common period for PROD and PAR, all sites exhibited a negative PROD peak in 1988 and in 1993 (except Laanila); the three northernmost ones exhibited a negative PROD in 1985 (Fig. 3a). High positive values were found in 1986 and/or 1987 at all sites. In 1989–1991 the indices were clearly above the average in the three northernmost sites, but clearly below them in the two southernmost sites, Sodankylä and Rovaniemi. Since 1993 PROD seems to have increased towards the year 2000 with high recordings in Rovaniemi and Laanila in 1998 and 2000, suggesting that growing conditions for height growth have improved a lot in Lapland during the 1990s. The development in July temperature supports this (Fig. 3c).

In comparison with PROD the year-to-year agreement was even stronger in PAR among the five mire sites in 1982–2000 (Fig. 3b). The correlation coefficient (r) between the sites varied from 0.889 to 0.294, all except one being statistically significant. Typically a very high pollen accumulation year was followed by a few very low years in PAR in all areas. The highest PAR values, however, were recorded in the southern and the lowest in the northern sites. Increased PAR years were 1986, 1989, 1994 and/or 1995 and 1998, while years with low PAR were 1982–1983, 1985, 1987–1988, 1993, 1996, and 1999–2000. The year 2001 was also a good PAR year (not shown).

Similarly, the five-year forest PAR chronologies exhibited the same good year-to-year agreement that was found in the mire centre; with high values in 1998 and low ones in 1999 even though the actual PARs were significantly higher in the forest than in the centre of the mires, as predicted by models of pollen dispersal (Parsons & Prentice 1981, Prentice & Webb III 1986).

3.2 Relationships between Temperature, PROD and PAR

Mean July temperature of the previous year (T_{JUL-1}) correlated statistically significantly with PROD at all five sites (Table 2). This relationship was weakest in the two southernmost sites and strongest in the northern sites, especially in Kaamanen (r=0.77). Also T_{JUN-1} correlated significantly at all five sites but the coefficients were lower (r=0.38 to 0.56). No other clear monthly signal appeared in any of the sites.

PAR correlated significantly (r=0.51 to 0.67) with T_{JUL-1} in all except in the southernmost site, Apukka, and the climate signal strengthened towards tree line (Table 3). T_{JUN} (Palomaa, Kevo) also correlated significantly with PAR (r=0.51 to 0.59). In most sites T_{JUL-2} or T_{AUG-2}, and PAR correlated negatively, supporting the alternation of good and bad pollen years indicated earlier.

PROD and PAR correlated significantly in the three northern sites within the continuous pine forest region, Laanila/Ukonjärvi (r=0.51) and Kaamanen/Palomaa (r = 0.63), and north of the region at Kevo/Kevo (r=0.61) (Table 4). Cross-correlations were insignificant in the two southernmost sites.

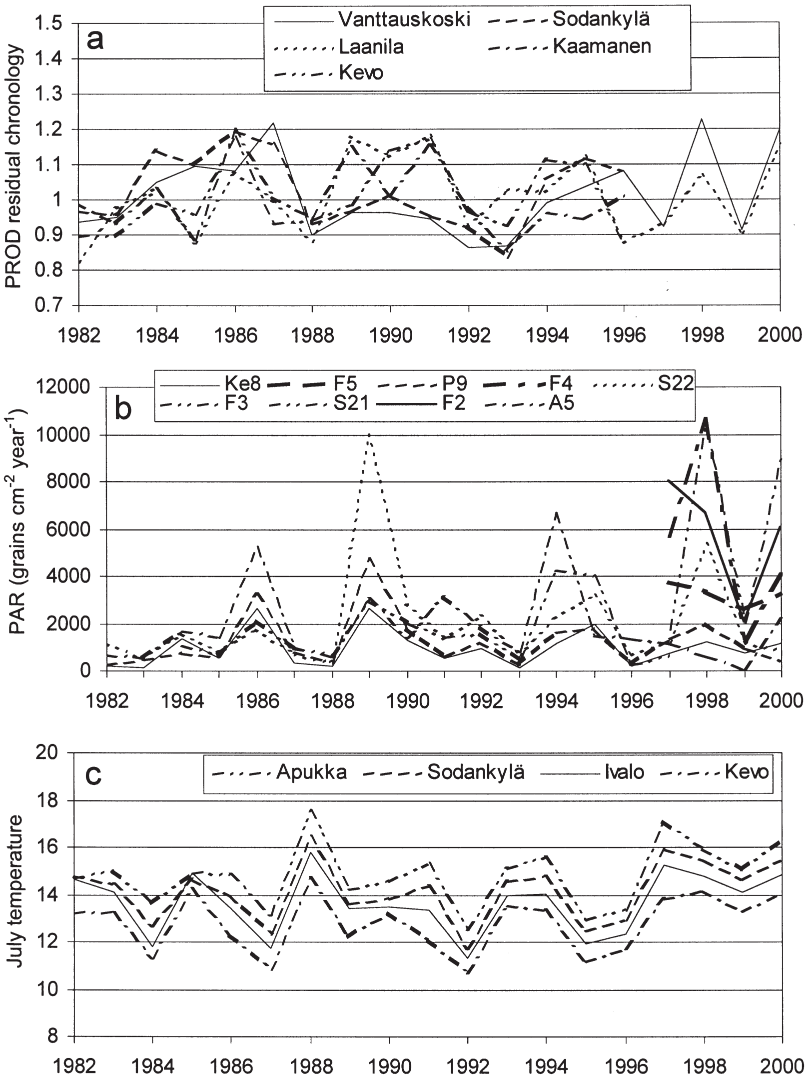

Fig. 3. Annual variation in PROD and PAR of *Pinus sylvestris*, and July temperature in their common period along the south–north transect in northern Finland in 1982–2000. a. Residual chronologies of needle production (PROD); b. raw pollen accumulated rate (PAR), and c. mean July temperature.

3.3 Reconstruction of Past PAR with July Temperature and PROD

Since T_{JUL-1} proved to be the most significant predictor for both PROD and PAR, it is used here to produce reconstructions of past PAR and thus test the robustness of the relationship (Fig. 4). At Kaamanen/Palomaa, Laanila/Ukonjärvi and Kevo/Kevo, the correlation between PROD and PAR was also significantly high (Table 4), PROD is used for reconstructing past PAR at these three sites (Fig. 5).

The PAR reconstructions either with PROD or T_{JUL-1} differ in magnitude, but the years with minimum and maximum values are generally the same. Both PROD and T_{JUL-1} are able to recon-

Table 2. Cross-correlation between PROD and mean monthly temperature with a lag of 0 to 2 years. Significant values are in bold. Standard error is 0.14–0.16.

Lag	Variable	Vant-taus-koski	Sodan-kylä	Laa-nila	Kaa-manen	Kevo
2	TJan	0.04	0.04	0.25	0.07	**0.36**
2	TFeb	–0.18	–0.06	0.01	0.08	0.00
2	TMar	**–0.32**	–0.12	0.07	0.05	–0.04
2	TApr	0.02	–0.01	0.02	0.04	0.00
2	TMay	–0.07	0.00	**0.32**	0.18	0.26
2	TJun	–0.14	0.07	–0.04	0.17	0.02
2	TJul	–0.04	0.03	0.26	0.09	0.18
2	TAug	–0.05	0.08	0.07	0.05	–0.01
2	TSep	0.04	0.02	0.00	–0.03	–0.01
2	TOct	–0.04	–0.09	0.00	–0.05	0.11
2	TNov	–0.15	–0.22	–0.26	**–0.33**	–0.31
2	TDec	–0.05	0.01	0.04	0.08	–0.06
1	TJan	–0.05	0.00	0.23	0.09	0.26
1	TFeb	0.02	–0.20	0.06	–0.15	0.11
1	TMar	0.10	0.24	**0.41**	0.24	**0.44**
1	TApr	0.08	0.09	0.14	0.05	0.09
1	TMay	0.17	0.13	0.03	–0.09	–0.01
1	TJun	**0.46**	**0.56**	**0.44**	**0.38**	**0.47**
1	TJul	**0.42**	**0.37**	**0.66**	**0.77**	**0.67**
1	TAug	0.08	–0.07	0.19	0.30	0.22
1	TSep	0.21	–0.08	0.14	0.01	0.08
1	TOct	0.20	0.17	0.00	0.06	0.03
1	TNov	0.08	–0.01	–0.05	–0.03	0.05
1	TDec	0.05	0.21	0.24	–0.05	0.23
0	TJan	0.09	–0.07	0.22	0.07	0.15
0	TFeb	0.11	0.20	**0.36**	**0.35**	**0.43**
0	TMar	–0.09	0.06	0.12	0.29	0.19
0	TApr	0.10	0.20	**0.42**	**0.35**	**0.49**
0	TMay	–0.06	–0.19	–0.01	–0.02	0.13
0	TJun	–0.10	–0.04	–0.03	0.23	–0.01
0	TJul	0.03	–0.05	–0.24	–0.06	–0.23
0	TAug	–0.16	0.03	–0.15	–0.04	–0.15
0	TSep	–0.07	–0.01	0.10	0.21	0.05

Table 3. Cross-correlation between measured PAR and mean monthly temperature with a lag of 0 to 2 years. Significant values are in bold. Standard error is 0.23.

Lag	Variable	A5	S21	S22	P9	Ke8
2	TJan	0.14	0.20	–0.10	–0.13	0.01
2	TFeb	0.42	0.24	–0.04	0.11	0.15
2	TMar	0.03	–0.09	–0.35	–0.35	**–0.48**
2	TApr	0.01	–0.42	–0.21	–0.21	–0.14
2	TMay	**0.65**	0.35	–0.12	0.20	0.23
2	TJun	0.11	–0.09	–0.27	–0.11	–0.36
2	TJul	**–0.52**	–0.22	–0.40	**–0.51**	–0.28
2	TAug	**–0.46**	–0.35	–0.24	–0.34	–0.32
2	TSep	0.29	0.08	0.00	0.00	–0.11
2	TOct	–0.43	–0.45	0.40	0.22	0.07
2	TNov	–0.15	–0.10	–0.02	–0.18	–0.08
2	TDec	0.37	0.23	–0.14	–0.05	0.10
1	TJan	–0.05	0.03	0.14	–0.02	–0.28
1	TFeb	–0.04	–0.22	–0.08	–0.37	–0.41
1	TMar	0.06	–0.17	–0.05	–0.06	–0.13
1	TApr	–0.01	0.15	–0.22	–0.27	0.00
1	TMay	0.02	–0.08	–0.03	–0.16	–0.24
1	TJun	–0.20	–0.08	0.13	0.03	0.10
1	TJul	0.18	**0.51**	**0.59**	**0.61**	**0.67**
1	TAug	0.14	0.17	0.40	0.44	0.39
1	TSep	–0.32	–0.14	0.23	0.09	0.20
1	TOct	–0.13	–0.13	–0.06	0.02	0.05
1	TNov	–0.05	0.10	–0.14	–0.01	–0.08
1	TDec	–0.18	0.04	–0.04	–0.26	–0.28
0	TJan	–0.07	0.06	0.26	0.04	0.00
0	TFeb	–0.19	0.25	0.08	0.09	0.20
0	TMar	0.20	0.41	0.36	**0.49**	**0.47**
0	TApr	0.28	**0.47**	0.38	0.30	0.28
0	TMay	0.01	0.03	0.29	0.26	**0.48**
0	TJun	0.19	0.35	0.24	**0.51**	**0.59**
0	TJul	0.01	–0.18	–0.10	–0.11	–0.28
0	TAug	0.13	0.03	0.07	–0.03	–0.06
0	TSep	–0.32	–0.06	–0.03	–0.12	–0.23

struct the highest recorded PAR values in 1986 and 1989 at Ukonjärvi and Palomaa but at Kevo PROD is unable to reconstruct the high recorded PAR in 1989 (Fig. 5c). Reconstruction of PAR with PROD for the period from the 1950's to 1980 suggests relatively high PARs in the years 1973–1975 and 1961 in all three northern sites. The highest reconstructed values are for the years 1955, 1961 and 1974. The use of T_{JUL-1} for PAR reconstructions results in 2 to 4 times higher values than the use of PROD during the highest reconstructed peak in 1972–1973. However, the values with lower PAR, independent of the reconstruction parameter, are generally similar and reconstructed PAR minima correspond well with those of recorded PAR minima (Figs. 4 and 5).

PROD-based models (Table 5; the significant models are shown) explained most of the variation (51%) at Kevo, but the explained variation decreases southward (Table 6). At Kevo the model based on PROD was stronger than the model based on T_{JUL-1} but from Kaamanen to Sodankylä T_{JUL-1} explained variation more than PROD.

In order to evaluate the robustness of the recon-

Table 4. Cross-correlation between measured PAR and PROD with a lag of –3 to 3 years. Significant values are in bold. Standard error is 0.23–0.26.

Lag	Apukka/ Vanttauskoski	Petkula/ Sodankylä	Ukonjärvi/ Laanila	Palomaa/ Kaamanen	Kevo/ Kevo
3	–0.29	–0.30	–0.16	–0.01	–0.29
2	–0.20	–0.25	0.28	0.26	0.11
1	0.12	0.09	0.09	0.03	0.01
0	0.06	0.26	**0.51**	**0.63**	**0.61**
–1	–0.30	–0.40	–0.17	–0.23	–0.15
–2	–0.06	–0.32	–0.20	–0.18	–0.43
–3	–0.22	0.00	0.32	0.48	0.12

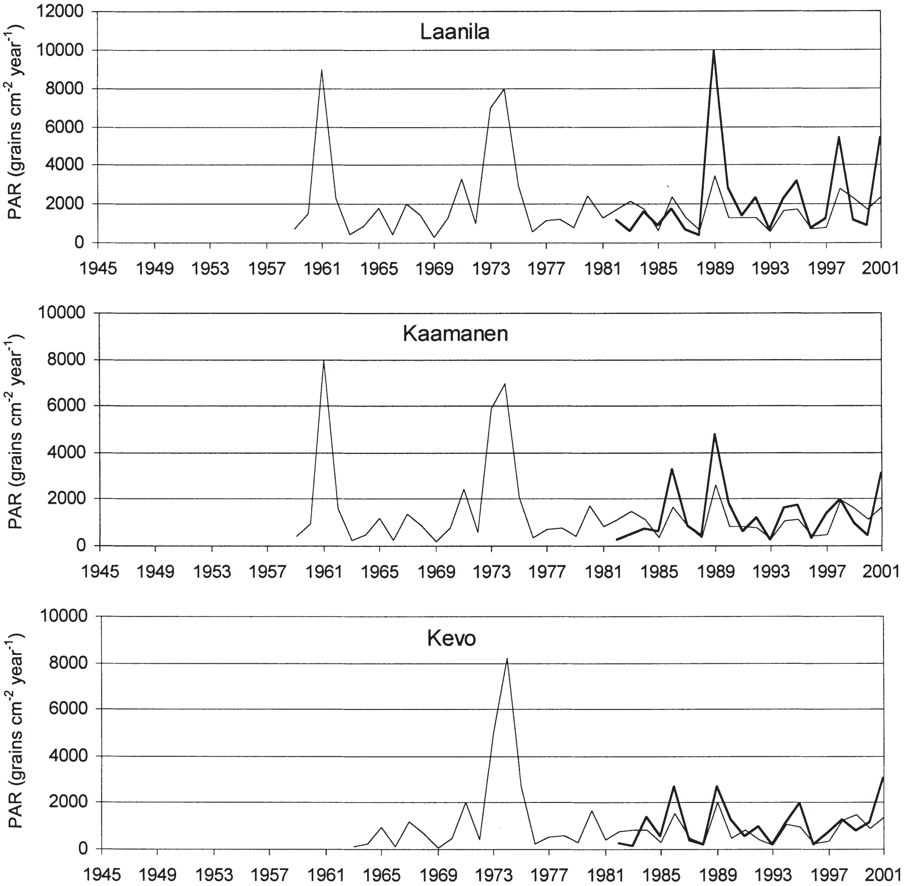

Fig. 4. Reconstruction of pollen accumulation (PAR) by T_{JUL-1} in *Pinus sylvestris* in Laanila, Kaamanen and Kevo near the northern timberline in Finland as compared with the recorded PAR at Ukonjärvi, Palomaa, and Kevo, respectively.

Table 5. Estimated model parameters for PAR based on PROD in the three northernmost sites.

Stand	Variable	Estimate	Error	t-value	Pr0>|t|
3	α	–4.51	1.52	–2.97	0.0085
	β	4.04	1.49	2.69	0.0154
4	α	–5.84	2.17	–2.69	0.0184
	β	5.34	2.15	2.49	0.0272
5	α	–7.68	1.93	–3.97	0.0016
	β	7.08	1.91	3.70	0.0027

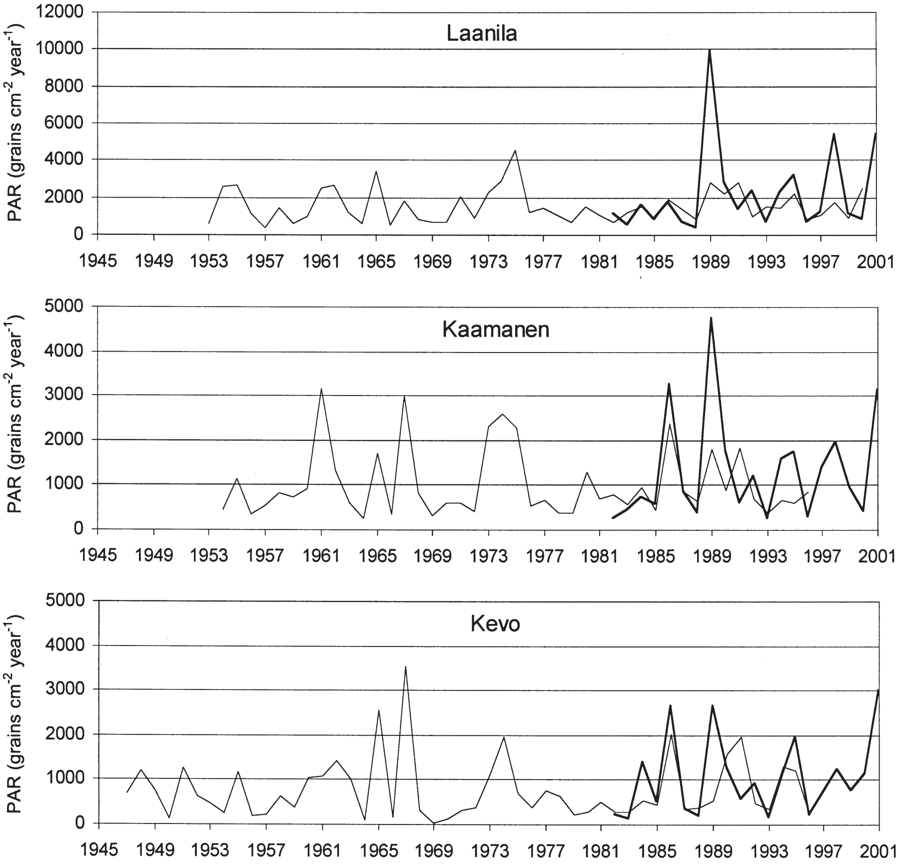

Fig. 5. Reconstruction of pollen accumulation (PAR) by PROD in *Pinus sylvestris* in Laanila, Kaamanen and Kevo near the northern timberline in Finland as compared with the recorded PAR at Ukonjärvi, Palomaa, and Kevo, respectively.

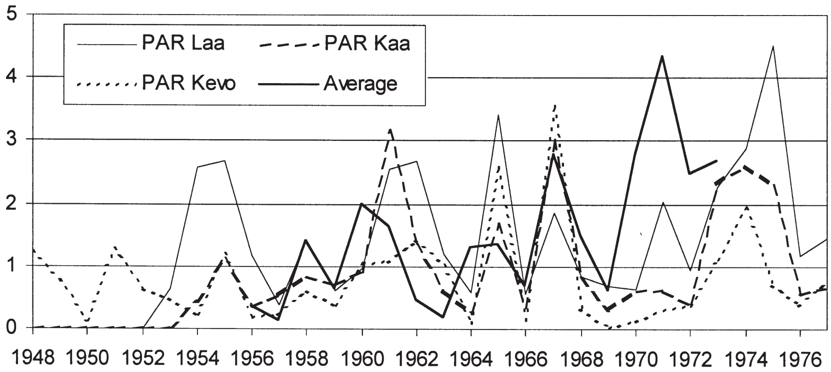

Fig. 6. Reconstructed pollen accumulation (PAR) of *Pinus sylvestris* in Laanila, Kaamanen and Kevo, and an averaged male-flower deposition of ten sites from Rovaniemi to Utsjoki (recalculated from Koski and Tallqvist (1978)).

Table 6. Explained variation of the models for PAR based on PROD or T_{JUL-1}.

Site	Explained variation in the independent variable, %	
	PROD	T_{JUL-1}
Vanttauskoski	3	0
Sodankylä	4	62
Laanila	30	41
Kaamanen	32	47
Kevo	51	45

structed PAR for the period before PAR records are available, i.e. pre 1982, the reconstructed values are compared with the record of pine male flowers for the period 1956–1973 (Koski and Tallqvist 1978, Koski 1981). As both the reconstructed series and the male-flower series retain the high-frequency signal by showing a good year-to-year agreement between the chronologies (Fig. 6), the reconstructed PAR models encourage their use in dating past pollen years.

4 Discussion

4.1 Chronologies for PROD and PAR

There is a good year-to-year agreement between the site chronologies of PROD for the period from 1950's to 1990's. In most years and for most sites high and low years alternate. There is a clear reason for this. Jalkanen and Tuovinen (2001) have found a strong relationship between PROD and July temperature of the previous year both close to the northern timberline and over a larger area. Since the July temperature records of the northern Finnish climate stations are highly correlated with each other (Pensa et al. 2005), so is the temperature-dependent PROD. However, this agreement in PROD was not strong in all periods. Between the years 1989 and 1991 the two southernmost sites, Rovaniemi and Sodankylä, have below-average values, instead of the high index values recorded in the northernmost sites. Pines in the southern part of the transect experienced an exceptional frost-to-roots damage and a root-decline phenomenon in the winter 1986/1987 (Jalkanen et al. 1995), which resulted in a shortage of carbohydrates, and a reduced number of needle initials in the following years until the trees recovered (Jalkanen 1998, Tuovinen et al. 2005).

The annual PAR has a high year-to-year agreement over the 20-year period between all sites since PAR at any one site reflects pollen production for a relatively wide area. PAR, therefore, contains inherent 'smoothing' compared with PROD, which is the record for a specific tree stand. The reason why a clearly high pollen year is often followed by at least one low pollen year must be linked with the physiology of the tree.

It is commonly observed in birch that massive pollen and seed production in one year uses up the reserves of the tree so that the same amounts cannot be produced in the following year and a similar mechanism seems to be present in pine with respect to pollen production but not needle production.

Although PAR chronologies between the sites are in agreement, the actual values are consistently higher in the southern than the northern sites. This reflects both the general health status of the trees and their overall abundance. At the two northernmost PAR sites (Kevo and Palomaa) pine is at its ecological limit; pollen production is less successful than in areas further south, where climate conditions are more favourable

Another reason for the variation in pollen quantity may be the wind direction during the period of pollen emission. In any year in which the dominant wind direction during the time of pollen emission is southerly, there is a greater chance of ‘southern’ pine pollen being abundantly deposited in the north. The year 1989 was such a year (Oikonen et al. 2005).

PAR at the ‘within forest’ traps is considerably higher than at the comparable mire centre traps but their annual fluctuations are in good agreement since the climate signal is the same.

4.2 The Chronologies and Climate

In monocyclic Scots pine, needle formation is predetermined by the climatic conditions of the previous summer, i.e. the needle initials of the short shoots developing in year two are formed in the lateral buds in year one (Duff and Nolan 1953, Hustich 1978). As the summer is shortest in the northern boreal zone, needle initials are formed during a very short period, at and soon after the time when shoot extension ceases, in late June–early July (Junttila and Heide 1981, Salminen and Jalkanen 2007). Needle production (PROD) generally decreases towards the north (see also Pensa and Jalkanen 2005). Since July temperature also decreases towards the north, this is in good agreement with the hypothesis that the mean temperature of the previous July is the main factor controlling PROD (Jalkanen and Tuovinen 2001, Salminen and Jalkanen 2004), the significance increasing towards the tree line. A lower but significant correlation of PROD with June temperature of the previous year suggests that it is not solely July temperature that determines the number of needle initials. This may also mean that the most effective period is shorter than one month, and is located in late June to early July.

The results presented here demonstrate that T_{JUL-1} is the main explanatory factor (see also McCarroll et al. 2003). The correlation between PAR and T_{JUL-1} increases towards the north. Temperature becomes a critical regulator of pollen production when the trees are growing close to their ecological limit and the calibrations suggest that the critical limit for pollen production is 10.5°C in the furthest north but a little above 11°C further south.

The significant correlation between PAR and T_{JUL-1} indicates that, at this temporal resolution (annual), variations in pine PAR can be used as a proxy for variations in summer temperature and specifically July temperature. This is in keeping with the findings from an altitudinal transect within the spruce dominated area of western Finnish Lapland (Autio and Hicks 2004).

The correlation between PAR and T_{JUN} at the two northernmost sites, the time of year when pollen is being emitted to the atmosphere, is more difficult to explain. T_{JUN} should not affect pollen productivity, only the timing of pollen emission. If July temperature is so low in one year (below 10°C) that no male-flower initials are formed, then pollen emission in the following year must also be low, however high the June temperature in that year is. It is conceivable that in years of low June temperature (especially if coupled with wet days) pollen emission to the atmosphere is so inhibited that any pollen produced cannot be efficiently dispersed and, therefore, is not recorded in the pollen trap, thus providing a correlation with low temperature.

4.3 Relations between PROD and PAR

It is evident that needle production, PROD, and annual pine-pollen accumulation rate, PAR, correlate with July temperature of the previous year. Thus it can be expected that they correlate with each other and that, taken together, the fossil records of both should form a strong proxy for July temperature. The feasibility of using these two parameters jointly to reconstruct past temperature will be tested in more detail in future studies once longer near-annual fossil pollen records exist from the same area.

Of the five sites along the transect PROD and PAR show a significant correlation at Laanila/Ukonjärvi, i.e. within the continuous pine forest, at Kaamanen/Palomaa, i.e. at the northernmost limit of continuous pine forest and at Kevo/Kevo, i.e. at the isolated pine population. Although PROD and PAR have a good year-to-year agreement in all sites, there are factors affecting their values differently even though both are strongly determined by T_{JUL-1} and the stronger the more northern site, suggesting that the short time during which needle and male-flower initials are formed is very strongly controlled by the temperature.

4.4 Reconstructing Past PAR

When PROD and T_{JUL-1} were used to reconstruct PAR, the models normally resulted in values 25 to 50% of the recorded ones, July temperature fitting better than needle production. Although temperature, rather than needle production, gives the best reconstruction for the time of instrumental records it is the period before the climate recordings that frequently needs verification and needle production provides a tool for this at near tree line conditions. When using PROD to reconstruct long chronologies of PAR, the resulting event years, if they can be identified as pollen peaks in the fossil record, can form a means of validating the dating of peat profiles. The uppermost layers of peat profiles, representing the very recent past have been dated by wiggle matching the ^{14}C content of the peat with that of the atmosphere (Goslar et al. 2005). This enables a near annual sampling resolution to be achieved, allowing annual PARs to be calculated. However, this resolution is insufficiently precise to produce calendar years incorporating only one growing season. A comparison between peaks and lows in PAR with the predictions of pointer years based on PROD can be of great help in evaluating the robustness of the ^{14}C based age-depth chronologies.

There are some publications, which verify both the measured and reconstructed pollen chronologies in terms of independently measured pollen production. These either cover just a short part of the PAR or reconstructed period of our study, or they originate in southern Finland. Pakkanen and Pulkkinen (1991) have assessed pollen production in two Scots pine seed orchards, which are situated in southern Finland but established with northern Finnish trees. For the period 1987–1990 pollen production was the lowest in 1989, which conflicts dramatically with our results (based on both recorded and reconstructed values) that 1989 was a good pollen year in all northern sites but especially good in the northernmost sites. Pollen production in seed orchards in southern Finland was lower in 1989 or 1988 than in 1987 or 1990 (Pakkanen and Pulkkinen 1991). Our hypothesis is that temperature plays a decisive role for pollen production in northern sites where the trees are at their ecological limit. The seed orchard calculations could be taken as being in line with this in that temperature does not seem to play the same dominant role in the south. On the other hand, according to Koski (1981) the year 1980 was clearly a better pollen year than 1978 and 1979. These relative levels are in agreement with our reconstructed values. Material from 1997 to 2000 at four locations from Rovaniemi to Kevo, collected by A. Pakkanen (unpublished data), also fits well with our records, having the best year in 1998.

All the above-mentioned pollen material was trapped in the air, i.e. it describes the pollen concentration in the air. Koski and Tallqvist (1978), who have produced 8 to 13-year-long series of male flowering in Scots pine throughout Finland, collected their data as dried male-flower remnants deposited in litter funnels (Sarvas 1962). Since the results of Koski and Tallqvist (1978) cover a time beyond our pollen-trapping period, we used this material to verify the reconstructed PAR. There is a good year-to-year agreement between the two data sets in the late 1950's to early 1970's (Fig. 6). These results strongly suggest that, although based on male flowers, needle production can be used to reconstruct past pollen chronologies. However, this has to be confirmed with further studies on peat profile, ^{14}C dating, and needle production.

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