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Age-dependent climate sensitivity of *Pinus sylvestris* L. in the central Scandinavian Mountains

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Twentieth century climate–radial growth relationships of *Pinus sylvestris* L. at the central Scandinavian Mountain tree line were analyzed. Some differences in growth responses to climate were evident among age classes, where the old pines (> 250 years old) retained their climate sensitivity throughout the analysed period better than the middle-aged pines (100–250 years old). However, the pines in the oldest age class responded less to unfavourable climate than the pines in younger age classes. The pines in all the age classes displayed significant changes in climate/radial growth relationships from the 1940s and onwards. From the 1970s, pines in the youngest age class (about 35 years old) displayed a higher climate sensitivity than the older pines, in addition to which they had high growth rates not previously seen in the past five centuries. Changes in climate/radial growth relationships were related to a twentieth-century climate change. Finally our results illustrated the importance of including trees of all ages when building a tree-ring chronology for climate research.

Introduction

The annual growth of high-latitude trees growing in natural environments is dependent mainly on the climate of the vegetation period, but also on additional factors such as the microclimate, past year's growth, tree age, ground surface slope and soil conditions (Fritts 1976). Close to their latitudinal and altitudinal limits of distribution in Fennoscandia, the main growth-limiting factor of Scots pine (*Pinus sylvestris* L.) is the summer temperature, mainly that of July (e.g. Briffa *et al*. 1992, Lindholm *et al*. 1996, Gunnarson and Linderholm 2002). Tree-ring data from Fennoscandia have been used for making high-resolution reconstructions of past regional temperatures (Briffa *et al*. 1992, Kalela-Brundin 1999, Lindholm and Eronen 2000), and have also been included in most high-resolution reconstructions and evaluations of past temperatures in the northern hemisphere (Mann *et al*. 1999, Crowley 2000, Briffa *et al*. 2001, Esper *et al*. 2002, Mann and Jones 2003). When reconstructing climate, the non-climatic "noise" is removed from the tree-ring data, to maximise the climate signal in the tree-ring data, in a process called standardisation (Fritts 1976, *see* below). Usually, it is assumed that after the standardisation the relationship between the tree growth and climate is independent of the age of the tree, i.e. at a given time trees of different age will respond equally to climate. However, if trees of different ages responded differently to climate, a climate reconstruction based on tree-ring data from uniformly-aged trees might not capture the full range of climate variability throughout the length of the chronology.

In recent years, an increasing number of publications reported a reduced sensitivity to temperature during the last decades for trees growing at high latitudes in the northern hemisphere (e.g. Briffa *et al*. 1998a, 1998b). Furthermore, negative growth trends of high-latitude trees in Eurasia and North America have been reported for the late twentieth century (e.g. Jacoby and D'Arrigo 1995, Hughes *et al*. 1999, Gervais and MacDonald 2000). The reduced climate sensitivity and decreasing growth have been related to global warming (Jacoby *et al*. 1999, Barber *et al*. 2000, Biondi 2000), or anthropogenic emissions of greenhouse gasses leading to increasing CO_2, tropospheric ozone or ultra violet radiation levels (Briffa *et al*. 1998a, 1998b). Twentieth century changes in climate–radial growth relationships of Scots pine and Norway spruce (*Picea abies*) in west-central Scandinavia have been linked to changes in wintertime climate (Linderholm 2002, Solberg *et al*. 2002). The implication of the above mentioned studies is that contemporary climate change has led to changes in tree-growth responses to climate. However, the full reason for the reduced climate sensitivity in high-latitude trees has yet to be fully explained.

Usually modern (i.e. based on samples from living trees) chronologies contain a majority of samples from old trees in order to reach as far back in time as possible. Consequently, when reconstructing climate from such tree-ring data, it is assumed that a tree will respond to climate regardless of its age. Yet, should the tree growth responses to climate change vary with age, it would bias climate reconstructions/interpretations. Past studies of an age-dependent climate sensitivity in trees have given ambiguous results. Gray (1982) found a discrepancy in climate responses of French oaks of different age, caused possibly by differences in the physiological processes of differently aged trees. Szeicz and MacDonald (1994) showed that growth responses to summer temperatures of *Picea glauca*, at the alpine tree line in Canada, declined with the tree age. On the other hand, Colenutt and Luckman (1991) found no discrepancies between the climate response of young and old *Larix lyalii* in the Canadian Rocky Mountains, and in the Italian Alps Carrer and Urbinati (2002) noted that *Pinus cembra* and *Larix decidua* displayed age consistent climate–growth relationships, but that sensitivity increased with the age.

In this paper the relationship between climate and radial Scots pine growth during the twentieth century is explored in five age classes. Pines were sampled at their limit of distribution at the tree line in the central Scandinavian Mountains, where there is a strong relationship between annual Scots pine radial growth and summer temperatures (Gunnarson and Linderholm 2002). Furthermore, previous studies in which the tree-ring data mainly consisted of samples from old trees, have shown that Scots pine in this area has displayed distinct changes in the climate–radial growth relationship throughout the twentieth century (Linderholm 2002, Linderholm *et al*. 2003).

Materials and methods

Study area

The study area, located within the northern boreal zone, lies just east of the Scandinavian Mountains main divide (Fig. 1). The main topography ranges from 800–1000 m above sea level (a.s.l.), but scattered alpine massifs to the south reaches approximately 1700 m a.s.l. The climate east of the Scandinavian Mountains can be described as continental, but the proximity to the Norwegian Sea and lack of high mountains in the west provide an influence of mild and moist westerly winds to the area. Consequently, the study area is located in a border zone between oceanic and continental climates. The average temperature is –7.5 °C in January and 11.3 °C in July, and the average annual precipitation is 846 mm (Storlien/Visjövalen 1901–1996). The local pine tree-limit is at about 700 m a.s.l.

Dendrochronology

Increment cores were collected from Scots pine, growing in the upper parts of the Handölan

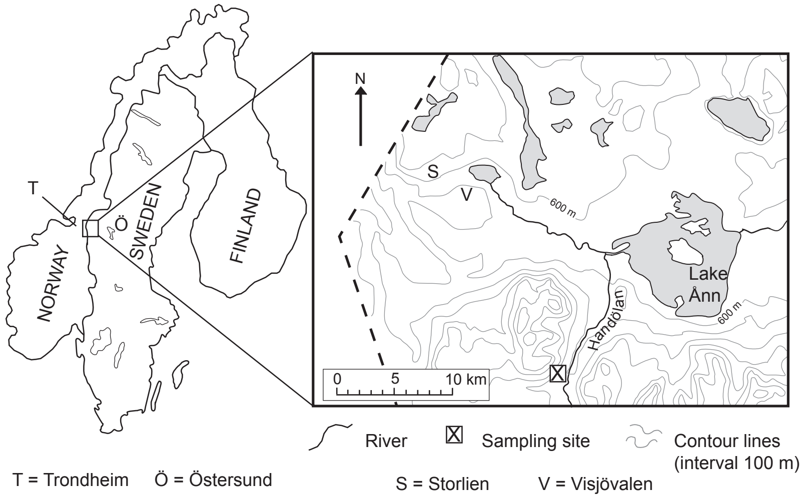

Fig. 1. Map showing the location of the sample site in the Handölan valley, central Scandinavian Mountains (63°15´N, 12°30´E), Sweden. Also shown are the locations of the metrological stations used in the study. 42 samples of Scots pine (*Pinus sylvestris* L.) of different age were collected at the tree limit (about 700 m above sea level) in the river Handölan valley.

Valley (63°10´N, 12°25´E, Fig. 1), at about 700 m a.s.l. Here the pines of different size and age grow in scattered stands on well-drained outcrops of glacial lake sediments with no signs of human activities. The sampled pines, in total 42, were selected to represent different age classes from young to mature and old. Two cores were extracted from each pine at approximately 1.3 m above the ground. The annual tree-ring widths of each core were measured with a precision of 0.01 mm, and if cross-dated averaged to a tree-ring series for each tree. To ensure correct dating, all tree-ring series were checked visually as well as with a COFECHA software which analyses the quality of a set of tree-ring measurements, verifies cross dating among tree-ring series and indicates possible dating or measurement problems (Holmes *et al*. 1986). The pines were grouped into five age classes:

I: 100–175 years old (nine trees),
II: 176–250 years old (ten trees),
III: 251–325 years old (nine trees),
IV: > 326 years old (five trees),
V: (nine trees) pines younger than 100 years of which six pines were younger than 50 years.

It should be noted that the given age is that at breast height, so in reality the trees were older.

A tree-ring series can be expressed as a linear composition of several sub-series (Cook 1990). These sub-series include an age-related growth trend, a climatic signal common to all trees at the site, and the influence of endogenous (single tree) and exogenous (common to most trees) disturbances in the stand. In order to remove the effects of a changing age and geometry of the tree that are unrelated to climate, all tree-ring width series were standardised (Fritts 1976). The standardisation included negative-exponential or straight-line curve fits. The obtained indices were then averaged into a master chronology for each age class. The standardisation was performed with a software ARSTAN (Cook 1985, Holmes 1994) using negative exponential functions or regression lines. For comparison between the age-class chronologies, descriptive statistics were used such as the mean sensitivity (MS) that is a measure of the relative change in ring widths from one year to the next, standard deviation (SD), first order autocorrelation (AC) that is the strength of dependence of a given year's chronology value on the value immediately preceding it, and variance explained by the first principal component (PC1) that is the variation held in common among the samples in the chronology, for the common analysis period 1900–1998.

Dendroclimatic analyses

To establish the climate–radial growth relationships for Scots pine in the first four age

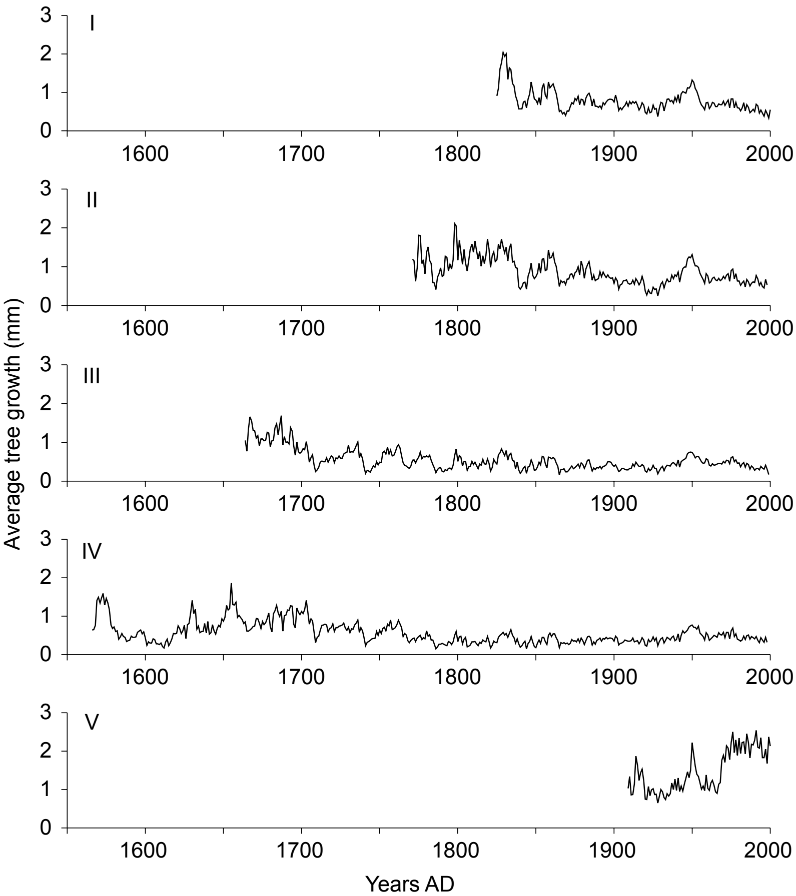

Fig. 2. Comparison of the raw-data age-class chronologies I–V.

classes, correlations were calculated between the ARSTAN chronologies, mean monthly temperature and total monthly precipitation. We used data from the closest meteorological station Storlien (68°19´N, 12°06´E, 595 m a.s.l.). In 1962 the station was moved to Visjövalen (68°18´N, 12°07´E, 642 m a.s.l.). The Storlien/Visjövalen meteorological data (1901–1996) were tested for homogeneity by comparison with regional Swedish and Norwegian stations, and was regarded as appropriate for the study due to the proximity to the study area (Fig. 1) and elevation of the stations. A 12-month period of analyses, from September of the preceding year to August of the growth year, was used to incorporate the effect of the previous winter's climate on the pine growth as well as climate during the growth season. Linderholm (2002) showed that the Scots pine growth responses to climate in the area varied throughout the twentieth century, so a correlation analysis was performed on the chronologies of age classes I–IV in three sub periods (1907–1936, 1937–1966 and 1967–1996). Only the correlation analysis was performed in the last sub-period on age class V chronology, since the chronology mainly consisted of young trees.

Table 1. Correlation matrix for the raw data age-class chronologies from the Handölan valley. Regular numbers indicate correlation over the entire chronology spans while those in boldface indicate correlation in the twentieth century.

Age class	I	II	III	IV	V
I	1	**0.87**	**0.80**	**0.75**	**–0.04**
II	0.89	1	**0.90**	**0.87**	**0.25**
III	0.81	0.72	1	**0.86**	**0.20**
IV	0.53	0.34	0.82	1	**0.29**
V	–0.04	0.25	0.20	0.29	1

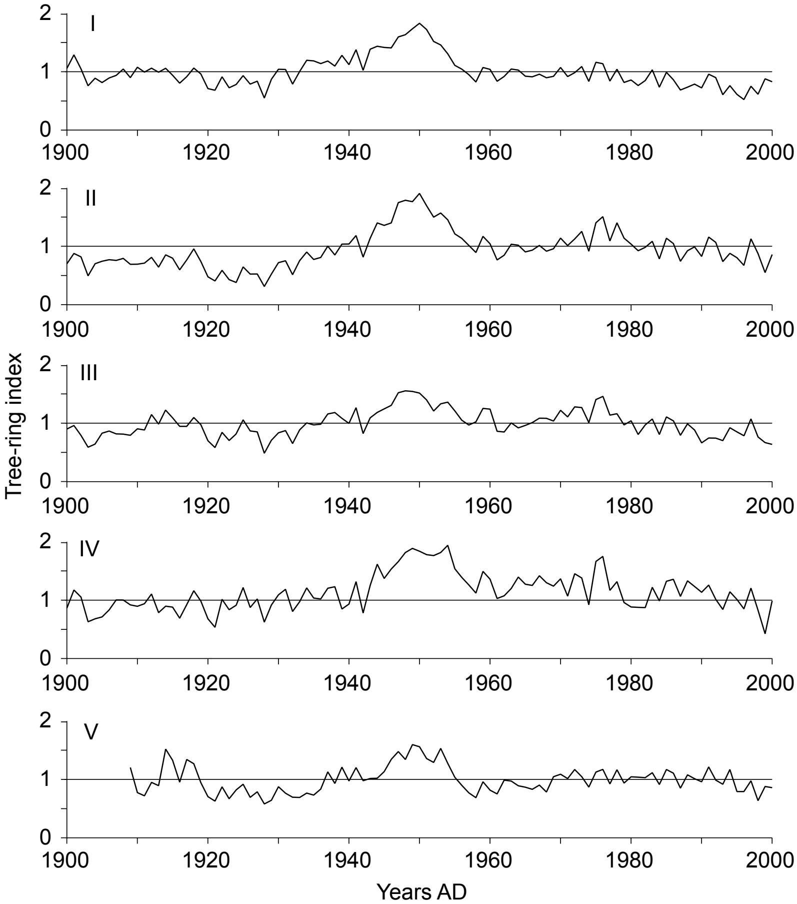

Fig. 3. Comparison of the standardised age-class chronologies I–V in 1900–2000.

Results

Similarities in growth patterns among certain of the age classes were apparent; growth variability and average annual growth were highly similar in age classes III and IV, and also in age classes I and II (Fig. 2 and Table 1). The average annual growth in age class V was far higher than that in the other age classes, especially around 1970 when the young trees were introduced. The growth patterns of the standardised age-class chronologies displayed a common variability in the twentieth century, with around or below average growth in the beginning of the century, a growth surge in the 1940s–1950s and a following growth decline (Fig. 3). Nevertheless, the correlation among the standardized chronologies indicates differences in growth variability, especially prior to the twentieth century (Table 2). Throughout most of the century, the oldest pines (age class IV) displayed the highest average standardised growth, especially in 1950–1970. Radial growth decline in 1920–1940 was most pronounced in group II, while the radial growth decline from the late 1970s and onwards was present in all the age classes. Chronology statistics (Table 3) revealed common features among

Table 2. Correlation matrix for the standardised age-class chronologies from the Handölan valley. Regular numbers indicate correlation over the entire chronology spans while those in boldface indicate correlation in the twentieth century.

Age class	I	II	III	IV	V
I	1	**0.77**	**0.78**	**0.73**	**0.66**
II	0.74	1	**0.85**	**0.87**	**0.75**
III	0.71	0.79	1	**0.83**	**0.70**
IV	0.65	0.62	0.69	1	**0.61**
V	0.66	0.75	0.70	0.61	1

the age classes, but the mean sensitivity (MS) and standard deviation (SD) were lowest in the youngest age classes. The auto correlation (AC) was consistent for all the age classes, except for pines younger than 100 years, where it was slightly lower, suggesting that the dependency of previous years' growth is independent of the tree age. The variation held in common among the samples in the age-class chronologies (PC1) was higher in the oldest age classes.

Correlation analyses disclosed similar but not equal climate–radial growth relationships among the age classes within the three analysed 30-year periods, as well as significant changes of the climate–radial growth relationships through time (Fig. 3). In 1907–1936, the summer temperatures were significantly correlated with the Scots pine growth in all the age classes and there was an additional strong influence of late fall–early winter temperatures in the age class I. In age classes I and II correlations with June temperatures were the highest, while correlations with July temperatures were the highest in age classes III and IV. Summer precipitation was negatively correlated with the pine growth in all the age classes. The variance in pine growth explained by climate (r^2) ranged from 0.6 (II) to 0.8 (III). The influence of climate on radial pine growth weakened drastically in 1937–1966, which is seen both in the correlation coefficients and the r^2 values, implying that neither temperatures nor precipitation were growth-limiting factors during this time in any of the age classes. The reduced importance of growth season temperatures was especially clear for the oldest pines in age class IV. In 1967–1996 r^2 values were almost equal to the preceding period, but there was no strong relationship between pine growth and summer temperatures. Instead radial pine growth was negatively (and significantly) correlated to April temperatures in age classes I to IV. Only pines in age class V displayed a strong and significant correlation with July temperatures.

In an attempt to test if tree age governs the response of its growth to climate, the standardized age-class chronologies were plotted against a summer (June–August) temperature index derived by averaging Trondheim and Östersund temperatures (100 km west and east respectively of the study area) over the period 1861–2000 (Fig. 4). Despite the large distances from the study area and differences in elevation among the sites, there was a strong coherency in summer temperature variability among the sites (correlation in 1901–1996 was 0.96 between Storlien and Östersund and 0.94 between Storlien and Trondheim). Consequently, this summer temperature index was regarded to be valid for Handölan. Over the 140 years, there were little differences among the age classes in terms of co-variation with summer temperatures. However, in the last decade of the twentieth century age classes I–III displayed growth indices below the temperature index, which was particularly evident in age class I. On the other hand, the oldest (IV) and youngest age classes (V) followed the temperature record reasonably well during that period. Only trees in age class IV did not respond with decreased growth to the cooling in the 1960s and in the period between 1910 and 1940 when especially pines in age-class II displayed growth indices well below the temperature index.

Table 3. Statistics of five age classes of Scots pine growing at the species tree line in the Handölan valley, central Scandinavian Mountains, Sweden. Statistics are presented for the common period 1900–1998. MS = mean sensitivity, SD = standard deviation, AC = auto correlation, PC1 % = variance in first principal component.

Age class	Tree age span	Mean tree age (yrs)	Average annual increment (mm)	Number of trees	MS	SD	AC	PC1 %
I	100–175	162	0.78	9	0.15	0.27	0.77	51.7
II	176–250	195	0.88	10	0.21	0.32	0.70	54.7
III	251–325	284	0.55	9	0.17	0.28	0.69	65.7
IV	> 326	369	0.56	5	0.19	0.34	0.76	60.0
V	< 100	49	1.49	9	0.16	0.23	0.61	48.3

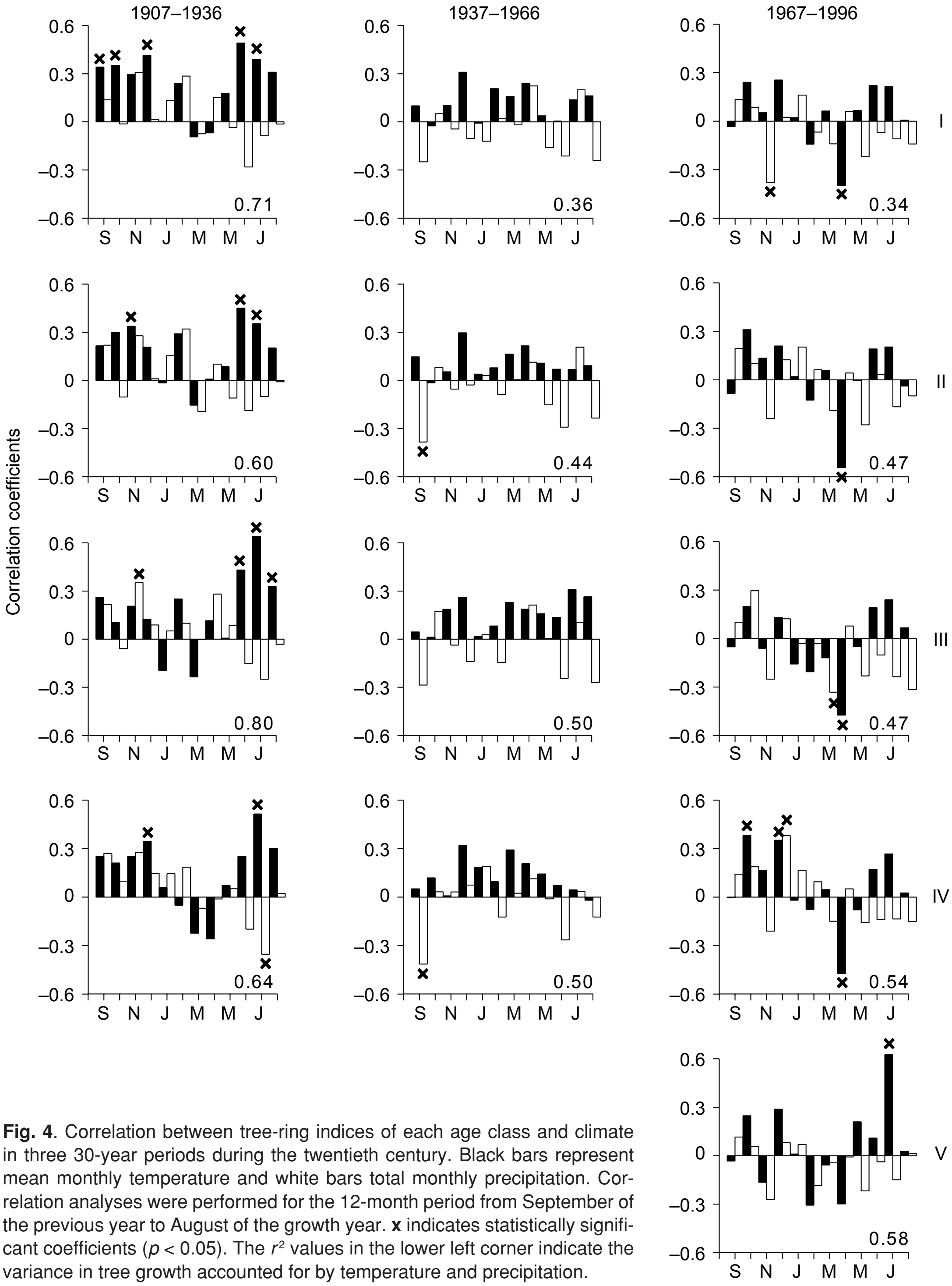

Fig. 4. Correlation between tree-ring indices of each age class and climate in three 30-year periods during the twentieth century. Black bars represent mean monthly temperature and white bars total monthly precipitation. Correlation analyses were performed for the 12-month period from September of the previous year to August of the growth year. **x** indicates statistically significant coefficients ($p < 0.05$). The r^2 values in the lower left corner indicate the variance in tree growth accounted for by temperature and precipitation.

Discussion

Our results show that there are no large differences among the age classes in terms of radial Scots pine growth variability and growth responses to climate in the studied area. However, the occurrence of age-class specific features should be taken into consideration when creating a tree-ring chronology for climate reconstructions purposes. Since the sample size of each studied age class was relatively low, the results of this study should be viewed as an indication, rather than firm evidence.

In general, looking at the actual (unstandardised) radial growth rates for Scots pines during the first decades of each age class (i.e. tree ages rather than calendar years), there are little differences among the age classes, except for the youngest trees in age class V (*see* below). Consequently, the growth pattern of young pines has been quite consistent since the sixteenth century but has altered for pines established in the late twentieth century. Although the growth increases/decreases occurred simultaneously in all the age-class chronologies, it is evident that inter-annual radial growth variability, in terms of amplitude, decreased with the tree age. Neither growth patterns nor radial growth/climate relationships showed large discrepancies among the age classes I to IV in the twentieth century; all the age classes followed the same basic growth pattern, and the variability in temperature sensitivity throughout the twentieth century was common to all age classes. However, the best agreement between the growth and summer temperatures was found in the oldest age class (IV), while pines in the youngest age class (V) showed a strong dependency on high temperatures during the peak of the growing season (July) in the late twentieth century. This suggests there is a decline in the climate–radial growth relationship in middle-aged (here 176–250 years old) pines as compared with that in younger and older age classes. The implication is that in open stands close to the tree limit, the growth of middle-aged pines is less limited by the temperature than the growth of younger or older pines, which is in agreement with the findings in Canada for 100–200-year-old *Picea glauca* (Szeicz and MacDonald 1994). However, since the pines in age class II displayed a low growth during the first 30 years of the century, especially in the 1920s, and the pines in age class I pines showed the lowest growth in the last decades of the twentieth century, it appears that middle-aged pines respond more readily to periods of unfavorable climates (e.g. periods of colder summers or wetter winters) than do older and younger pines.

The variability in the climate–radial growth relationship in the twentieth century showed two important features: a growth increase in 1940–1960 that does not correspond to high summer temperatures in the meteorological record, and a subsequent growth decline and lowered pine growth sensitivity to climate as compared with that in the early part of the century. A highly increased growth and low climate–radial growth relationships in 1937–1966, showing a dramatic decrease in temperature as a limiting growth factor, suggest that this period must have been highly favourable for the Scots pine growth. The pines in age class V that were introduced around 1970 displayed much higher growth rates than young pines in the other age classes. These pines were estimated to have germinated in the 1950s (increment cores were taken at the base of the tree and at the general sampling height, and the difference in annual rings between the samples was counted). A new establishment of pines in the Handölan valley further supports that summers were warm at that time. In addition, in a surveillance of the Scots pine tree limit in the central Scandinavian Mountains, Kullman (1993) disclosed a peak in pine germination yielding an elevated tree limit in the 1950s, and at Sylglaciären — a glacier 30 km south-southwest of the study area — a substantial volume loss which seems to have occurred during that period (Østrem 1985). Altogether, the evidence suggests that the increased growth could be an effect of a lengthening of the growing season that, in combination with a drier climate, temporarily resulted in a reduction in the importance of temperature as a growth-limiting factor (Linderholm 2002). Since increased Scots pine growth in the 1950s has also been observed at sites in Norway just west of Handölan (Linderholm *et al.* 2003), but not in Femundsmarka about 140 km SSW of Handölan, it is likely that the dominating wind direction at that time was more SW orientated, so that most precipitation would fall in the southern and south-central parts of Norway rather than further north and east of the Scandinavian Mountains.

The negative growth trends displayed in all age classes from the late 1970s, together with

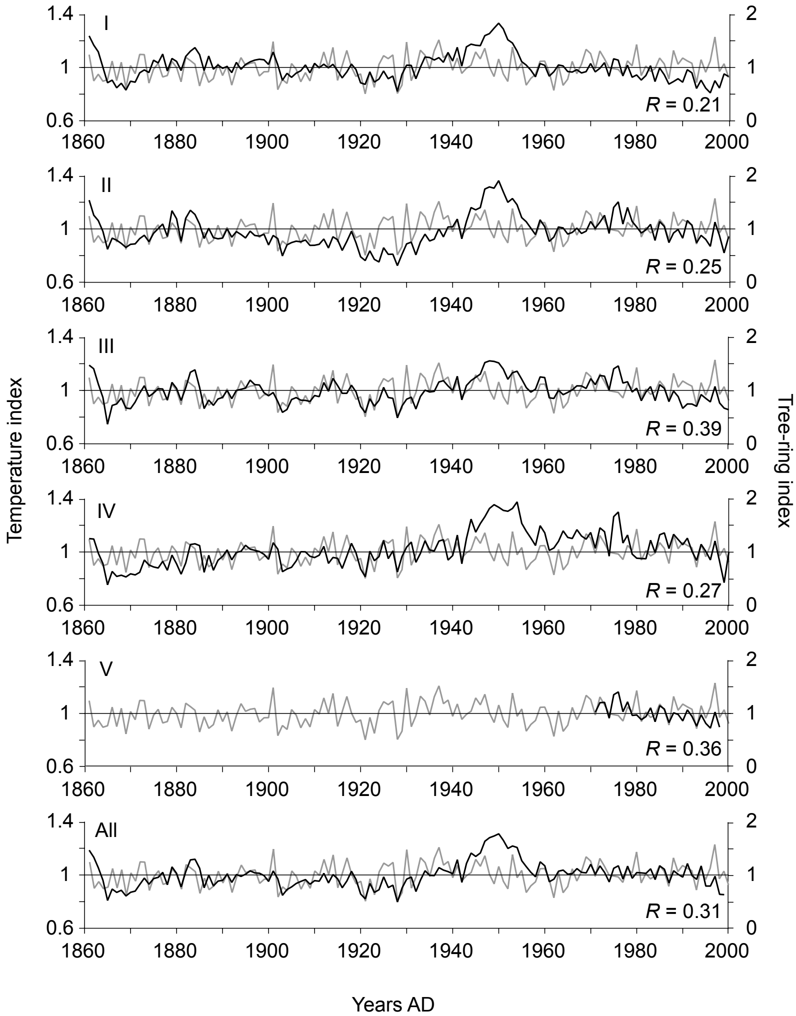

Fig. 5. Comparison of tree-ring indices of age classes I–V, a composite chronology (the average of all age classes) and a summer (June–August) temperature index. *R* values indicate correlation between the two records.

low climate–radial growth relationships, despite a slight increase in summer temperatures, suggests that a change in climate has affected the Scots pine growth in the area. Middle-aged pines (age classes I to III) were more affected than the young or old pines, especially age classes I and III. Correlation coefficients of 1967–1996 indicate a stronger negative influence of spring than summer temperatures on radial pine growth, except in age class V. This response is most likely due to increased wintertime warming since the 1980s associated with a strong and positive phase of the North Atlantic Oscillation (NAO). A link between the positive winter NAO and conifer growth decline in Scandinavia since the 1980s has previously been suggested (Linderholm 2002, Solberg *et al*. 2002). The periods of high winter temperatures may potentially represent a stress factor for pine due to increases in freeze–thaw cycles and more unfavourable soil conditions (Kramer and Kozlowski 1979). Evidently, this has not had a negative effect on the young pines in age class V in which the growth rates remained high. Having been established in a warm period, they seem to have retained their dependency on summer temperatures.

It is evident from Fig. 5 that the best fit between summer temperatures and radial tree growth is found when trees of all age classes are combined into a chronology. An overrepresentation of trees of a certain age class might bias a climate reconstruction. Consequently, equal amounts of trees of different ages should be used when creating a tree-ring chronology for climate reconstructions.

Conclusion

The results of this investigation show that there is no clear-cut relationship between the climate and Scots pine radial growth in a given age of a tree. However, there were indications that middle-aged pines of about 175–250 years old respond stronger to periods of unfavorable climate than do older or younger pines. Furthermore, pines in the oldest age class were less inclined to respond to late twentieth century climate with decreasing growth. The radial growth rates of Scots pines established in the late twentieth century differed significantly from those of the trees established in the previous five centuries, indicating a change in the local growth conditions probably due to a recent climate change. Although this study did not show any large discrepancies in the growth variability and climate sensitivity among the age classes, it does stress the importance incorporating trees of all ages into the chronology. Preferably an equal number of trees from different age classes should be used, including young trees, since a dominance of a certain age class might bias the climate–growth relationship.

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