

**Effects of climatic change on the growth of dominating
tree species along major environmental gradients**

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Dr. scient. thesis

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Preface

The world of tree-rings was new for me when I started my PhD in March 1998. During these years, I have learned that tree-rings are an amazing historical source of information for a wide range of scientific disciplines, among them is climatology. I still remember sitting on a tree-ring lab at 2800 m a.s.l. in the Rocky Mountains at the eighth North American dendroecological fieldweek (1998) and counting an individual tree back to the 13th century. That is more than 700 years of information on ecology and climate, amazing.

This work has been carried out at the Norwegian University of Science and Technology at the Department of Botany. The department ended its history a few weeks before this thesis was fulfilled, and merged with the Department of Zoology into Department of Biology. The Research Council of Norway financed my PhD scholarship through a grant for my supervisors Annika Hofgaard and Håkan Hyttborn (project no. 122176/720).

To accomplish a doctoral thesis is like mountain walking. When you think you are at the top it is always a new one, and often a steeper one. Without the encouragement and stimulating supervising from Annika and Håkan, this thesis would never have been finished. Thank you very much both of you.

The dendroclimatological scientific environment is very small in Norway. My travel and participants in international meetings, conferences, and courses have been necessary in respect to methodological aspects of coring and analysing tree-rings, and also to enhance the scientific perspective of my own research. An especially thanks goes to Dr. Hans Linderholm and Dr. Markus Lindholm, who are co-writing paper III in this thesis. Furthermore, I want to thank my PhD colleagues Dagmar, Ingar, Kristian, Linda, and Olga for a nice social environment during the years of my thesis; Terje Thun at the dendro lab.; Geir Løe for excellent field work assistance; and Tove Trondvold at the Departments office. Many others of you is not mentioned, but still not forgotten.

I wish to thank my parents who thought me respect and love for nature during my childhood, and later on always have supported me.

I remember after the summer in 1998 when I have been away for more than one month both abroad and on fieldwork. Finally coming back, Henrik (2 years old at that time) ran up in front of me and stopped on a certain distance. Stared me in my eyes. Then he said; "Daddy, you don't take care of me!", turned around and ran away. However, we have been in touch since that. I thank Henrik and Ane for being the most wonderful children and making each day, a day of happiness.

Finally, I wish to thank my wife Ellen for her patience and love during my PhD-period. "You never stopped to believe in me, though I did all the time."

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List of papers

The thesis is based on the following individual papers:

- Paper I Solberg, B.Ø., Hofgaard, A. & Hytteborn, H. 2002. Shifts in radial growth responses of coastal *Picea abies* induced by climatic change during the 20th century, Central Norway. *Ecoscience* 9: 79-88
- Paper II Solberg, B.Ø. Spatiotemporal changes in radial growth and response to climate for *Picea abies* along environmental gradients. (Submitted)
- Paper III Linderholm, H.W., Solberg, B.Ø. & Lindholm, M. (in press). Tree-ring records from central Fennoscandia: The relationship between tree growth and climate along a west east transect. *The Holocene* 13(5): xxx-xxx
- Paper IV Solberg, B.Ø. & Hofgaard, A. Tree growth and decadal climate oscillations in the north-eastern Atlantic sector: species specific and general responses. (Manuscript)

The papers are referred in the text by their roman numerals.

Paper I is included with permission from the publisher.

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1 General introduction

1.1 Climate variability and forest responses

On long time scales and large regional scales, the character of the macroclimate exerts an overwhelming influence on vegetation (Prentice 1986). The migration of trees and changes in their relative abundance during the Holocene have been interpreted as responses to climate changes (Ritchie & Yarranton 1978; Huntley & Webb 1989; Huntley 1990; Pitelka et al 1997). Tree-line fluctuations (Payette & Lavoie 1994; Kullman 1990, 2002) and changes in vitality (Kullman & Högberg 1989; Hofgaard et al. 1991) are well known responses to changes in climate. Range margin rise and invasion into alpine tundra is seen for widely separated regions of Europe and North America during the last 10-20 years (Jacoby & D'Arrigo 1995; Luckman & Kavanagh 2000; Kullman 2002). This phenomenon is paralleled by a tree-limit and range-margin rise amounting to 100-150 m, for the principal trees in Scandinavia, since the close of the Little Ice Age (Kullman 2001). Tendencies of a reversal of this centenary trend were recorded during some colder decades prior to the late 1980's (Kullman 1990, 1997). When changes in vegetation and forest composition is considered over smaller regional scales, and over decades and centuries, edaphic factors, succession, human impact and other disturbance factors are important. In this respect, forest fires are one of the most important disturbance factors in boreal forests (e.g. Payette 1992; Engelmark 1999). Spatial difference in fire regimes in northwestern Europe determines species distribution, abundance and range.

The climatic system is a dynamic system, which in historical time have changed continuously due to natural driving forces like e.g. solar radiation and volcanic activity (Briffa et al. 1998c; IPCC 2001a). To day it is evident that global temperatures have increased throughout the 20th century with approximately 0.6-0.7°C (IPCC 2001a and references therein), and there are indications that the 20th century have been the warmest for the last 1000 years (Briffa et al. 1995, 2001; Mann et al. 1999). Major effort has been put on to understand the driving forces behind this global temperature increase. In the centre of the debate is the question if this temperature increase is a natural phenomenon or if human influence on the climatic system has brought about this trend. Several lines of evidence points to that the human emission of greenhouse gases has, at least partly, caused this temperature increase (IPCC 2001a). This ongoing climate change is expected to distribute unevenly in different part of the world, and the climate warming is predicted to be more extensive at

higher latitudes and in the winter, which has been the case for the temperature trend during the last decades. Furthermore, the temperature increase in the Northern Hemisphere has been stronger in interior land areas than in oceanic areas (Chapman & Walsh 1993).

At present, there are an extensive research effort to elaborate the consequences of climate change on ecosystems and their biological components (IPCC 2001a, b). There has also been produced several scenarios for increased greenhouse effect on biological system sustainability and future survival and distribution of individual species. Small changes in different climatic variables cause shifts in environmental conditions and may effect species dominance, have profound effects on species distribution and effect survival and fecundity (Payette & Lavoie 1994; Kullman 1996; Mysterud et al. 2000; Kullman 2002). Thus, it is of vital importance to study small changes in climate and the effect on species and biological systems to understand consequences of future climate changes.

There is a general lack of long (several centuries) instrumental records of climate variables (Bradley & Jones 1992). Long series of climatic information is necessary to gain insight into the natural variability of climate. Due to these shortcomings, information on past climate must be derived from natural climate proxy data like tree-rings, pollen, diatoms, chironomids, ice layers and corals (Jones et al. 1996; IPCC 2001a). Different proxy data are fundamental in reconstructing long climate series and predictions of future climate, and long tree-ring series plays an important role in this context (Mann et al. 1999; IPCC 2001a). Different proxies reflect different climate variables in different seasons, and limitations of single climate proxies may, at least partly, be overcome by using multi-proxy analyses (e.g. Biegler et al. 2002; Cook et al. 2002).

Substantial portions of the climate variability in the North Atlantic area are associated with atmospheric and oceanic circulation. A major source of the interannual variability in the atmospheric circulation is the North Atlantic Oscillation (NAO) (e.g. Hurrell 1995 and references therein). The NAO is strongly correlated to temperature and precipitation, especially in the winter season (Hurrell 1995; Chen & Hellström 1999). Since the 1970's the NAO has been in a positive phase forcing a substantial amount of mild and wet air masses over northern Europe. This has resulted in mild and wet winters and cool and moist summers over this area (Hurrell 1995; Hanssen-Bauer & Førland 2000). The high positive phase of NAO is partly a result of anthropogenic influence (Paeth et al. 1999; Cook et al. 2002). Interaction between the ocean and atmosphere form a dynamic system, exhibiting complex patterns of variation, which may profoundly influence ecological processes in a number of ways (Ottersen et al. 2001).

1.2 Natural environmental gradients and the temporal component

Natural gradients consist of variations in environmental conditions, e.g. temperature, precipitation, moisture, snow conditions, disturbance regime. Such natural gradients are demonstrated to be well suited to study changes in tree growth responses to climate (Kienast et al. 1987; Villalba et al. 1997; Hofgaard et al. 1999; Mäkinen et al. 2000; Gedalof and Smith 2001; Peterson & Peterson 2001). The effect of climate variables is known to change impact on radial tree growth at lower and higher parts of an altitude gradient, for example. Generally, radial tree growth is restricted by low summer precipitation at lower latitudes and altitudes, and by low summer temperatures at higher latitudes and altitudes (Woodward 1987; Bonan & Shugart 1989; Villalba et al. 1994; Lindholm et al. 2000). Climate gradients have long been recognised as determinants of composition and distribution of boreal ecosystems. Tree growth responses to climate variables are of major importance to understand the effect of climate change on future tree growth under a climatic regime with enhanced temperatures. In this thesis, the climate transition since the close of the Little Ice Age and throughout the 20th century up to present is used to gain knowledge about tree growth response to a changing climate. Such knowledge is also crucial to understand growth-climate relations in the future.

Climate variation and its influence on tree growth could be divided into three different time scales after Prentice (1992): 1) short term, or the domain of decades; 2) long term, or the domain of vegetation history on time scales of millennia; and 3) the middle range, or the domain over centuries. Climate changes in the decadal band have been attributed to various external causes like volcanic and solar activity. These changes are not recorded in sampling of most sedimentary records, but have been detected in tree-ring series (Guiot 1987). Climate changes in the millennial band include phenomenon such as the Medieval Warm Period and the Little Ice Age (Grove 1988). These phenomena have been attributed to variations in volcanic activity, changes in solar output and surges in the Antarctic ice sheet, and are detected in climate records from tree-rings, small glaciers and pollen records (Bradshaw & Zachrisson 1990; Briffa et al. 1992; Luckman 2000). Additionally, climate changes in the interannual band are attributed to oscillations in the climate system, especially interactions between the atmosphere and oceans like El Nino/Southern Oscillation and NAO. In this study, the strongest emphasis is put on climate variations and radial tree growth dynamics on decadal and interannual time scales. Furthermore, the time scales in target are pushed towards centenary perspectives.

1.3 Tree rings and climate

Climate forcing on hemispheric, regional and local scale has strong implications for tree growth (Bradley & Jones 1992). Additionally, several other factors like disturbance, anthropogenic influence, bedrock, soil conditions and biotic interactions have also implications for tree growth (Schweingruber 1996). Tree ring data are thus difficult to interpret because tree growth rarely, if ever, is limited by a single environmental factor. Despite this problem, dendrochronological timeseries have at least three important attributes (citation from Schweingruber & Briffa 1996):

- all rings are absolutely dated so that tree-ring data can be compared with precisely dated climatological parameters
- genetical and ecological variability within groups of individual trees can be minimised by building mean tree-growth curves, so-called chronologies
- networks of tree-ring parameter time series allow direct spatial reconstructions of tree-growth patterns and their interpretation in terms of climate parameters

Tree-rings are a unique proxy of climatic information (Fritts 1976). Among different proxy data, tree rings have, although time consuming, the advantage of being easily sampled and the annual ring width is easily measured. Tree-ring analyses offers absolute time resolution at an annual time scale and are applicable over large areas. Due to the principles of uniformitarianism and limiting factors, tree rings offer an opportunity to exactly date the year when a ring is formed (Fritts & Swetnam 1989). Crossdating refers to the general year-to-year agreement or synchrony between variation in ring width characteristic of different trees. By coupling this to climate data (e.g. temperature), it is possible to establish a connection between critical climatic variables and tree growth. Furthermore, this make it possible to understand variation in tree growth during time, and how changes in climate may influence tree growth and forest development. Especially, narrow tree-rings are suitable to discover harsh climatic conditions and extreme events (Schweingruber 1996). Long tree-ring chronologies are frequently used to reconstruct past climate variations, and at high latitudes several networks of tree-ring chronologies are used to reconstruct past variations in summer temperature (e.g. D'Arrigo & Jacoby 1993; Mann et al. 1999; Briffa et al. 2001). To predict a possible global warming, tree-ring data are an important component. Furthermore, tree-ring chronologies are also used to understand ecological processes related to forest dynamics (e.g. Fritts & Swetnam 1989; Schweingruber 1996; Niklasson & Granström 2000).

2 Aims of the thesis

This thesis deals with effects of climate on tree growth of the dominating conifer species, *Picea abies* (L) Karst. (Norway spruce) and *Pinus sylvestris* L (Scots pine), in central Norway and Fennoscandia. Both species are sampled along major environmental gradients, i.e. altitude and oceanicity, and growth responses to climate, i.e. temperature and precipitation, are examined along these gradients. Additionally, time is considered as an environmental gradient and temporal responses are carefully deciphered. Special attention is given to large-scale climate oscillation and their effect on tree growth. In the individual papers the specific aims have been to:

1. identify climate variables (all seasons) with significant influence on radial tree growth of *P. abies* and *P. sylvestris* along major environmental gradients (Paper I-IV)
2. identify if and how the growth response to climate has changed through time along these gradients (Paper I-IV)
3. make interregional comparisons of *P. sylvestris* growth pattern across Fennoscandia from oceanic western Norway to continental eastern Finland (Paper III)
4. analyse to what degree large-scale circulation patterns of air masses are registered in regional tree growth of both *P. abies* and *P. sylvestris* (Paper I, III and IV)
5. discuss possible effects on radial tree growth of a predicted warmer climate (Paper I, III and IV)

3 Study area

3.1 Environmental gradients and study sites

The study area is situated in boreal forests in central Norway, 64°N 10°-14° E. Three areas (A-C) along a coast-inland gradient were sampled. This gradient reflects a precipitation gradient with diminishing amount of precipitation eastwards. Additionally, the coast-inland gradient reflects an oceanicity-continentally gradient with an oceanic climate at the coast and elements of a more continental climate in the east. In each area, three to four sites are sampled

along altitude gradients from lowland forests to forest line, reflecting a summer temperature difference of approximately 2°C. The dominating conifer species in the study area is *P. abies* and *P. sylvestris*. Both species coexist in all sites and *P. abies* occupies concave micro sites while *P. sylvestris* occupies convex and relatively xeric micro sites. For each site, species specific tree-ring width chronologies are constructed. Further details of the site characteristic, geology, vegetation etc. are elaborated in the individual papers. Furthermore, the oceanicity-continently gradient is extended to include several sites from central Sweden and Finland (62-64°N 10-30°E).

3.2 Climate

In central Norway, the climate is strongly influenced by westerly winds from the North Atlantic Ocean. Generally, this gives a relatively high amount of precipitation throughout the year and a typical oceanic climate with cool summers and mild winters. The impact from the westerlies declines eastwards and area C have elements of a continental climate. Consequently, the climate in the three areas is regarded as oceanic (A), sub-oceanic (B) and a transition zone between oceanic and continental climate (C) (censu Moen 1999). The three areas along the coast-inland gradient reflect a total yearly precipitation of 1500, 900 and 600 mm, respectively (Førland 1993). Furthermore, the mean annual temperature in the three areas was 5.0°C, 4.2°C and 0.9°C, respectively (Aune 1993). Snow covers the ground for approximately 120, 165 and 195 days at area A, B and C (Bjørnbæk 1993). There are however, large variations between the lowland sites and the forest line sites at each area in respect to snow conditions and duration of snow cover. In the more continental sites in eastern Finland, the yearly precipitation is below 600 mm with colder winters and warmer summers than in central Norway.

4 Methodology and data

This thesis applied standard methods of dendrochronology (Stokes & Smiley 1968; Fritts & Swetnam 1989) and dendroclimatology (Fritts 1976; Cook & Kairiukstis 1990). When analysing the tree-ring data, software Time Series Analysis and Presentation (TSAP;

Rinn 1996) and the International Tree-Ring Data Base Program Library, particularly COFECHA for crossdating and ARSTAN for tree-ring standardisation and chronology building (Holmes 1994), were used. The tree-ring series were processed by standard methods and measured with a precision of 0.01 mm using LINTAB measuring equipment (Frank Rinn, Heidelberg). Climate-growth relationships were analysed using correlation and response function analyses in the software PRECON (Fritts et al. 1991), version 5.17b. Temporal aspects of climate-growth relationships were analysed by Moving Response Function Analyses (Biondi 1997, 2000) which is a refined version of response function analyses. Spatiotemporal aspects of interregional connection between species and along environmental gradients were analysed by Pearson's correlation and Principal Component Analyses (Peters et al. 1991). Further details of the use of the different methods are given in the individual papers.

The tree-ring data in this thesis consisted of 10 spruce and 9 pine tree-ring chronologies sampled along coast-inland gradient and altitude gradients in central Norway. Further, one Norwegian, three Swedish and two Finnish pine chronologies were used to extend the oceanicity-continentally gradient. The climate data used were: homogenised and standardised regional monthly mean temperatures and monthly totals precipitation values (Norwegian Meteorological Institute; Hanssen-Bauer & Nordli 1998; Hanssen-Bauer & Førland 1998), the NAO index (<http://www.cru.uea.ac.uk/cru/data/nao.htm>; Hurrell 1995; Jones et al. 1997), the Arctic Oscillation (AO index; http://www.atmos.colostate.edu/ao/Data/ao_index.html; Thompson & Wallace 1998), the Zonal Index (ZI; Frich et al. 1996; Tuomenvirta et al. 2000), and the Meridional Index (MI; Frich et al. 1996; Tuomenvirta et al. 2000). The NAO is expressed by the differences in sea-level pressure between Iceland and the Azores and is strongest during the winter (Rogers 1990). The AO reflects the mean deviation from the average sea level pressure measured throughout the Northern Hemisphere at longitudes poleward of 20°N (Thompson & Wallace 1998). The AO resembles the NAO in many respects, but its primary centre of action covers more of the Arctic than the NAO. The ZI and the MI are regional climate indexes that are valid to a somewhat smaller geographical area (Frich et al. 1996; Tuomenvirta et al. 2000). These indexes are determined from the difference in monthly mean sea level pressure between Hammerodde (Denmark) – Bodø (Norway) and Helsinki (Finland) – Bergen (Norway), respectively. The ZI resemble the NAO and the AO in that it expresses the zonal influence of air masses. The MI however, expresses the meridional influence of air masses flowing over Fennoscandia, and thus represents a different weather pattern than the zonal indexes.

5 Major results in a broader context

5.1 Climate influence on tree growth

In central Norway and Fennoscandia, summer temperature and the growth season length are the main decisive factor controlling radial tree growth for both *P. abies* and *P. sylvestris* (Papers I-IV). Tree-ring data from this region is also extensively used to reconstruct summer temperature (e.g. Briffa et al. 1990, 1992; Lindholm 1996; Kalela-Brundin 1999; Kirchhefer 2001), and is used as a major contribution in the calibration models to predict future climate changes (Mann et al. 1999; IPCC 2001a). In the past, pine has been overemphasised in dendroclimatic work in Fennoscandia compared to spruce. This thesis shows that spruce contains a stronger climate signal than pine in central Norway, which initialises a stronger focus on spruce in the future (Paper IV). There should be a large potential to build long spruce chronologies from living material at tree-line sites in the region. In the cold, moist boreal forests, precipitation have considerably less influence on tree growth than temperature (Papers II and III). Consequently, precipitation signals are seldom emphasised and/or reconstructed in tree ring series from the boreal forest (but see Szeicz & MacDonald 1996). Recently, there are found indications on declining radial tree growth in especially dry and continental areas in north-American boreal ecosystems (e.g. Barber et al. 2000). The increase in temperature during the 20th century has given signs of drought stress in boreal conifers due to lack of a simultaneously increase in precipitation (Jacoby & D'Arrigo 1995; Kirchhefer 1999; Barber et al. 2000; Biondi 2000; Lloyd & Fastie 2002). Such mechanisms are less likely in central Norway due to less temperature increase in oceanic areas compare to interior land areas (Chapman & Walsh 1993), and considerably wetter conditions in central Norway with increasing precipitation during the last decades (Hanssen-Bauer & Førland 1998).

5.2 Coherency between large-scale climate variation and radial tree growth

Traditionally, climate variables used in growth-climate analyses are temperature and precipitation. However, during recent years is indexes reflecting large-scale climate patterns used more frequently. Contemporarily, there has been an increasing interest to understand the influence that large-scale climate variations have on populations on both plant and animals (e.g. review by Mysterud et al. 2002). In the north-east Atlantic sector there has been special

emphasise on the NAO. Such large-scale indexes are interesting because they capture variations on both temperature and precipitation, and influence plants and animals.

Correlation between large-scale climate indexes and radial tree growth showed contrasting patterns depending on species, position along west-east gradients and analysed time period (Papers I, III and IV). Generally, during winter, spruce responded negatively to the NAO in western Fennoscandia and pine responded positively to the NAO in eastern Fennoscandia (Paper I, III and IV). In Paper I, a significant negative correlation between spruce radial growth and the winter NAO is present for shorter time periods during the first half of the 20th century, but not for the entire analysed period 1873-1997. In Paper IV, however, spruce showed some weak but significant negative correlations with the NAO for the period 1901-1990. This point to the fact that significant correlation between the NAO and spruce radial growth is sensitive to changes in climate and choice of analysed period. Additionally, analyses of pine radial growth responses to the NAO along the Fennoscandian transect showed that tree growth in nearby sites, with more or less similar response to temperature and precipitation, distinguished in their response to the NAO (Papers III and IV). Running correlation series between surface temperature and atmospheric circulation, i.e. the NAO, revealed significant non-stationarities in the correlation patterns (e.g. Chen & Hellström 1999; Slonosky et al. 2001), suggesting that caution must be used in interpreting correlation between atmospheric circulation and climate-related biological responses during different time periods. These non-stationarities does not seem to be systematically associated with the mean strength of the circulation (Chen & Hellström 1999). Radial tree growth responded more or less in the same fashion with the AO as with the NAO, confirming the strong similarities between the two indexes (Thompson & Wallace 1998). The ZI showed a more detailed and better-adapted response to radial tree growth than the NAO and the AO (Paper IV). During summer, both pine and spruce responded negatively to the ZI (Paper IV). A high ZI during summer indicate a relatively strong influence of cool, moist air masses from the Atlantic Ocean (Slonosky et al. 2001 and references therein). This negative correlation is in accordance with the general positive response to summer temperature for both species.

Generally, for the studied region the response pattern to temperature and precipitation turned out to be more robust than the response pattern to large-scale climate indexes (Papers I, III and IV). Thus, the results from this thesis gave evidence for that temperature and precipitation are superior compared to large-scale climate indexes to gain knowledge of climate-growth relationship for conifers in central Norway (Papers I, III and IV). However, there are indications that the NAO is a better proxy for North Atlantic climate now than it has

been in the past (Ottersen et al. 2001), though there is no results indicating that the NAO is better capturing radial tree growth at present (Linderholm 2002; Paper I and III). Numerous models predict that the current positive phase of the NAO will persist at least for the first decades of the 21st century (Paeth et al. 1999). Conclusively, ecologist should as part of their investigations of climate influence on biological components in ecosystems, include possible effects of large-scale climate patterns like the NAO.

Pines from Fennoscandia have been used to reconstruct the NAO (Cook et al. 1998, 2002; Lindholm et al. 2001). Results from this thesis suggest that spruce have stronger correlation with the NAO than pine, at least in western Norway. Consequently, spruce should be considered to be included in reconstructions of atmospheric circulation indexes. Local climate and tree growth were stronger related to other zonal indexes than to the NAO (Slonosky et al. 2000; Paper IV), which put emphasise that other zonal indexes should in addition be considered in reconstructions of large-scale climate variability.

5.3 Dynamic change in tree growth response to climate

Several climate variables change their strength in impact on radial tree growth during slightly different climate regimes (Papers I-IV). At the coast, both May and June temperatures were found to be less important for spruce radial growth during periods when the mean of these climate variables was higher than the long-term mean (Paper I). Concomitantly, climate variables during other parts of the year showed increased importance, as exemplified by a significant correlation with winter climate (the NAO index) during mid 20th century. During the 20th century, the climate in central Norway changed to a warmer and wetter climate compared to the 19th century (Hanssen-Bauer & Førland 1998; Hanssen-Bauer & Nordli 1998). This includes a generally increased oceanicity over larger areas, and, climatically, a more homogenous environment (Tuomenvirta et al. 2000). Along the coast-inland gradient, spruce gradually showed a more similar response to climate and also stronger inter-site correlations towards present (Paper II). This is reflected by a stronger emphasis on June temperature along the entire gradient and an increasingly stronger response to May temperature in the inland areas.

Principal component analyses showed that species was the strongest separating factor for all 19 tree-ring chronologies in central Norway (Paper IV). Secondly, the individual sites were separated due to their position along the coast-inland gradient (Papers II and IV). Thirdly, altitude above sea level also turned out to be an important environmental variable

contributing to different growth responses to climate (Paper II). In a temporal perspective, tree growth along the revealed separating variables (species, coast-inland and altitude) became more similar at present compared to the situation 100-150 years ago. These findings should be considered in the development of models over future responses to climate influence on tree growth at both spatial and temporal scales.

The recently reduced climate sensitivity in high latitude trees (Briffa et al. 1998 a, b; Jacoby et al. 2000) is to some degree reflected in the tree-ring series from central Norway (Papers I and III). Both spruce and pine showed slightly reduced growth sensitivity to climate in the last half of the 20th century compared to the first half (Papers I and III). In eastern Fennoscandia, however, pine showed indications of increased growth sensitivity to climate in the last half of the 20th century (Paper III). This put attention to that growth response to climate not only is species-specific, but also additionally, shows different directions depending on prevailing climate.

The increased oceanicity with increase in both temperature and precipitation has both physiological and ecological implications for tree growth (Körner 1998; Crawford 2000). Physiologically, damage might be brought about by depletion of carbohydrate reserves, ice-encasement and frost or exposure to injury either in carbohydrate depleted shoots or from precocious shoot growth in spring. Ecologically, increased oceanicity might include bog growth, wind throw, soil leaching and mid-winter removal of snow (Crawford 2000). The Atlantic component in winter climate with increased oceanic conditions since the 1960's, conduct mild and wet air masses over Western Europe and a possible increase in stressful conditions with frequent freeze-thaw cycles. If, in a future climate, occasional periods of deep frost occur, the probability of frost damage may increase despite a significant warming (Kramer et al. 2000). In the last half of the 20th century, there was increased separation between area A and B for spruce radial growth along the altitude gradient (Paper II). This points to increased differences in growth conditions along altitude in (sub)-oceanic areas. The amount and duration of snow-cover is a critical determinant for the onset of tree growth in spring (Villalba et al. 1997; Vaganov et al. 1999; Peterson & Peterson 2001). Warm and wet winters are generally associated with more snowy winters inland and at high altitudes (Myserud et al. 2000). However, in lowland coastal western Norway, with winter temperature close to 0°C the winter precipitation will mainly fall as rain, and so shorten both the amount and duration of the snow cover. Potentially, this may produce difference in growth conditions resulting in varying tree growth response to climate along altitude gradients (Villalba et al. 1997; Paper II).

5.4 Climate change and regional tree growth

Generally, increased temperatures are expected to give a longer growing season and consequently increased tree growth in the northern part of the European boreal forest (e.g. Spiecker et al. 1996; Kellomäki & Kolström 1994; Myneni et al. 1997; Talkkari 1998; Menzel & Fabian 1999; Chimielewski et al. 2001). In northern Europe, *P. abies* and *P. sylvestris* dominate boreal forests, and these species grow well across most of their current distribution ranges. Hypothetically, these species will respond differently in different regions depending on prevailing climate. In oceanic areas, a retreat in range is possible due to warmer climate with mild winters (Sykes & Prentice; Bradshaw et al. 2000; Paper I, II and IV), while in more continental and interior mountain areas both species are likely to invade higher altitudes and tundra regions (Kellomäki & Kolström 1994; Sykes & Prentice 1996; Kullman 2002). In the southern boreal forests, the same species are expected to decline because of a concurrent increase of deciduous tree species and a less favourable climate (Sykes & Prentice 1996; Bradshaw et al. 2000).

The development of climate in central Norway during the 20th century has been characterised by maximum temperatures in the 1930's and around 1990 (Jones et al. 1986; Hanssen-Bauer & Nordli 1998). The trees have responded differently to these temperature optimums. In the 1930's the diameter growth of the trees responded sensitively to the temperature increase, while the 1990 maximum was not followed by increased tree growth (Papers I, II and III). A qualitative difference in these two maxima may have caused the difference in diameter growth response. During the 1930's high summer temperatures largely caused the high annual temperatures, while around 1990 high winter and spring temperatures caused the high annual temperature (Hanssen-Bauer & Nordli 1998). Additionally, the 1930's included a period with decreased intensity of the NAO, while the period around 1990 represented a period with increased intensity of the NAO (Hurrell 1995). Climate changes during the last 150 years with increasing temperature and precipitation have led to increased oceanicity over larger areas at present (Hanssen-Bauer & Førland 2000; Tuomenvirta et al. 2000; Cook et al. 2002). At present, there are stronger correlations between spruce and pine and also stronger correlation between the different areas along the coast-inland gradient and between the different sites along the altitude gradients (Papers II and IV). Consequently, the increased oceanicity has led to a more homogenous environment for tree growth along the studied environmental gradients (Papers II and IV). The effect of changes in climate due to increased oceanicity, especially increased precipitation and winter temperatures, have

potentially negative impacts on tree growth from both a physiologically and ecologically point of view (Crawford 2000).

Generally, it is quite naive to anticipate that all species will increase their biomass and growth under a warmer climate (e.g. IPCC 2001b). It is more likely that different species respond individually and that specific species respond differently according to local/regional climate and in interactions with other species and disturbance. One important question in this respect is: Will spruce and pine benefit from increased temperatures in central Norway? Results produced so far indicate that spruce probably will respond negatively to the ongoing climate changes (increased oceanicity), at least in coastal and lowland areas (e.g. Huntley 1990; Prentice et al. 1991; Skre & Nes 1996; Sykes et al. 1996; Papers I and II). The situation is somewhat more obscure for pine, but probably pine is more tolerant for a warmer climate with a thinner and more unstable snow cover (Huntley 1990; Linderholm 2002; Paper III). In conclusion it can be stated that detailed multi-species studies of growth response to climate are necessary to understand future tree growth responses to climate changes. Tree growth responses to climate are not only species specific, but also dependent on prevailing climate, other environmental variables, disturbance regime and temporal aspects.

6 Conclusions and future studies

Summer temperature is the main climatic factor important for radial tree growth for spruce and pine in central Norway. However, the strength and importance of different climate variables change influence through time. This is important knowledge for modelling of future tree growth under a changing climate, and for constructions of transfer functions when reconstructing past climate. The stronger response to climate from spruce compared to pine revealed in this study, requires a stronger emphasise on spruce in future dendroclimatological work from the region. Both species showed significant correlation with climate outside the growing season, emphasising the importance of a heterogeneous tree growth response on climate. Significant correlations with large-scale climate indexes were present, though generally weak. At the coast, the correlation between spruce radial growth and the NAO varied temporarily in concordance with variations in climate. Furthermore, radial tree growth were stronger correlated with a regional zonal index than the more hemispheric NAO and AO. Pine radial growth had no significant correlation between western and eastern Fennoscandia,

and also more or less opposite responses to climate. Consequently, it is not possible to combine tree-ring width chronologies from western and eastern parts of central Fennoscandia expecting them to yield a common climate signal. This supports the general picture that one cannot expect uniform tree growth responses to future climate changes.

Generally, there is a need to extend the sampling network to the entire spruce and pine distribution area of Fennoscandia and probably European Russia to identify crucial climatic factors important to growth under a changing climate throughout northern Europe. Such information would improve our ability to accurately predict species growth responses to climate in forest simulation models and better predict community and ecosystem responses to future climatic variability.

Several directions of future research are possible:

1. Expand the network of chronologies to include the entire distribution area for spruce in Scandinavia. This will adjust for a regional comparison of spruce growth and response to climate on a large scale, which is especially important in the context of climate change.
2. There is also a need to sample spruce from true continental sites in Russia, with the similar ecological conditions in respect to soil properties, soil moisture, nutrient conditions, slope and exposition.
3. There is also a need to sample pine over larger areas to fill in gaps where dendrochronological series are not available: central to northern Norway between the chronologies presented in this thesis and chronologies presented by Kirchhefer (1999); western Norway and eastern Norway. In this way, available data from southern Norway (Kalela-Brundin 1999 and pers. comm.), central Norway (this study) and northern Norway (Kirchhefer 1999) can be extended to a more complete national network.
4. Build millennial long pine tree-ring chronologies. Such chronologies are available from northern Finland, northern Sweden, central Finland and central Sweden. To gain an improved understanding of Holocene climate in Fennoscandia it would have been of most importance to have equivalent tree-ring chronologies from western Norway and even southern Norway.
5. Due to the stronger climate signal in spruce chronologies compared to pine chronologies in central Norway, it would have been of great importance to build long spruce tree-ring chronologies along relevant environmental gradients.

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Paper I

Ecoscience 9: 79-88

Shifts in radial growth responses of coastal *Picea abies* induced by climatic change during the 20th century, Central Norway

by

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Shifts in radial growth responses of coastal *Picea abies* induced by climatic change during the 20th century, central Norway¹

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Abstract: Climate-growth relationships since the end of the 19th century were analysed by using regional climate data and North Atlantic Oscillation index data, together with spruce (*Picea abies* (L.) Karst.) tree-ring data from an altitudinal gradient close to the coast in central Norway (64°N). Correlation and response function analyses were used to decipher both spatial and temporal diameter growth responses. A positive response for May and June temperatures dominated along the entire gradient, but the importance of individual months shifted through time. In periods when May and June temperatures were above their long-term means, the importance of other climate factors increased. Winter climate was significantly related to radial tree growth mainly for periods up to the 1940s, but not during the second half of the 20th century. This pattern was principally caused by changes in the response to winter precipitation. The summer climate acquired increased importance in periods with warm and moist winters. The climate-growth relationship in this study changed continuously and dynamically during the studied period; this might be a general phenomenon that should be carefully considered in dendroclimatological studies. In scenarios for forest development, it is of vital importance to build on detailed knowledge of growth responses to multiple climate variables for all seasons, particularly where the oceanic influence is predicted to be spatially extended.

Keywords: *Picea abies*, tree growth response, dendroclimatology, climate change, oceanic impact, NAO.

Résumé : Nous avons étudié les relations qui existent entre le climat et la croissance des épinettes (*Picea abies* (L.) Karst.) depuis la fin du 19^e siècle dans le centre de la Norvège (64° N). Plusieurs ensembles de données ont été analysés, dont des données climatiques régionales, d'autres sur l'oscillation nord-atlantique, et enfin des mesures des cernes de croissance des arbres prélevés le long d'un gradient altitudinal dans une région côtière. Des corrélations et des fonctions de réponse ont été calculées afin de détecter de possibles liens entre la croissance en diamètre des arbres et le climat. Une réponse positive a été détectée pour les températures des mois de mai et juin le long du gradient, mais les températures de ces mois n'ont pas toujours eu la même influence sur la croissance des arbres. Par exemple, lorsque les températures de mai et juin étaient supérieures à la moyenne, l'importance des autres facteurs climatiques augmentait. Le climat de la saison hivernale a été associé de façon significative à la croissance radiale jusque dans la décennie 1940, mais ce ne fut pas le cas au cours de la seconde moitié du 20^e siècle. Cette modification a été causée par un changement de la réponse des arbres aux précipitations hivernales : le climat de la saison estivale a en effet d'autant plus d'influence sur la croissance lorsque les hivers sont doux et humides. En fait, les relations entre le climat et la croissance des arbres ont changé de façon continue au cours du 20^e siècle; toute étude dendroclimatique devrait tenir compte de l'existence possible d'un tel phénomène. Lorsque l'on propose des scénarios de croissance forestière, il est d'une importance cruciale que ceux-ci se fondent sur une connaissance approfondie des influences du climat de toutes les saisons sur la croissance des arbres, et plus particulièrement dans les régions de plus en plus marquées par un climat océanique.

Mots-clés : *Picea abies*, réponse de la croissance des arbres, dendroclimatologie, changements climatiques, impact océanique, oscillation nord-atlantique.

Introduction

Growth of boreal tree species is generally restricted by direct and indirect climatic factors. In the long term, these factors determine altitudinal and latitudinal distribution limits of the boreal forest (Bryson, 1966; Larsen, 1971; Huntley, 1990). In the short term, climate factors set limits and prerequisites for annual tree growth (Fritts, 1976). Consequently, tree growth in terms of radial growth varies in a spatiotemporal manner, largely mediated through gradients in precipitation and temperature, and depending on geographical location, habitat, and species (Kienast *et al.*,

1987; Villalba *et al.*, 1997; Briffa *et al.*, 1998; Hofgaard, Tardif & Bergeron, 1999). Time dependent site- and species-specific radial growth patterns suitable for detailed analyses of climate growth relationships are thus produced (Hofgaard, Tardif & Bergeron, 1999). In this way, transient responses and/or directional trends in tree growth may be elucidated for a variety of climate variables, time periods, geographical areas and along environmental gradients (*e.g.*, latitude, altitude, continentality). Such data is essential in predictions of the future development of boreal forest communities.

Temporal variation in oceanicity in northern Europe is largely governed by the behaviour of the North Atlantic

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Oscillation (NAO) (Hurrell, 1995). Since the 1970s there has been an apparent change towards milder and wetter winters in northern Europe compared with earlier decades of the 20th century (Hurrell, 1995). Changes in oceanicity through time and their effects on terrestrial ecosystems have recently received increased scientific interest (Post & Stenseth, 1999; Crawford, 2000). However, most dendroclimatic studies from the boreal region consider inland areas and to a lesser extent coastal areas (but see Wiles, D'Arrigo & Jacoby, 1996). Potentially, coastal boreal forests are sensitive indicators of even minor changes of the climatic system due to their exposed geographic position. Increases in oceanicity are generally seen as promoting plant growth but may also create unfavourable growing conditions through causing physiological problems by prolonged metabolic activity during unfavourable periods (Crawford, 2000). Negative correlations between warm winter temperatures and diameter growth for conifers have been reported in some boreal environments (D'Arrigo, Jacoby & Free, 1992; Carrer *et al.*, 1998; Mäkinen, Nöjd & Mielikäinen, 2000), but as Mäkinen, Nöjd and Mielikäinen (2000) correctly stated, the causal physiological mechanisms are still uncertain. However, high winter temperatures may have a negative effect on tree growth due to increasing respiration and evapotranspiration during a period when the losses cannot be replaced by photosynthesis and water supply (Tranquillini, 1979; Crawford, 2000). Additionally, positive growth response at one altitude may be changed into a negative response at another altitude in the same area and time period due to altitudinal change of growth-related thresholds in, for example, soil temperature, snow duration, and exposure to frosts.

In northern Europe, tree-ring growth increased during the 20th century up to *ca* 1940, after which there was a slightly decreasing trend until the 1980s (Briffa *et al.*, 1992; Kullman, 1996; Kirchhefer, 1999). This growth pattern broadly corresponds with the regional summer temperature development during the 20th century (Jones, Wigley & Wright, 1986; Hanssen-Bauer & Nordli, 1998). In general, April through September is the most important growing season in boreal forests (Briffa *et al.*, 1992; Jacoby *et al.*, 2000). However, significant climate-growth relationships during other parts of the year may be found for certain areas and/or time periods (Kalela-Brundin, 1999; Mäkinen, Nöjd & Mielikäinen, 2000). Climatic events during the winter might have long-lasting ecosystem consequences (Kullman & Högberg, 1989; Hofgaard, Kullman & Alexandersson, 1991). An example of such an event is the coincidence of shallow snow cover and severe cold, which occurred in north Sweden from mid-December 1986 to mid-January 1987, resulting in unprecedented needle loss in a natural forest (Kullman & Högberg, 1989). Most climate change scenarios for high latitudes predict that pronounced changes predominantly will occur during the winter (Kattenberg *et al.*, 1996; IPCC, 2001). Thus, dendroclimatological studies need to focus more strongly on the importance of winter climate for radial tree growth during the subsequent summer. In this study we focus on Norway spruce (*Picea abies* (L.) Karst.) along an altitudinal gradient in an oceanic environment in central Norway. The aims are to *i*) determine which climate variables influence diameter growth of Norway

spruce at its most westerly and oceanic distribution limit, *ii*) determine if the importance of these climate variables has changed through time, *iii*) investigate if and how winter climate is translated into the growth pattern through time, and *iv*) analyse if changes in spatiotemporal growth response pattern are related to changes in the regional climate.

Methods

STUDY AREA

The study area is situated in the community of Flatanger, central Norway (64° 22' N, 10° 55' E; Figure 1), in the inner part of the Jøssund-fjord about 15 km east of the outer coastline. A rough terrain composed of steep hills, deep valleys, and several small summits where the local treeline is reached dominates the area. Three sites along an altitudinal gradient were chosen for the study. Site A is situated close to the fjord at 75 m a.s.l., and sites B and C are situated five km east of site A at 200 and 290 m a.s.l., respectively. Site C is situated just below the treeline, close to a small summit. Minor logging activities have occurred in the study area during the last 100 years, but this is only evident at site B, where a limited number of stumps are present. Mixed coniferous forests dominate the area, with Norway spruce the dominating tree species and *Pinus sylvestris* L. as sub-dominant tree species. *Betula pubescens* Ehrh., *Sorbus aucuparia* L., *Populus tremula* L., and *Alnus incana* (L.) Moench occur with lower frequencies in the tree layer. A sparse shrub layer consists of *Juniperus communis* L. The field layer in the studied sites is dominated by *Vaccinium*

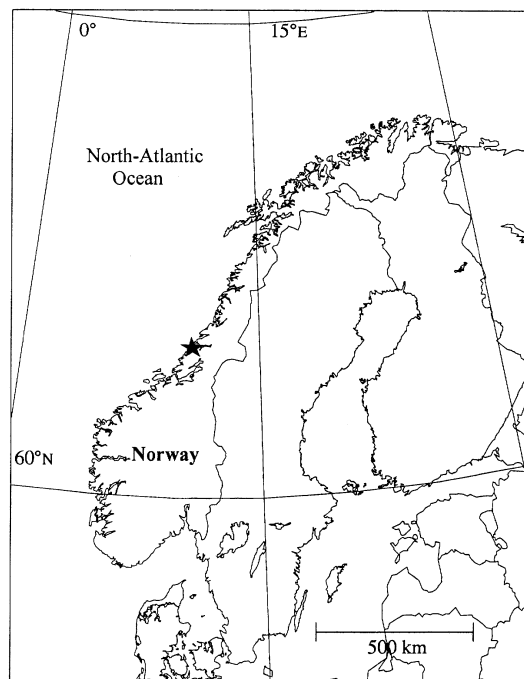


FIGURE 1. Location map of the study area (star).

myrtilus L., *V. uliginosum* L., *Cornus suecica* L., *Nartheceium ossifragum* (L.) Hudson, and *Molinia caerulea* (L.) Moench, and the bottom layer is dominated by *Hylocomium splendens* Hedw. and *Rhytidiadelphus loreus* (Hedw.) Warnst. Phytogeographically, the area belongs to the oceanic section of the middle and northern Boreal Zone (*sensu* Moen, 1999). The bedrock in the area consists of nutrient-poor gneiss-granite rocks (Sigmond, 1985) covered with a thin soil layer. A sparse and thin layer of moraine occurs in the valleys.

CLIMATE

The climate is oceanic, with *ca* 1300 mm annual precipitation and a mean annual temperature of 3.6°C (January = -5.5°C, July = 12.9°C) (Førland, 1993; Aune, 1993). Precipitation data show a maximum in the autumn and early winter (September-December), and a minimum in April-June (Førland, 1993). The area is normally snow-covered from late November to April (Bjørnbæk, 1993). However, the duration and stability of the snow cover varies between sites, with an increase of both variables along the altitudinal gradient. A stable and continuous snow cover is interrupted by mild spells with freeze and thaw cycles during the winter. All data refer to the normal period 1961-1990. From 1898 to 1997, annual and seasonal temperatures have increased, with the most pronounced changes during the first half of the period up to *ca* 1940 and in the spring (Figure 2a,b; Hanssen-Bauer & Nordli, 1998). Additionally,

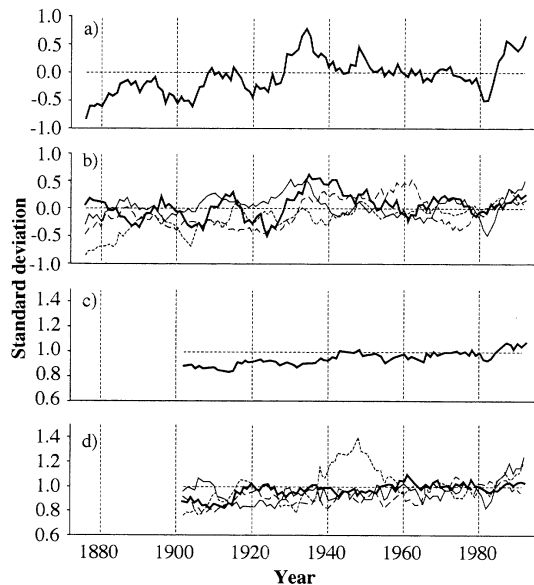


FIGURE 2. Regional climate development during the 20th century given as standard deviation relative to the 1961-1990 mean: a) annual temperature, b) seasonal temperature, c) annual precipitation, and d) seasonal precipitation. In b) and d) the thin line shows winter (Dec.-Feb.), dotted line spring (Mar.-May), thick line summer (Jun.-Aug.), and dashed line autumn (Sep.-Nov.). All series are 10-year running means of regional standardised values (data from Hanssen-Bauer & Førland, 1998; Hanssen-Bauer & Nordli, 1998). The dotted horizontal line is the mean for 1961-1990.

annual precipitation has shown a continuous increase since the end of the 19th century (Figure 2c; Hanssen-Bauer & Førland, 1998). The increase includes all seasons but is only significant for spring and summer. Spring precipitation had a major maximum during the period 1938-1954 (Figure 2d). The area is under the influence of North Atlantic air masses throughout most of the year, and the dominating wind direction is west. The climatic conditions during winter are strongly determined by the position and strength of lows originating from the North Atlantic. At the large scale, alternation of the intensity and position of these low pressures is described by the NAO index (Rogers, 1984; Hurrell, 1995). Air pressure data for the months December through March are quantified in the index. High positive values of the NAO index are associated with relatively warm and moist winters in western Scandinavia, and high negative values with relatively cold and dry winters (Hurrell, 1995). Mild and moist winters increase the amount of precipitation in western Norway. Whether the precipitation is rain or snow depends on the position of the actual site along both latitudinal and altitudinal gradients (Mysterud *et al.*, 2000). Cold and dry winters produce a thinner snow cover along the entire altitudinal gradient but increase the length of the snow-covered period close to the fjord.

SAMPLING AND PREPARATION

Altogether, 31 trees were cored at each site, and two samples from each tree were collected at 0.5 m above ground in opposite directions. The cores were sanded and visually cross-dated by the use of negative pointer years (Schweingruber *et al.*, 1990). The ring width was measured with a precision of 0.01 mm using LINTAB (Frank Rinn, Heidelberg) measuring equipment. Dating and measurement errors were tested for using the TSAP (Rinn, 1996) and COFECHA (Holmes, 1994) computer programs. Cores showing low correlation values (*r* < 0.5) with the mean site chronology were excluded from further analyses, resulting in 148 cores in total (Table I). Additionally, periods of

TABLE I. Chronology statistics (residual chronologies) calculated for the common period 1898-1996. Signal to noise ratio (SNR), expressed population signal (EPS), the explained variance for the first principal component (PC1) and standard deviation (SD).

CHRONOLOGIES	A	B	C
Number of trees (cores)	27 (45)	30 (57)	26 (46)
Autocorrelation*	0.25	0.33	0.50
Autoregression order*	1	1	1
SNR	16.6	33.1	24.9
EPS	0.94	0.97	0.96
EPS > 85% since	1844	1803	1812
No trees EPS > 85%	10	6	6
PC1	40.3%	54.1%	51.0%
Mean sensitivity	0.26	0.26	0.25
SD	0.21	0.22	0.22
MEAN CORRELATION			
Between trees	0.38	0.53	0.49
Within trees	0.57	0.71	0.69
CORRELATION BETWEEN CHRONOLOGIES			
A-B	0.90		
A-C	0.84		
B-C	0.94		

* Refers to statistic from the standard chronologies.

suppressed growth at the beginning of individual series were omitted.

CHRONOLOGY CONSTRUCTIONS

The ARSTAN program in the Dendrochronology Program Library software package (Holmes, 1994) was used for the standardization and construction of two different types of chronologies, standard and residual.

In the construction of the standard chronology, the raw ring-width records of each tree were standardized by a negative exponential curve or, if that failed, by a regression line, and further averaged together to one standard chronology per site (Cook *et al.*, 1990). With this type of standardization, low-frequency variability is kept and used for analyses of long-term and decadal trends. This conservative standardization method thus corrects for the biological age trend and transforms the actual ring-width data to dimensionless index series (Fritts & Swetnam, 1989).

In constructing the residual chronology, each individual series was first detrended by a spline function and the degree of smoothing was fixed at 50% frequency response of 60 years. A 60-year spline will keep 99% of the variation within the individual series at time scales shorter than 19 years. This means that common trends (< 19 years) between trees are conserved. All chronologies were computed by applying bi-weight robust means to discount outliers, and autocorrelation was removed from the individual series through autoregressive modelling (Cook, Shiyatov & Mazepa, 1990). This method removes lower-frequency variation and enhances the common high-frequency climatic signal, which generally has a better correlation with yearly climate variation. These residual chronologies were used for analyses of climate-growth relationships. The mean correlation technique (Briffa & Jones, 1990), the expressed population signal (EPS), and the signal to noise ratio (SNR) (Wigley, Briffa & Jones, 1984) were applied to estimate measures of common signal between trees in each RESIDUAL chronology. EPS was used to define the reliable part of the chronologies. The threshold EPS = 0.85 was selected for this purpose (Briffa & Jones, 1990).

CLIMATE-GROWTH ANALYSES

Climate-growth relationships were analysed using the PRECON software program (Fritts *et al.*, 1991), version 5.17b. Regional monthly mean temperature and regional monthly precipitation values (Hanssen-Bauer & Førland, 1998; Hanssen-Bauer & Nordli, 1998) were used in the analyses for the period from May in the year prior to growth to August in the year of growth (*i.e.*, 32 analysed variables). Response function analyses were performed for the period 1898-1997. One hundred bootstrap iterations were computed to assess statistical significance of the results (Guiot, 1990). The residual chronologies were set as predictands and climate variables as predictors. Moving response functions (MRF) were used to compute response functions for multiple time intervals (Biondi, 1997; 2000). To maintain enough degrees of freedom in the statistical model, the calibration period was set to 48 years, that is, 150% of the number of predictors (Biondi, 1997). Moving response function analyses were also performed with NAO index (December through March) as predictor variable and the residual chronology as predictands. The analysed time

window was 10 years, and the analysed period was 1873-1997. NAO data were downloaded from the Internet site <http://www.cru.uea.ac.uk/cru/data/nao.htm>. Additionally, temporal patterns in the climate-growth relationship were tested by the use of Pearson correlation analyses. In these analyses, the relationships between the residual chronologies and regional climate data and NAO index were analysed for the entire data period 1898-1997 and 1873-1997, respectively, and for 50-year sub-periods overlapping by 25 years.

Results

CHRONOLOGY CHARACTERISTICS AND LONG-TERM GROWTH TRENDS

The tree age varied between 93 and 288 years for all three sites taken together. The mean tree ages for sites A, B, and C were 158, 183, and 166 years, respectively. The tree-ring series contained only few missing rings (0.04%, 0.16%, 0.26%, respectively), mostly located to years or periods of years with narrow annual ring width, as, for example, during the last two decades (Figure 3). All three chronologies are significantly correlated to each other, but the correlation decreases with the altitudinal distance between the sites (Table I). Chronologies B and C are more homogenous than A, as reflected by the EPS, the SNR, and the variance explained by the first principal component. All three sites have well-replicated chronologies from the mid-1840s and onwards (Table I).

Pronounced growth peaks are more or less common to all sites around 1860, 1890, 1910, 1940, and 1970, along with growth depressions in the 1920s and from 1945 to 1960 (Figure 3). Since the 1940s, the growth pattern of site A has deviated from those of sites B and C, with no major alternations between growth increases and growth decreases.

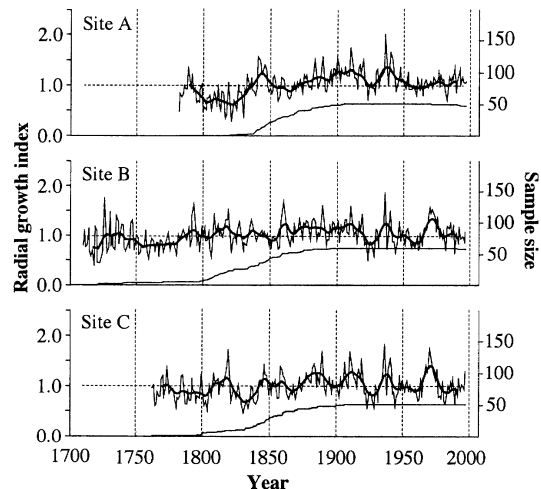


FIGURE 3. Standard chronologies for all three sites. The thin line shows the yearly tree-ring indices, and the thick line is a Gaussian low-pass filtered curve with a standard deviation of 3 years corresponding to a 10-year running mean. The thin line below shows the number of cores included in the mean. Total sample size for each site is given in Table I.

Additionally, the growth peak in the 1860s is less expressed in site A (Figure 3).

CLIMATE-GROWTH RELATIONSHIPS

RESPONSES TO SPRING AND SUMMER CLIMATE

May and June during the year of growth have the strongest correlation with diameter growth along the altitudinal gradient. Above average temperatures for both these months enhance annual ring width (Figure 4; Table II), and above average precipitation in May and June reduces the annual ring width (Table II). Additionally, there is a weak positive response to below average temperatures during April at the two uppermost sites (B and C) (Figure 4). During the summer prior to growth, a moist July has a positive correlation with diameter growth along the gradient (Figure 4), which is also indicated by a negative response to temperature (Table II). Additionally, site A has a positive correlation with above average August precipitation (Figure 4), but the signal is only related to the second half of the 20th century (Table II).

The general pattern for the period 1898-1997 changes somewhat when the data is analysed for responses through time. The influence of April and May temperatures during the year of growth decreases throughout the studied period, and April is only significant in the beginning of the analysed period and during a few shorter periods in the 1930s and 1950s at the treeline site (Figure 5). May temperature is an important climatic variable up to the 1930s whereupon it drops significantly in impact at all three sites, even though there are weak significant responses after 1960 at the lower sites (Figure 5; Table II). June has a significant correlation on annual ring width throughout the whole analysed period at all three sites but shows a less significant relationship from the 1930s to mid-1950s (Figure 5). Additionally, a negative correlation with May and June precipitation is evident for the year of growth. However, its importance has shifted from May to June during the analysed period along the entire gradient (Table II).

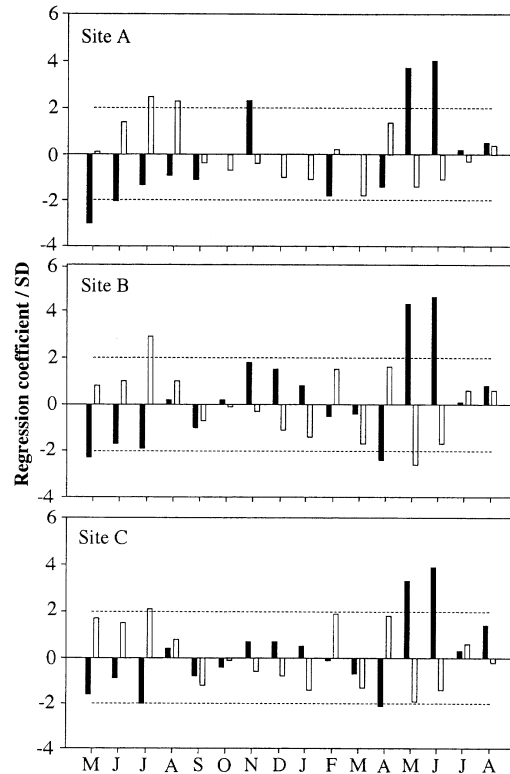


FIGURE 4. Effect of temperature (filled bars) and precipitation (open bars) on ring width indices from all three sites (A-C) shown by the regression coefficient divided by its standard deviation (based on the residual chronologies) for the period 1898-1997. Data are shown for May_{t-1} to August_t. Dotted horizontal lines indicate significance level ($p < 0.05$) above and below the mean, where the ratio > 2 between the regression coefficient and its standard deviation was used as a guideline. The explained variances of the three sites are 0.55, 0.64, and 0.55, respectively.

TABLE II. Significant correlations ($p < 0.05$) between the residual chronologies and regional climate data (Hanssen-Bauer & Førland 1998; Hanssen-Bauer & Nordli, 1998) for the period 1898-1997 and three 50-year sub-periods with 25 years overlap. Analysed months are from May_{t-1} to August_t.

Time period	Previous year Temperature					Precipitation		Current year Temperature					Precipitation		
	May	June	July	Sep.	Nov.	June	July	Aug.	Feb.	May	June	Aug.	Apr.	May	June
SITE A															
1898-1947	-0.32		-0.34		0.34		0.31		-0.30	0.41	0.51			-0.37	
1923-1972			-0.33						-0.31	0.31	0.50			-0.28	-0.32
1948-1997	-0.39	-0.45		-0.32			0.31	0.29			0.49				
1898-1997	-0.35	-0.29	-0.28	-0.24				0.28	-0.21	0.31	0.49			-0.28	-0.22
SITE B															
1898-1947			-0.36		0.36		0.31			0.41	0.52			-0.42	
1923-1972			-0.36							0.39	0.53			-0.33	-0.41
1948-1997	-0.37									0.35	0.56				-0.29
1898-1997	-0.31		-0.31					0.21		0.37	0.52			-0.33	-0.27
SITE C															
1898-1947			-0.30							0.43	0.49			-0.36	
1923-1972			-0.36							0.29	0.52				-0.41
1948-1997	-0.37										0.51	0.37			-0.33
1898-1997	-0.28		-0.30							0.30	0.49	0.22	0.21	-0.27	-0.26

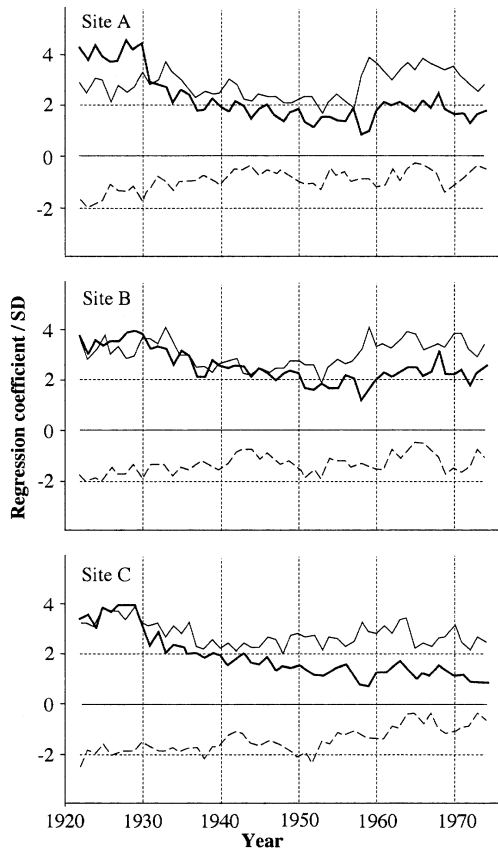


FIGURE 5. Course of April_t (dashed line), May_t (thick line) and June_t (thin line) temperature effect on growth for all three sites during the period 1898-1997, using moving response function with a 48-year time window (this means, for example, that the value for year 1922 comprises the time period 1898-1945). Dotted horizontal lines indicate significance level ($p < 0.05$) above and below the mean, where the ratio > 2 between the regression coefficient and its standard deviation was used as a guideline.

RESPONSES TO AUTUMN AND WINTER CLIMATE

Above average November temperature during the previous year is positively correlated with annual ring width at site A (Figure 4). This influence of November temperature is restricted to the first part of the analysed period, during which significant values are shown also at site B (Figure 6; Table II). Additionally, the decreasing correlation of November temperature throughout the analysed period is paralleled by a continuous increase in the correlation of December temperature during the previous year. The same shift in response is indicated at the treeline, although not significant. November and December precipitation during the previous year are both negatively correlated to annual ring width, but at site A the response is only significant for shorter periods prior to the 1950s, and at sites B and C only between the 1930s and 1950s (Figure 6). After the 1950s, there is no effect of November and December precipitation on diameter growth.

There is no evident relationship between diameter growth and the NAO index when analysed over the period 1873-1997 (Table III). In the analyses of 50-year periods and the MRF analyses, periods with significant correlations are evident (Table III; Figure 7). Negative significant response to the NAO index is mainly restricted to periods around 1920 and around 1940 (Figure 7). At site A, these periods are more or less the only ones with a significant response. The response through time has generally followed the same pattern along the altitudinal gradient (Figure 7). Differences in response are only evident during shorter periods prior to the 1920s and in the 1950s to 1970s. At the treeline, a significant positive response around 1880 and during the first decade of the 20th century is apparent. During the second half of the 20th century, the correlation

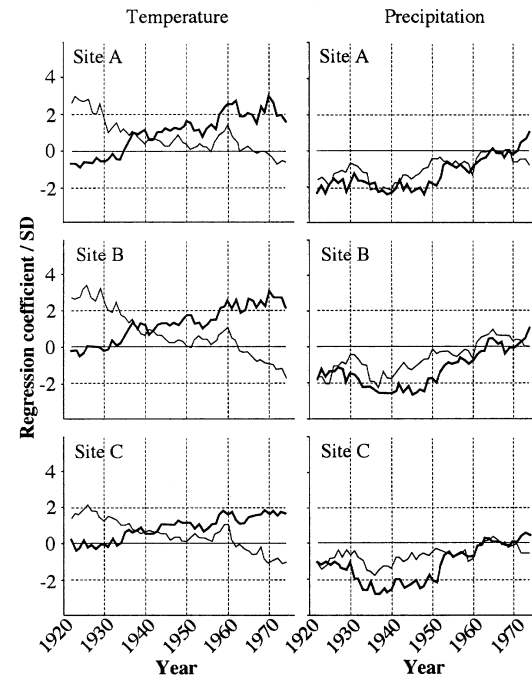


FIGURE 6. Course of November_{t-1} (thin line) and December_{t-1} (thick line) temperature and precipitation effect on growth, shown by moving response function (48-year time window, cf. Figure 5) values for the period 1898-1997. Dotted horizontal lines indicate significance level ($p < 0.05$) above and below the mean, where the ratio > 2 between the regression coefficient and its standard deviation was used as a guideline.

TABLE III. Correlations between the NAO index (Hurrell, 1995) and the residual chronologies for four 50 years periods with 25 years overlap and for the period 1873-1997. Significant values are given in bold, and significance level in parentheses.

	A	B	C
1873-1922	-0.11 (0.453)	-0.04 (0.784)	0.09 (0.555)
1898-1947	-0.42 (0.002)	-0.34 (0.015)	-0.26 (0.072)
1923-1972	-0.38 (0.007)	-0.41 (0.003)	-0.44 (0.001)
1948-1997	0.01 (0.970)	-0.06 (0.690)	-0.12 (0.410)
1873-1997	-0.18 (0.049)	-0.17 (0.053)	-0.14 (0.119)

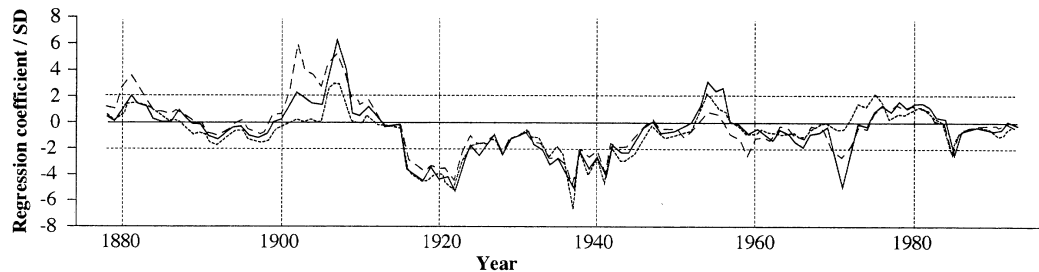


FIGURE 7. Correspondence between the NAO index (December-March) and diameter growth, shown by moving response function (10-year time window) values for 1873-1997, for site A (dotted line), site B (thin line), and site C (dashed line). Dotted horizontal lines indicate significance level ($p < 0.05$) above and below the mean, where the ratio > 2 between the regression coefficient and its standard deviation was used as a guideline.

between NAO and diameter growth is not significant except for a few occasions (Table III; Figure 7).

Discussion

The close relationship between early summer (May-June) temperature variations and the long-term (century) diameter growth pattern is an oceanic characteristic for *P. abies* in western Scandinavia, caused by earlier cessation of the winter and the subsequent earlier start of the growing season compared with more continental areas (Tuhkanen, 1984). Consequently, the result differs somewhat from findings in continental parts of central and northern Fennoscandia, where radial growth response to June-July temperature variation is dominating (Hofgaard, Kullman & Alexandersson, 1991; Kullman, 1996; Mäkinen, Nöjd & Mielikäinen, 2000). In the study area, the recorded shift with gradually reduced sensitivity to May temperature occurred along with a constant increase in May temperature during the 20th century. Both May and June temperatures were found to be less important to radial tree growth during periods when the mean of these climate variables was higher than the long-term mean. Hypothetically, May temperature passed a threshold somewhere around the middle of the analysed period, above which it became less restricting to spruce diameter growth, and June thus became the dominating early summer variable. Concomitantly, climate variables during other parts of the year showed increased importance (*i.e.*, variables that cause increased restrictions to diameter growth), as exemplified by the significant correlation with winter climate (NAO index) during the mid-century.

Generally, in coastal regions of southern and central Norway, the NAO index is negatively correlated to snow depth at low altitudes and positively correlated at higher altitudes (Myrsterud *et al.*, 2000). At low altitudes, high NAO index values are thus indicative of a relatively insufficient snow cover to prevent soil frost formation. With increasing latitude and still with a thin snow cover, this fact is likely to increase due to generally decreasing temperatures. Consequently, mild winters in the study area might have a negative effect on radial tree growth during the subsequent summer due to ground frost formation and a delayed start of the growing season (Kullman, 1996). In addition, unusually mild winters may cause conditions without ground frost and subsequent damage due to, for exam-

ple, pre-season bud burst (Crawford, 2000). How the effect of winter climate is mediated into radial growth response along the studied gradient thus depends on the altitudinal threshold position for snow cover/snow duration during individual years and periods of years, and the duration and altitudinal position of temperatures $< 0^{\circ}\text{C}$ during snow-free winter periods. Changes of such threshold positions have possibly occurred during the studied period but generally seem to have comprised the entire gradient. The MRF between NAO and annual ring width show a highly correlated pattern between the sites, except for shorter periods with altitudinally separated response. Conceivably, the general pattern with no separation between altitudes is due to the fairly short distance between sea level and the treeline. However, it also shows the dominating influence that different modes of the North Atlantic weather system have on nearby terrestrial ecosystems (D'Arrigo *et al.*, 1993; Post & Stenseth, 1999).

The evident temporal and spatial variation seen in the response to NAO variation is caused by a combined effect of changes in a range of climate variables with individually only weak or without significant correlation to radial growth. For example, during the 1920s, 1930s, and 1940s, there was only a weak signal for individual climate variables, but there were marked signals for the NAO index. After the mid-20th century, there seems to be no correlation between winter climate and diameter growth except for a few shorter periods. Generally, the trees appear to have had a reduced ability to respond sensitively to climatic variability during the last decades, a tendency that is also reported from other areas and for other species from the boreal region (Jacoby & D'Arrigo, 1995; Kullman, 1996). Additionally, reduced sensitivity to summer temperature during recent decades has been discussed for several boreal tree species (Kullman, 1996; Briffa *et al.*, 1998; Vaganov *et al.*, 1999; Jacoby *et al.*, 2000). This reduced sensitivity has been discussed in terms of several explanations, including changes in winter conditions such that stress during the winter induces needle damage and needle loss, reducing the opportunity to take advantage of subsequent favourable growth conditions. Besides decreased growth, deep ground-frost formation may cause retrogression of trees and decreasing stand vitality due to root damage (Kullman & Högberg, 1989; Kullman, 1996; Crawford, 2000; Sveinbjörnsson, Hofgaard & Lloyd, in press), which might lead to destabilisation of the forests. It is not likely

that the recorded temporal differences in radial growth response are caused by stand age, as the mean tree ages are far from the potential maximal age of the species (Niklasson & Zielonka, 1999; Kullman, 2000). Further, an old-growth *P. abies* forest in northern Sweden regained vitality and radial growth after a period of low vitality, providing further evidence of the strong linkage between climate variation and radial tree growth (Hofgaard, Kullman & Alexandersson, 1991).

According to climatic records (Jones, Wigley & Wright, 1986; Hanssen-Bauer & Nordli, 1998), the late 1930s and the years around 1990 were the warmest periods during the 20th century. The maximum in the 1930s was well reflected in the diameter growth of the trees along the gradient, but the 1990 maximum was not. A qualitative difference in these two maxima may have caused the difference in diameter growth response. While high summer temperatures largely caused the high annual temperature in the 1930s, mainly high winter temperatures caused the warm period around 1990 (Hanssen-Bauer & Nordli, 1998), to which the trees were unable to respond positively. During periods with a predominant oceanic climate pattern (late 20th century), as well as during periods with cold climate (early 20th century), the course of the summer is of increased importance (mainly through the increased importance of June) for the growth of coastal spruce forests. In the light of present results, the mid-century period (characterised by a more continental climate type), with a significant correlation between diameter growth and the NAO index, appears to be an exception from a longer-term perspective. The situation during recent decades, with no significant correlation, might be closer to what could be a more common long-term pattern. Such fluctuations in the climate/growth relationship have to be seriously considered in dendroclimatological studies (Kullman, 1996), both in retrospective analyses and in scenarios for the future.

Climate scenarios for northern Europe predict a non-uniform distribution of temperature increase throughout the year, with evident warming mainly during late autumn and winter (Kattenberg *et al.*, 1996; IPCC, 2001). Most scenarios predict a 3–4°C increase in winter temperature during the 21st century (Kattenberg *et al.*, 1996; Jones *et al.*, 1997; IPCC, 2001). Given that the present mean winter temperature for the area is -4.7°C (1961–1990; Aune, 1993), the predicted mean winter temperature would be close to -1°C according to these scenarios. Consequently, mild spells in winter would most likely be more regular events and the precipitation would to an increasing degree fall as rain. Our results indicate that the response of spruce would involve a decrease in radial growth rate and a further increase in the importance of June temperature. However, this response would be highly dependent on the seasonal timing of temperature changes and on soil frost formation controlled through precipitation quantity and quality during winter along the altitudinal gradient. Further, the given scenarios would most likely produce a climatic pattern characterised by increasing oceanicity over larger areas both along coastal-inland gradients and altitudinal gradients of northern Scandinavia compared with the current situation (Kattenberg *et al.*, 1996; IPCC, 2001). The radial growth

response pattern currently prevailing in coastal areas would thus be spatially extended to areas with currently more continental climate and growth pattern. However, further studies along extended natural gradients are needed before conclusive growth response scenarios for Scandinavian spruce forests at the interface between oceanic and continental regions can be made.

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Paper II

Submitted manuscript (Canadian Journal of Forest Research)

Spatiotemporal changes in radial growth and response to climate for *Picea abies* along environmental gradients

by
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**Spatiotemporal changes in radial growth and response to climate for
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Abstract: Tree-ring data from *Picea abies* (L.) Karst. was sampled at 10 sites at three different areas along gradients of oceanicity and altitude in central Norway. Correlation and response function analyses were applied to decipher spatiotemporal growth patterns and correlation with climate along the studied gradients. *P. abies* from all sites showed a positive response to summer temperature, although the response shifted through time and from May_t and June_t at the coast, to May_t, June_t and August_t in the most continental part of the studied area. During the 20th century the climate in the region changed and the whole region was more oceanic in late 20th century than earlier. Contemporary, there was an increase in correlations between the tree chronologies from the three different areas and more similar growth responses to climate along the oceanicity gradient. Trees along the altitudinal gradients at the coast showed larger dissimilarities at the end of the 20th century. This may have been caused by an alteration in winter climate due to milder winters with precipitation more likely falling as rain instead of snow. This put the trees under increased stress and worsened the growth conditions for *P. abies* in this oceanic region.

Introduction

Dendroclimatological methods are useful tools for analysing the climate factors that influence radial tree growth (Fritts and Swetnam 1989). Tree-rings from high elevation and high latitude sites provide climatically sensitive records that may extend over centuries to thousands of years with annual resolution (Briffa 2000). Climate sets prerequisites for tree growth and determines limits for the distribution and abundance of different tree species (Payette and Lavoie 1994; Kullman 1996; Hofgaard 1997; Bradshaw et al. 2000). In high latitudes, there is a general strong influence from mid summer temperatures on radial tree growth for conifers (c.f. Briffa et al. 1990; D'Arrigo and Jacoby 1993; Lindholm 1996). However, tree growth responses to climate differ in a spatiotemporal manner determined by climate variations along natural environmental gradients (Briffa et al. 1998; Kalela-Brundin 1999; Kirchhefer 1999; Hofgaard et al. 1999; Mäkinen et al. 2000; Allen et al. 2001; Gedalof and Smith 2001). Such natural gradients are demonstrated to be well suited to study changes in response pattern of tree growth (Kienast et al. 1987; Villalba et al. 1997; Hofgaard et al. 1999; Mäkinen et al. 2000; Gedalof and Smith 2001). The spatial component in climate variation is seen over geographical areas, e.g. along altitudinal, longitudinal and latitudinal gradients. Scandinavia stretches over 14° in latitude and this gives a high natural variation in climate from the south to the north.

Climate varies temporally over years, decades and centuries. For example, one deviating period in the last millennium was The Little Ice Age, which was a prolonged cold period, ca 1430-1850 (Grove 1988). It was characterised by a relatively cool period in a Holocene perspective, but interrupted by warmer periods. After the termination of the Little Ice Age, the climate in Central Norway changed to a warmer and wetter climate (Hanssen-Bauer and Førland 1998; Hanssen-Bauer and Nordli 1998). The temperature increase reached a maximum around 1940 and again in the 1990's, after a period with decreasing temperatures. The increase in precipitation has been almost linear since the end of the 19th century. Thus, in the studied region the climate has changed from a relatively cold climate to a relatively warmer and wetter climate during the last 150 years or so. Such transient changes in climate have consequences for radial tree growth and trees response pattern to climate (Kullman 2001; 2002; Tardif et al. 2001; Solberg et al. 2002).

Generally, there is a positive correlation between summer temperature and radial growth for conifers in Fennoscandia (Briffa et al. 1990; Hofgaard et al. 1991; Kalela-Brundin 1999; Mäkinen et al. 2000; Solberg et al. 2002). However, northern conifers have shown to change their response and sensitivity to climate variables through time (cf. Briffa et al. 1998; Hofgaard et al. 1999; Solberg et al. 2002), for example a reduced sensitivity to summer temperature for the last decades at high latitudes in the Northern Hemisphere is evident (Briffa et al. 1998). Furthermore, there is a variation between species and regions within Fennoscandia in the specific months where radial tree growth correlates with climate (e.g. Briffa et al. 1990; Kalela-Brundin 1999; Mäkinen et al. 2000; Solberg et al. 2002). Norway spruce (*Picea abies* (L.) Karst.) has changed response to both summer and winter climate during the 20th century (Solberg et al. 2002). This non-linear response has implications for retrospective studies of radial tree growth and the use of tree-rings as proxy data in reconstruction of climate and understanding of past natural climate variation.

Important insights into the magnitude of the tree growth response to climate variability and/or change can be gained from species-specific dendroclimatic investigations along natural environmental gradients (Kienast et al. 1987; Villalba et al. 1997; Hofgaard et al. 1999; Mäkinen et al. 2000; Solberg et al. 2002). In order to elucidate tree growth response to both spatial and temporal climate variations this study uses *P. abies* ring-width chronologies from altitudinal gradients along a coast-inland gradient in central Norway.

The principal aims of the study are i) to identify climate variables with significant influence on radial tree growth of *P. abies* along oceanicity and altitudinal gradients ii) to identify how the growth response to climate has changed through time along these gradients iii) to evaluate conceivable growth responses to predicted changes of the regional climate along the analysed spatial gradients.

Material and Methods

Environmental gradients and regional climate

The study is performed in the boreal forest in central Norway along a coast-inland gradient spanning a distance of approximately 200 km (64°N 10°-14° E; Fig. 1). Along this gradient three areas from west to east (A, B and C) are sampled reflecting a total yearly precipitation of 1500, 900 and 600 mm, respectively (Førland 1993). In each area, three to four sites (a-d) are sampled along altitudinal gradients from lowland forests to forest-line, reflecting a summer temperature difference of approximately 2°C (Table 1).

On a regional scale, the climate is influenced by westerly winds from the Atlantic Ocean, with reducing oceanicity towards east (Table 1). Area A is in the oceanic zone, B in the sub-oceanic zone and C in a transition zone between oceanic and continental climate (c.f. Moen 1999). The mean annual temperature along the coast-inland gradient goes from 5.0°C (20 m a.s.l.) in area A to 0.9°C (433 m a.s.l.) in area C (Aune 1993). Due to the influence of the Atlantic Ocean the winter is mild at the coast with a mean January temperature of -2.4°C, and considerably colder in the east with a mean January temperature of -10.4°C (Fig. 2). The climate during the growing season (May-August) does not show such big differences along the gradient, with a July temperature of 13.3°C at the coast, and 11.8°C in the east (Fig. 2). Area A has maximum precipitation in autumn and winter, while area B and C in late summer and autumn (Fig. 2). At the coast May and June are the months with lowest precipitation; inland April and May have precipitation minimum (Førland 1993). Snow covers the ground for approximately 120, 165 and 195 days at area A, B and C, respectively (Bjørnbæk 1993). There are also differences along the altitudinal gradients within each area in respect to snow-cover, with prolonged snow cover at higher altitudes. All data refer to the normal period 1961-1990 (Aune 1993; Bjørnbæk 1993; Førland 1993).

The sites were selected to avoid influence from major anthropogenic disturbances, and both the sites and the individual trees were chosen to maximise the climatic signal in the tree ring series (Schweingruber 1996). Additionally, the sampling was performed to choose sites that are similar in respect to ecological factors like exposition, pH, nutrient status and soil-moisture conditions. Mixed boreal forests with *P. abies* and *Pinus sylvestris* L. (Scots pine) as the dominating tree species, and low occurrence of boreal deciduous tree species (e.g. *Betula*

pubescens Ehrh. (Birch), *Sorbus aucuparia* L. (Rowan), *Populus tremula* L. (Aspen) and *Alnus incana* (L.) Moench. (Grey Alder)), characterise all sampled sites. At area A, *P. abies* is sampled at its most westerly and oceanic part of its total distribution area (Schmidt-Vogt 1977). For a more detailed description of the area see Solberg et al. (2002). Area B is in Imsdalen valley where site Ba is at the valley bottom on glacial-fluvial deposits. This is a dense forest on a highly productive site with some disturbance from wind and logging. Site Bb and Bc is on the same valley side on thin soil with no signs from logging impact. All sites in area C were on the north to northwesterly slope of the Hestkjølen mountain massif (1300 m a.s.l.). The more southerly exposition for site Cb was due to the position of the site on a small hill in the valley bottom. Site Ca seems to have been disturbed in the 19th century, probably by logging and all sampled individuals from this site had approximately the same age (Table 1). Site Cb and Cc is old-growth forests with trees in all stages, dead standing trees and logs in different degree of decay. Site Cd is situated at the local forest-line where *P. abies* grows mostly in wet depressions in an area dominated by *B. pubescens*. *P. abies* is here growing both in clumped clones and as solitary individuals.

Sampling and chronology constructions

P. abies ring-width chronologies from 10 sites were sampled. On each site, minimum 30 trees were sampled and two cores from opposite sides (0.5-1.3 m) were extracted from each tree. The cores were mounted, sanded, crossdated and measured in the laboratory according to standard procedures. The cores were measured to the nearest 0.01 mm using LINTAB measuring equipment and the software Time Series Analysis and Presentation (TSAP) version 2.4 (Rinn 1996). The crossdating was performed both manually (Stokes and Smiley 1968) and with correlation coefficients (Holmes 1994). By using approaches in the TSAP and the COFECHA (Holmes 1994) computer programs, dating or measurement errors were tested. Cores showing low correlation values ($r < 0.5$) with the mean site chronology were excluded from further analyses resulting in 280 trees and 534 cores in total. Additionally, periods of suppressed growth at the beginning of individual series were omitted.

Through standardisation, the individual growth trends were removed and all tree-ring series on one site were averaged together to produce one chronology per site (Cook et al. 1990a). The tree-ring series were standardised by fitting the observed ring width series to a curve or a

straight line, and then dividing the ring width by the fitted curve (Fritts and Swetnam 1989). One STANDARD chronology that preserved low-frequency variations (long-term and decadal growth trends) was built for each site to facilitate analyses of growth trends. In these STANDARD chronologies, each individual tree-ring series was detrended by a negative exponential curve or, if that failed, by a regression line. Additionally, one RESIDUAL chronology was constructed for each site with the purpose of maximising high-frequency climate signals and eliminating non-climate variation in the chronologies. Autocorrelation was removed from the individual series through autoregressive modelling (Cook et al. 1990b). In this case, each tree ring series was detrended with a 60-year spline that maintained 99% of the variation within the individual series at time scales shorter than 20 years. As a side effect of this process, also long-term climate variation was removed (Cook et al. 1990a). These RESIDUAL chronologies were used for all correlation, principal component (PC) and climate-growth analyses.

Statistical analysis

The mean correlation technique (Briffa and Jones 1990), the expressed population signal (EPS) and the signal to noise ratio (SNR) (Wigley et al. 1984) were applied to estimate measures of common signal between trees in each RESIDUAL chronology. The EPS value 0.85 was used as a threshold to define the reliable part of the chronologies. Mean sensitivity is a measure of the relative change in ring width variations between years (Fritts 1976). Thus it reflects the potential of trees to respond to short time climate variation. Along an altitudinal gradient it is expected that the relative influence of climate on tree growth should increase, therefore mean sensitivity is expected to increase along altitudinal gradients (Fritts 1976). Mean sensitivity is calculated for the 1873-1997 period and additionally for 50 years sub-periods with an overlap of 25 years.

Correlation patterns along the environmental gradients and through time were investigated for the common period 1873-1997 by using Pearson's correlation and principal component analysis (PCA) (Peters et al. 1981). Additionally, the data set was split in 50-years sub-periods with an overlap of 25 years, and both correlation and PC analyses were carried out for all sub-periods. In the correlation matrix, years were used as variables and the ten RESIDUAL chronologies as observations.

Climate-growth relationships were analysed between ring width indices (RESIDUAL chronologies) and climate data. The climate-growth analyses were performed with response

function analyses (Fritts 1976) by using procedures in PRECON (Fritts et al. 1991) version 5.17b. One hundred bootstrap iterations were computed to assess statistical significance of the climate variable (Guiot 1990). The climate-growth relationships were analysed for two growing seasons in a sequence of 16 months from May_{t-1} to August_t with homogenised and standardised regional monthly means of temperature and monthly totals of precipitation values (Hanssen-Bauer and Nordli 1998; Hanssen-Bauer and Førland 1998). The analysed period was 1898-1997 and, additionally, the data were split in 50-years sub-periods overlapping with 25 years.

Results

Chronology characteristics and low-frequent growth patterns

All chronologies showed a strong climatic signal and are thus well suited to climate-growth analyses (Table 2). The chronologies from the eastern area had a more homogenous signal compared to the two western chronologies, i.e. stronger signal to noise ratio, a higher variation in PC1, a higher correlation both within and between trees and needed a lower number of trees to get a reliable chronology (Table 2). The mean sensitivity and standard deviation was highest in the coastal area and at the forest-line in the easternmost area (Cd) (Table 2). Mean sensitivity analysed over 50 year sub-periods revealed a common pattern where the 19th century generally had low year to year variation followed by a maximum in the first half of the 20th century and then subsequently dropped slightly in the sub-period 1948-1997 (Table 3). Additionally, the mean sensitivity showed a slightly increasing trend along the altitudinal gradients during the 20th century (Table 3).

Long term trends in tree growth are visualised by the STANDARD chronologies in Fig. 3. On a decadal scale, there are several differences between the sites, but also major similarities. The most evident growth pattern is slower growth in the 1920's and faster growth in the 1930's than long term mean. This pattern is more or less valid for all sites except site Cd, which had faster growth in the 1940's with a peak around 1950 (Fig. 3). Sites Ac, Ba, Cb, Cc and Cd had decreased growth in the end of the 18th century and the beginning of the 19th century (Fig. 3) followed by increased growth in the 1820's for most of the sites. Furthermore, there were

indications of a decreased growth for the last decades in the two eastern areas, which was not evident at the coast.

Regional tree growth correlations

When correlated both for the entire period and for 50-years sub-periods, all areas and sites was highly significant (Table 4 and 5). The correlations between areas decrease along the coast-inland gradient (Table 4). Further, there are indications of a decreasing correlation along the altitudinal gradients (Table 5), although not so evident as along the coast-inland gradient. The correlation between area A and B are stable for all analysed 50-years periods, except for a slightly lower correlation in the 1873-1922 sub-period (Table 4). On the other hand, the correlations between area C and A/B have increased continuously since the 1873-1922 sub-period (Table 4).

The PCA showed that 42.7% of the total variance in the series was related to PC1 (Table 6). The individual sites from the different areas were well separated and this axis was interpreted as a coast-inland gradient (Fig. 4). More than 16% of the total variance was explained by PC2, which was interpreted as an altitudinal gradient (Fig. 4). PC 3 and 4 seem to represent some area specific variables, but also environmental variables related to altitude that is not represented by PC2 (Fig. 4). However, each axis explained relatively lower fractions of the total variance than the two former axes and will not be treated any further (Table 6). The sum of eigenvalues showed a peak in the sub-period 1898-1947 and a minimum in 1948-1997 (Table 6), reflecting less total variance in the last sub-period. Furthermore, the eigenvalues for PC1 decreased relatively more than the sum of eigenvalues and this led to a reduction of explained variance from 52,4% in 1898-1947 to 37.5% in 1948-1997 (Table 6). This indicates that the external factor causing a long environmental gradient with a relatively large eigenvalue in the sub-period 1897-1947 is considerably weaker in the sub-period 1948-1997. Consequently, the PC1 gradient length is shortened. The eigenvalues for PC2 have been more or less stable for all sub-periods (Table 6). However, due to the decrease in the sum of eigenvalues between 1898-1947 and 1948-1997, PC2 showed an increase in explained variance (Table 6). The evolution of site positioning along the second axis has changed between the areas through time (Fig. 5). At the coast, there was a shorter gradient in the sub-period 1898-1947 than before and afterwards. For area B, there has been a

progressively longer PC2 gradient throughout the studied period, while in the easternmost area the site positioning has been relatively unchanged (Fig. 5).

Spatiotemporal variations in tree growth response to climate

Temperature

There was a strong positive correlation between radial tree growth and late spring to summer temperature the year of growth for all sites in the 1898-1997 period (Fig. 6). The response shifted along the coast-inland gradient from May_t and $June_t$ at the coast, while in the most continental part of the studied area radial growth responded to May_t , $June_t$ and $August_t$ temperatures. There is stronger emphasis on $June_t$ than on May_t in the two inland areas, compared to the maritime area. Several of the forest-line and near forest-line sites (Ab, Ac, Bb, Bc, Cd), had a negative response to $April_t$ temperature (Fig. 6). Further, the radial growth showed a negative correlation to temperature above mean in the summer prior to growth, especially for the easternmost area.

The correlation between radial tree growth and summer temperatures changed over the different sub-periods (Fig 7). May_t temperature was at the coast, but not in the most continental area, C, positively correlated with radial growth in the period 1898-1947. In the later sub-periods, radial tree growth in the coastal area was less correlated with May_t temperature, while in the more continental areas radial growth increased its response to May_t temperature (Fig. 7). Thus, for the two later sub-periods the response patterns to May_t temperature were more similar across the coast-inland gradient. June temperature and radial tree growth is highly significant correlated in all time periods at all sites. The positive influence of $August_t$ temperature in the easternmost area is not present during 1898-1947.

Radial tree growth responses to winter climate differ between the sites along both the coast-inland and the altitudinal gradients (Fig. 6). A significant positive response to $November_{t-1}$ temperature was present along the coast-inland gradient, with the strongest response in the inland. Through time, the significant correlation with $November_{t-1}$ temperature is shifted to correlation with $December_{t-1}$ temperature (Fig. 7). This pattern is more or less consistent for all areas and sites. Additionally, at area C there is a strong negative effect of $February_t$ temperature above mean (Fig. 6). The negative influence of $February_t$ temperature is most pronounced at area C during the sub-period 1923-1972 and less evident for the two other sub-periods (Fig. 7). Further,

the correlation between February_t temperature and radial tree growth is also present at site Bb and Bc for the same sub-period.

Precipitation

Generally, there are few significant correlations between precipitation variables and radial tree growth during the studied period 1898-1997 (Fig. 6). However, there are weak negative responses to early summer precipitation the year of growth at the coast (May) and in the easternmost area (June) (Fig. 6), which is probably a reflection of the temperature response. Additionally, there are positive responses to summer precipitation the year prior to growth, while the only significant response during winter is a positive response of February_t precipitation on site Bb and Bc (Fig. 6).

Radial tree growth over time showed different correlations with precipitation variables from September_{t-1} to August_t (Fig. 8). The growth responses for the two first sub-periods had approximately the same pattern with emphasis on December_{t-1}, March_t and June_t (Fig. 8). Though, for the sub-period 1898-1947 only a couple of the responses were significant. During the sub-period 1948-1997 the responses to precipitation variables were missing. A positive response to summer precipitation in the year prior to growth is present for the sub-period 1898-1947 and 1923-1972, but not for the sub-period 1948-1997 (Fig. 8).

Discussion

A variety of climatic factors influence tree growth (Fritts 1976), and the importance of different climatic variables shifts according to the species in target (e.g. Villalba et al. 1994), along environmental gradients, and during time (Kienast et al. 1987; Hofgaard et al. 1999; Peterson and Peterson 2001; Solberg et al. 2002). The dominating radial growth response to May temperature is a characteristic feature for spruce in coastal Fennoscandia (see Solberg et al. 2002). The deviating response pattern in the eastern area, C, shares strong similarities with more continental parts of Fennoscandia (Hofgaard et al. 1991; Kullman 1996; Mäkinen et al. 2000). However, in a temporal perspective the areas along the studied coast-inland gradient became

more similar towards the end of the 20th century. Hypothetically, this is due to an increased oceanicity over larger areas at present (Crawford 2000; Tuomenvirta et al. 2000). The increased oceanicity includes increased precipitation and temperatures, especially during winter, and decreased variability in intra-annual temperatures (Hurrell 1995; Hanssen-Bauer and Førland 2000; Folland et al. 2001; Frich et al. 2002). These changes in climate are strongly related to a general increase in the North Atlantic Oscillation for the last decades. In the inland, there is a negative correlation between radial growth and February temperature in similarity with central and northern Finland (Mäkinen et al. 2000), but this relationship is lacking at the coast. This indicates that this correlation is an inland characteristic of *P. abies* in northern Europe, and further fortifies radial tree growth differences along the coast-inland gradient. Ultimately, the similarity in site conditions among all sites indicates that the differences in growth responses are caused by a changing climate along the coast-inland gradient.

The different areas were well separated along the coast-inland gradient (PC1). Hypothetically, this separation is a result of different growth conditions between maritime and more continental parts of central Norway. Changes in climate throughout the 20th century with warmer temperatures and an increase in yearly precipitation towards present (Hanssen-Bauer and Førland 1998; Hanssen-Bauer and Nordli 1998; Folland et al. 2001) have encompassed changes in several climatic variables, included in the analyses. These changes have led to a more homogenous and oceanic climate in an extended area in the late 20th century compared to the conditions immediately after the Little Ice Age (Hurrell 1995; Crawford 2000; Tuomenvirta et al. 2000; Cook et al. 2002). Consequently, the trees from the different areas are responding more similarly to climate at present than at the beginning of the analysed period. These findings should be considered in the development of models over future responses of climatic influence on tree growth on both a spatial and temporal scale.

The Little Ice Age ended during mid 19th century and probably left behind a low-vitality forest after a long period where cold temperatures had prevailed (Grove 1988; Hofgaard et al. 1991; Briffa et al. 1992; Kullman 2001). During the 19th century, there had been a lower influence of mild and wet Atlantic air masses and a stronger dominance of colder and drier air masses than in the 20th century (Grove 1988; Hurrell 1995; Slonosky et al. 2000). The tree-ring series showed characteristics of a lower mean sensitivity at all sites in the 19th century compared to the 20th century. This is probably a result of low-vitality trees with a relatively low potential to

respond rapidly to high-frequent climatic variations (Hofgaard et al. 1991). Due to climate amelioration between ca 1880 till 1940 (Hanssen-Bauer and Nordli 1998), there was a general increase in radial tree growth at all sites. During this warming period, the easternmost area demonstrated lower correlations with the other areas, hypothetically, due to higher variance in the regional climate. In the northern boreal forest in North America, changes in influence from different air masses have importance for vegetation distribution and tree growth (Bryson 1966; Larsen 1971; Scott et al. 1988; Hofgaard et al. 1999). There is a lack of detailed studies of air mass distribution in northern Europe (but see Krebs and Barry 1970). The climate in Scandinavia is under influence from mild and wet Atlantic air masses, cold Arctic air masses and dry Siberian air masses (Wallén 1970). Thus, spatiotemporal changes in influence from these different air masses may influence radial tree growth differently on a regional scale in Scandinavia. The less strong oceanic influence along the coast-inland gradient during the sub-period 1898-1947 may have led to a stronger influence of other large scale air-masses (Hanssen-Bauer and Førlund 2000), especially in the eastern area.

During the sub-period 1948-1997, the coast-inland gradient became weakened pointing to more similar growth conditions along the entire gradient. In the same sub-period, there was increased separation in area A and B along the altitudinal gradient (PC2). This points to increased differences in growth conditions along altitude in (sub)-oceanic areas. The amount and duration of snow-cover is a critical determinant for the onset of tree growth in spring (Villalba et al. 1997; Vaganov et al. 1999). Warm and wet winters are generally associated with more snowy winters inland and at high altitudes (Mysterud et al. 2000). However, in lowland coastal western Norway, with winter temperature close to 0°C the winter precipitation will mainly fall as rain, and so shorten both the amount and duration of the snow-cover. Potentially, this may produce difference in growth conditions resulting in varying tree growth response to climate along altitudinal gradients (Villalba et al. 1997; Solberg et al. 2002).

In the last decades there has been an increased oceanicity in central Norway with increase in both temperature and precipitation. Climate scenarios for the future rely on a further increase in both variables for this region (Christensen et al. 2001; Folland et al. 2001). An increase in winter temperature followed by a change in precipitation patterns and quality may have different impacts on *P. abies* depending on how and to which degree these climate characteristics will vary along the coast-inland and the altitudinal gradients. The general exclusion of *P. abies* from

maritime climates in Europe is probably related to the development and maintenance of winter hardiness that is broken by repeated freeze-thaw cycles that characterise western Europe winters (Dahl 1990; Bradshaw et al. 2000). Given that the scenarios of a warmer climate are correct, one might hypothesise a poorer performance of spruce in oceanic central Norway in the future. Furthermore, modelling experiments predict a major withdrawal of *P. abies* from the coastal area of central Norway (Prentice et al. 1991; Sykes et al. 1996). The distribution of the species is predicted to shift uphill on the mountains and northwards. Further, increased oceanicity leads to increased cloudiness, with potentially lower tree growth, and a lower altitudinal position for the tree line (Körner 1998; Crawford 2000). It remains an open question how strong this effect will be in the interior more continental Scandinavia.

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Table 1. Site description including location, altitude above sea level, aspect and oceanicity. A-C indicates study areas from coast to inland, and a-d individual sites from lowland forests to forest line within each area.

Site	Locality name	Lat. N	Long. E	m a.s.l	Aspect	Oceanicity	Tree age (mean and range)	No of trees (cores)
Aa	Drossavikhaugen	64°22'	10°50'	75	NV	O2	140 (93-216)	27 (51)
Ab	Sørsætra	64°19'	10°56'	200	SV	O2	171 (103-288)	30 (59)
Ac	Salahalsen	64°19'	10°55'	290	S	O2	153 (92-236)	28 (51)
Ba	Kjenstad	64°10'	12°21'	150	NV	O1/O2	201 (119-276)	28 (52)
Bb	Kjenstadlia 1	64°09'	12°33'	310	V	O1/O2	205 (128-261)	29 (56)
Bc	Kjenstadlia 2	64°09'	12°34'	410	V	O1/O2	170 (111-223)	31 (60)
Ca	Murusjøen	64°28'	14°01'	330	N	OC	129 (117-137)	29 (54)
Cb	Skograudberget	64°27'	13°57'	410	S	OC	173 (112-270)	27 (51)
Cc	Middagshaugen	64°27'	14°00'	520	NV	OC	201 (120-312)	26 (51)
Cd	Storbekken	64°26'	13°56'	620	V	OC/O1	158 (91-293)	25 (49)

Note: Oceanicity according to vegetation (c.f. Moen 1999), O2: oceanic, O1: sub-oceanic, OC: oceanic-continental transition zone.

Table 2. Chronology statistics from RESIDUAL chronologies analysed for the common period 1873-1997.

	Aa	Ab	Ac	Ba	Bb	Bc	Ca	Cb	Cc	Cd
No of trees (cores)	23 (36)	28 (51)	25 (42)	27 (48)	27 (46)	26 (47)	22 (37)	24 (43)	25 (48)	16 (27)
Autocorrelation*	0.25	0.33	0.50	0.48	0.54	0.39	0.41	0.48	0.44	0.42
Autoregression order*	1	1	1	2	1	1	1	1	1	1
SNR	14.5	29.5	21.6	25.1	20.1	21.7	26.7	24.6	33.5	13.9
EPS	0.94	0.97	0.96	0.96	0.95	0.96	0.96	0.96	0.97	0.93
EPS > 85% since	1843	1803	1816	1747	1761	1799	1864	1773	1751	1800
No trees EPS > 85%	9	6	7	7	8	7	5	6	5	7
Variation PC1	41.1	53.0	48.6	50.0	44.8	47.4	56.2	52.6	58.9	49.5
Mean sensitivity	0.26	0.26	0.25	0.21	0.24	0.22	0.20	0.21	0.23	0.26
SD	0.21	0.22	0.22	0.18	0.21	0.19	0.17	0.18	0.20	0.23
Mean correlation										
Between trees	0.39	0.51	0.46	0.48	0.43	0.46	0.54	0.51	0.57	0.46
Within trees	0.54	0.70	0.67	0.66	0.58	0.64	0.69	0.70	0.73	0.72

Note: SNR is signal to noise ratio, EPS is expressed population signal, SD is standard deviation.

* Refers to statistic from the STANDARD chronologies

Table 3. Mean sensitivity for all RESIDUAL chronologies in successive 50-year sub-periods with 25-years overlap. Numbers in bold indicates maximum mean sensitivity, and numbers underlined minimum mean sensitivity for each individual chronology.

	Aa	Ab	Ac	Ba	Bb	Bc	Ca	Cb	Cc	Cd
1750-1799				0.19					<u>0.19</u>	
1775-1824				0.25	<u>0.20</u>			<u>0.18</u>	0.23	
1800-1849		0.20		0.21	<u>0.20</u>	0.20		<u>0.18</u>	0.21	0.27
1825-1874		<u>0.17</u>	<u>0.18</u>	<u>0.18</u>	<u>0.20</u>	<u>0.19</u>		0.20	0.21	0.26
1850-1899	<u>0.18</u>	0.20	0.19	<u>0.18</u>	0.21	<u>0.19</u>		0.22	0.21	0.23
1875-1924	0.20	0.24	0.24	0.19	0.22	<u>0.19</u>	<u>0.17</u>	0.20	0.21	<u>0.19</u>
1900-1949	0.22	0.31	0.30	0.25	0.28	0.26	0.20	0.25	0.29	0.25
1925-1974	0.21	0.26	0.26	0.23	0.25	0.25	0.18	0.21	0.26	0.24
1948-1997	0.22	0.26	0.26	0.24	0.26	0.24	0.20	0.20	0.26	0.25

Table 4. Correlation for RESIDUAL chronologies between study areas for the common period 1873-1997 (in italic), and four successive 50-year sub-periods with 25-years overlap. All correlations are significant at $p < 0.001$.

	A-B	A-C	B-C
<i>1873-1997</i>	<i>0.865</i>	<i>0.697</i>	<i>0.805</i>
1873-1922	0.806	0.605	0.726
1898-1947	0.880	0.664	0.771
1923-1972	0.882	0.711	0.762
1948-1997	0.882	0.762	0.872

Table 5. Correlation between RESIDUAL chronologies. All correlations are significant at the $p < 0.001$ level.

	Oceanic zone (A)			Sub-oceanic zone (B)			Transition* zone (C)			
	a	b	c	a	b	c	a	b	C	d
Oceanic Zone (A)	a	1								
	b	0.89	1							
	c	0.84	0.94	1						
Sub-oceanic zone (B)	a	0.77	0.78	0.72	1					
	b	0.72	0.83	0.78	0.79	1				
	c	0.75	0.85	0.83	0.79	0.92	1			
Transition zone* (C)	a	0.55	0.57	0.53	0.68	0.57	0.64	1		
	b	0.65	0.68	0.64	0.75	0.72	0.75	0.84	1	
	c	0.66	0.70	0.65	0.73	0.76	0.78	0.78	0.90	1
	d	0.59	0.64	0.59	0.69	0.68	0.73	0.69	0.79	0.88

* Oceanic-continental transition zone

Table 6. Eigenvalues and explained variance are shown for four principal components (PC1-4) in the analyses. Results for the period 1873-1997 (in italic) and four successive 50-years's sub-periods with 25-years overlap.

	<i>1873-1997</i>	1873-1922	1898-1947	1923-1972	1948-1997
Eigenvalues_PC1	<i>0,529</i>	0,215	0,321	0,251	0,154
Eigenvalues_PC2	<i>0,200</i>	0,102	0,082	0,084	0,084
Eigenvalues_PC3	<i>0,152</i>	0,065	0,066	0,059	0,051
Eigenvalues_PC4	<i>0,121</i>	0,046	0,050	0,036	0,039
Sum Eigenvalues	<i>1,239</i>	0,511	0,605	0,516	0,409
R ² _PC1	<i>42,7</i>	42,1	52,4	48,7	37,5
R ² _PC2	<i>16,2</i>	20,0	13,4	16,3	20,7
R ² _PC3	<i>12,3</i>	12,8	10,8	11,4	12,6
R ² _PC4	<i>9,8</i>	9,0	8,2	7,1	9,4

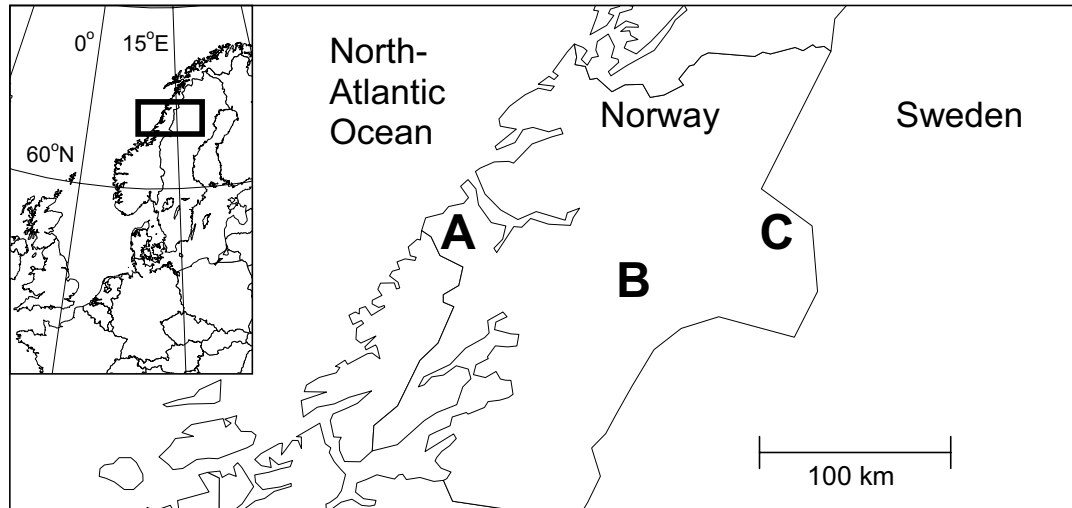


Fig. 1. Study region, with the three study areas indicated by A, B and C.

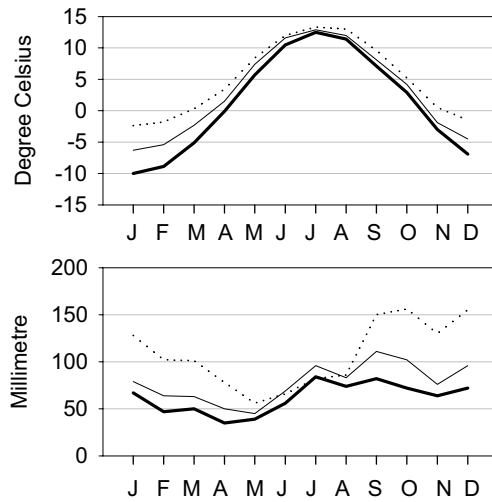


Fig. 2. Climate diagrams showing mean monthly temperature and total monthly precipitation from local climate stations during the period 1961-1990 (Aune, 1993; Førland, 1993; Swedish Meteorological and Hydrological Institute unpubl. data). Dotted line is Namsos (temp.)/Namdalseid (prec.) close to area A, thin line is Snåsa close to area B and thick line is Frostviken (Sweden) close to area C.

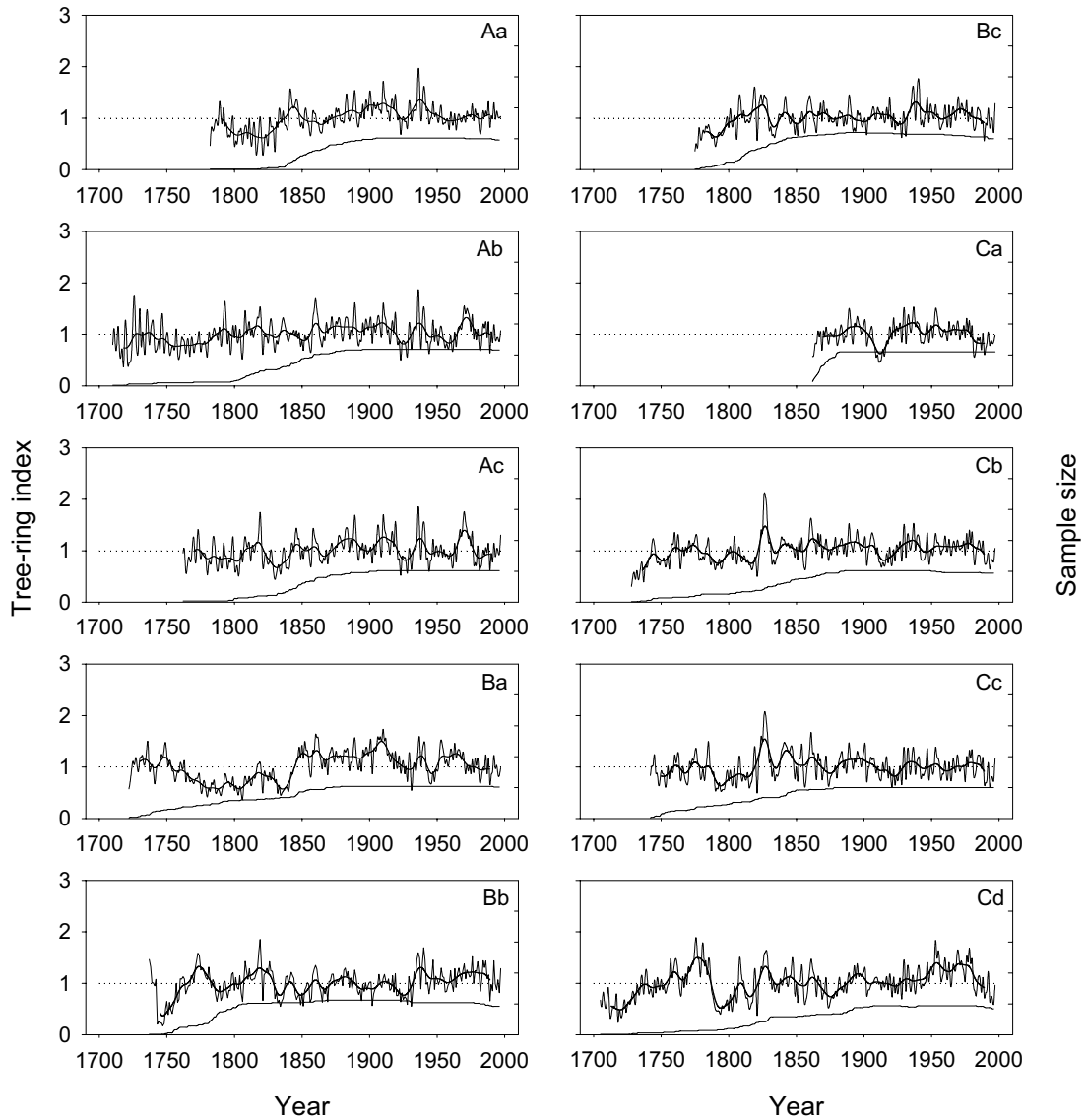


Fig. 3. STANDARD tree-ring chronologies from all sites. The thin lines show the annual indices and the thick lines are Gaussian filtered curves with a standard deviation of 3 year corresponding to a 10 year running mean. The thin lines below the curves show the number of cores included in the mean and refer to the right hand y-axis on a scale from 0-250. A-C indicates study areas from coast to inland, and a-d individual sites from low-land forests to forest line within each area.

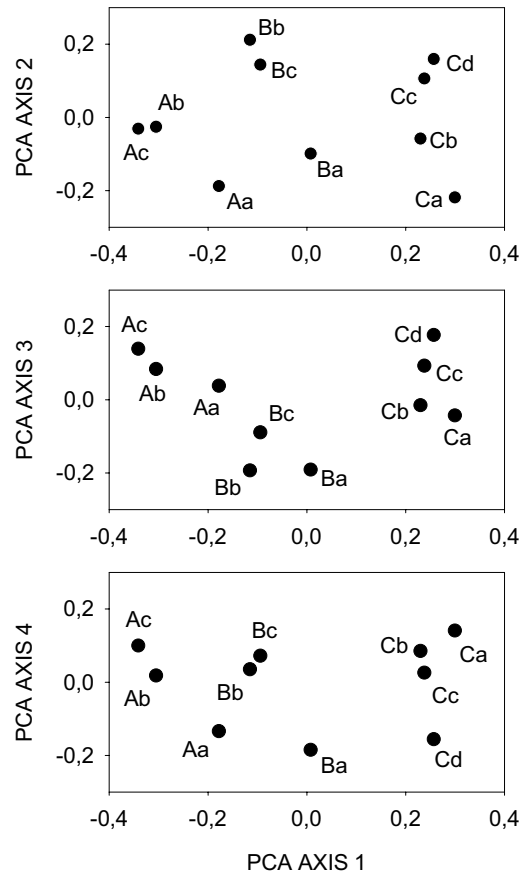


Fig. 4. Principal component scores of sites along axis 1 versus axis 2, 3 and 4 respectively. Years are used as variables and the ten RESIDUAL chronologies as observations. Analysed period is 1873-1997. A-C are study areas from coast to inland, and a-d individual sites from low-land forests to forest line within each area.

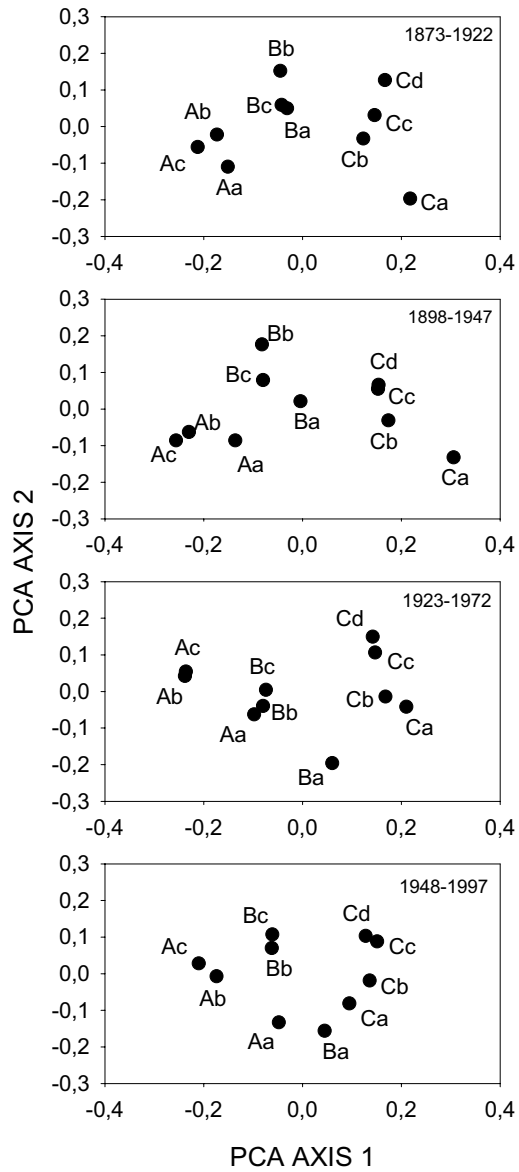


Fig. 5. Principal component scores, PC1 versus PC2, of sites for four successive 50-years periods with 25-year overlap for the period 1873-1997. For explanations, see Fig. 4.

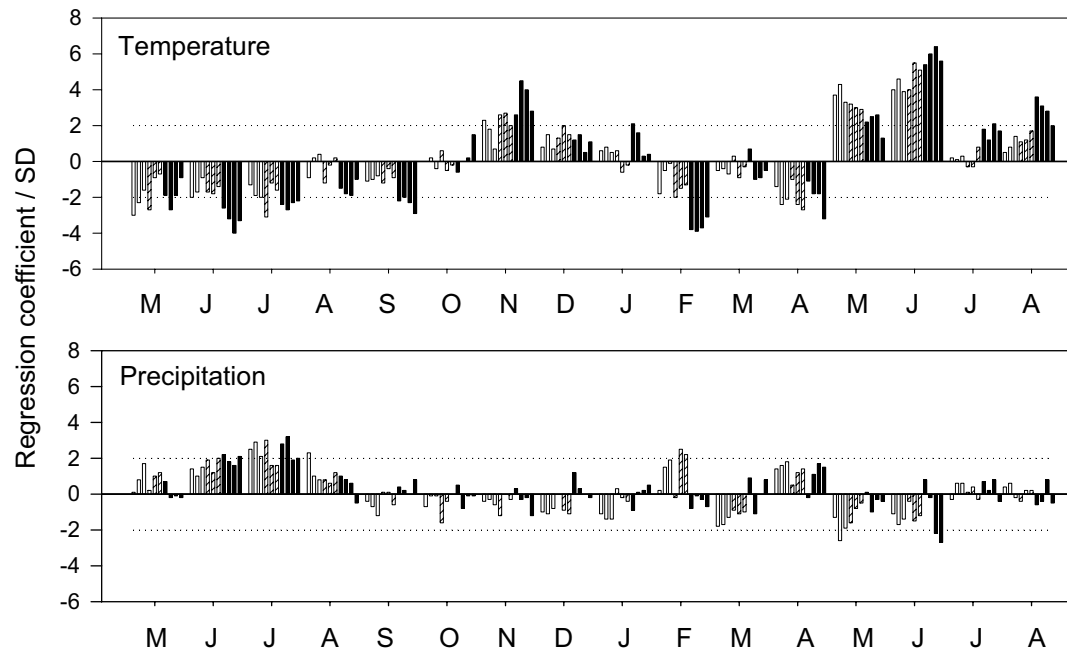


Fig. 6. Effect of temperature and precipitation on ring width indices from all ten sites, shown by the regression coefficients divided by its standard deviation for the period 1898-1997 given for May_{t-1} to $August_t$. Open bars are area A, shadowed bars are area B and filled bars are area C. Within each area are sites, a-d, shown from the left to the right. Dotted horizontal lines indicate significance level ($p < 0.05$) above and below the mean.

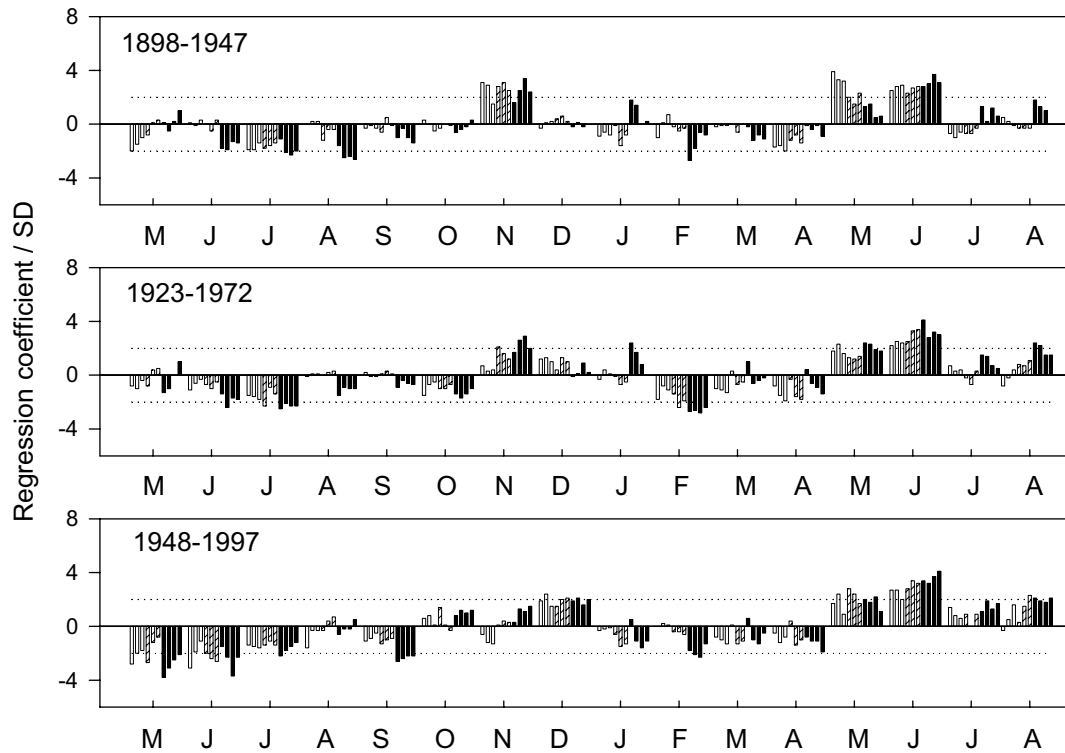


Fig. 7. Effect of temperature on ring width indices from all ten sites, shown by the regression coefficients divided by its standard deviation for three successive 50-years periods during 1898-1997 for May_{t-1} to August_t . Bars and horizontal lines as in Fig. 6.

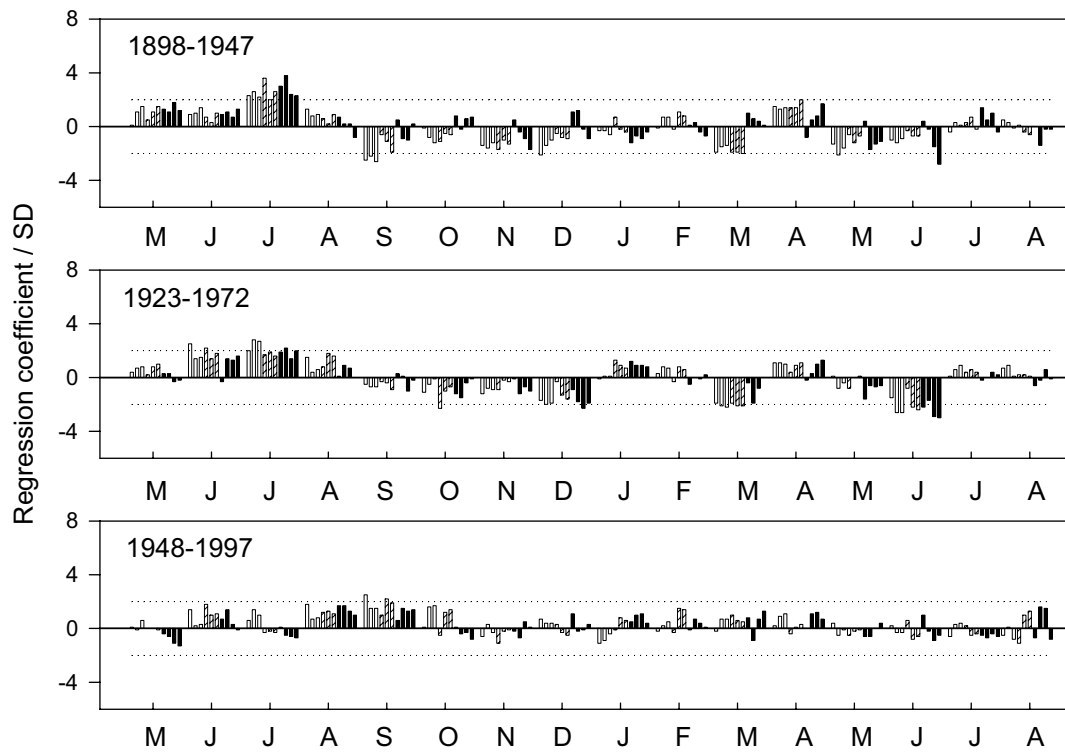


Fig. 8. Effect of precipitation on ring width indices from all ten sites, shown by the regression coefficients divided by its standard deviation for three successive 50-years periods during 1898-1997 for May_{t-1} to August_t . Bars and horizontal lines as in Fig. 6.

Paper III

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Tree-ring records from central Fennoscandia: The relationship between tree growth and climate along a west east transect.

by
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Tree-ring records from central Fennoscandia: The relationship between tree growth and climate along a west east transect.

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Abstract

Nine Scots pine tree-ring width chronologies were compared regarding growth variability and response to climate along a gradient of oceanicity-continentality at 62°-64°N in central Fennoscandia. The study revealed higher growth variance and stronger response to climate in the oceanic area west of the Scandinavian Mountains, compared to the more continental areas further east. However, there was a gradual change in radial tree growth and response to climate along the gradient, where tree growth in a transition zone between oceanic and continental climate showed positive correlations with radial tree growth in both oceanic and continental areas. Pine growth responded positively to summer temperatures in the western areas, and positively to summer precipitation in the east. Generally, pine growth showed a weaker relationship with the North Atlantic Oscillation (NAO) than with temperature and precipitation. During the summer, pine responded to the NAO only in western Fennoscandia, while during the winter pine responded to the NAO in both western and eastern Fennoscandia. This suggests that during winter, the NAO is an adequate measure for climate variations important for pine radial growth along the whole studied gradient, while in the summer, the NAO is an inadequate measure for climate variations important for pine radial growth east of the Scandinavian Mountains. During the last half of the 20th century, pine growth in western Fennoscandia displayed reduced sensitivity to climate, while the opposite was found in the east. Indications of growth stress were found in one site east of the Scandinavian Mountains, and as increasing temperatures have been accompanied by increasing precipitation in Fennoscandia throughout the 20th century, we suggest that a change in climate regime from sub-continental to sub-oceanic caused those trees to experience climatic stress. However, trees in either oceanic or more continental areas did not seem to respond negatively to recent climate change.

Key words: Central Fennoscandia, Scots pine, NAO, Climate change

Introduction

Tree ring records are valuable indicators of past climates as they have an extensive coverage, are precisely dated and may contain a highly resolved climate response (Briffa, 2000). Depending on the location and strength of the climate forcing, information concerning different climate variables (e.g. temperature and precipitation) can be recovered on yearly to decadal or centennial timescales. Trees growing close to the altitudinal or latitudinal tree line respond to summer temperatures and several regional reconstructions of high latitude temperatures have been made using tree-ring data from the northern boreal zone (D'Arrigo and Jacoby, 1993; D'Arrigo *et al.*, 1999; Hughes *et al.*, 1999; Lindholm and Eronen, 2000). Furthermore, recent global or hemispheric temperature reconstructions have largely relied on tree-ring data (Jones *et al.*, 1998; Mann *et al.*, 1999; Briffa *et al.*, 2001).

Along the altitudinal and latitudinal tree line in Fennoscandia, annual to decadal Scots pine (*Pinus sylvestris* L.) growth patterns are highly correlated and the growth-climate relationship is similar over large areas (e.g. Briffa *et al.*, 1990; Lindholm, 1996; Kirchhefer, 2001; Gunnarson and Linderholm, 2002). Below the altitudinal and latitudinal tree line a diminishing growth influence of summer temperature and increasing influences of other climate variables, such as precipitation and competition among trees, is expected (Fritts, 1976; Lindholm *et al.*, 2000).

In Fennoscandia, a significant proportion of the inter-annual precipitation and temperature variability is attributed to the dynamics of the North Atlantic Oscillation (NAO), which is a measure of the pressure difference between the Azores and Iceland and hence affects westerly winds blowing across the North Atlantic. Seasons of high positive NAO are associated with warming and increased rainfall over Northwest Europe (Hurrell, 1995). This relationship is most pronounced in winter and early spring and substantially weaker in summer (Rogers, 1990).

Since the late 1960's there has been a strengthening of the wintertime NAO, with unprecedented strongly positive NAO index values since the 1970's (Hurrell, 1995). This may account for some of the wintertime warming in recent decades and the steady increase in storminess in winter over the northeast Atlantic and the North Sea since the 1960s (Ulbrich and Christoph, 1999). Increased warming, as well as increased precipitation, indicates that the climate of Fennoscandia is becoming more oceanic (e.g. Tuomenvirta *et al.*, 2000).

As the strengthening of the NAO coincides with late 20th century global warming, the influence of large-scale atmospheric circulation on a variety of ecosystems has gained increased attention in the North Atlantic region (e.g. D'Arrigo *et al.*, 1993; Post and Stenseth, 1999; Weyhenmeyer *et al.*, 1999; Mysterud *et al.*, 2000; Solberg *et al.*, 2002). As a consequence, several recent studies have focused on making multi-proxy reconstructions of the NAO (e.g. Cook *et al.*, 1998; Glueck and Stockton, 2001; Cook *et al.*, 2002). However, few attempts have been made to understand the influence of the atmospheric circulation on tree growth in the Atlantic region (but see D'Arrigo *et al.*, 1993). It is our opinion that a reasonable understanding of these mechanisms is fundamental before using tree-ring data as proxies for NAO.

Lately, several accounts of reduced tree growth sensitivity to climate in the Northern Hemisphere have been presented (Jacoby and D'Arrigo, 1995; Briffa *et al.*, 1998; Linderholm, 2002). Although the mechanism behind this loss of climate sensitivity has yet to be confirmed, the evidence suggests that the temperature increase, especially in the last two to three decades, has caused trees to respond differently to climate than during earlier decades of the 20th century.

In a joint Fennoscandian project, growth patterns and growth-climate responses during the last 150 years of a Scots pine tree-ring width chronology network from central Fennoscandia (61°N to 64°N, 10°E to 30°E) are compared. Climate regions range from oceanic at the west coast of Norway, highland climate in the Scandinavian Mountains, and sub-continental to continental in Sweden and eastern Finland. Local studies of tree growth response to climate have been conducted in central Fennoscandia (e.g. Lindholm *et al.*, 1997; Kalela-Brundin, 1999; Linderholm, 2002), and regional comparisons of growth-climate relationships have been made along north south gradients in Finland and Sweden (Lindholm *et al.*, 2000; Mäkinen *et al.*, 2000, Linderholm *et al.*, 2002). The present work is the first comparative study of climate influence on tree growth along a west-east transect through central Fennoscandia. Our aims with this investigation were to:

1. Make interregional comparisons of Scots pine growth pattern variations across Fennoscandia from oceanic western Norway to continental eastern Finland.
2. Determine the influence of temperature and precipitation on Scots pine growth across central Fennoscandia.
3. Detect a signature of a large-scale atmospheric circulation system (i.e. the NAO) in tree-growth along this west east transect.

4. Detect possible changes in growth-climate relationships in the 20th century

Material and Methods

Regional climate and growth conditions

The regional climate in the studied region ranges from oceanic conditions in the west to a relatively continental climate in the east (Wallen, 1970). The oceanic climate is characterised by mild, wet winters, cool summers, high precipitation with maximum in autumn and winter, and relatively low variance in temperature between summer and winter. The more continental climate is characterised by colder winters, warmer summers, and considerably lower precipitation with maximum in summer and autumn, and higher variance in temperature between summer and winter. The strong impact of the westerlies is responsible for the oceanic climate in the west and several of the sites in and east of the Scandinavian mountain range are also strongly influenced by Atlantic air masses.

Site descriptions

We used Scots pine tree-ring width chronologies from 9 sites in the boreal forest of central Fennoscandia. The sampled sites represent mature and natural pine stands ranging from the west coast of Norway to eastern Finland (Figure 1, Table 1). The four westernmost sites (N1, N2, N3 and S1) are characterised by an oceanic – sub-oceanic climate with high amounts of precipitation, and together with N4 and S2 they are situated close to the local forest line. Furthermore, N4 and S2 lie in a transition zone between oceanic and continental climates. All Norwegian and Swedish sites are characterised by open forests dominated by Scots pine and Norway spruce (*Picea abies* (L.) Karst.). Furthermore, the sampled trees at these sites grew on relatively thin soil layers, mainly till. In this environment, pine occupies dry, convex micro sites while spruce occupies wetter, concave micro sites. The N1, N3, N4 and S1 are composite chronologies, each containing trees from two sites. The individual sites in each chronology are situated close to each other and are strongly correlated. At N1, N3 and N4 samples were taken at the upper boundary of Scots pine as well as 100 meters below. At S1 trees were collected at the Scots pine tree limit from two sites approximately 30 km apart. The two Finnish sites represent typical growing conditions for Scots pine in eastern Finland,

i.e. well drained, pine dominated heaths with coarse mineral soils and a thin humus layer. Most of the bedrock in the region is covered by glacial till, but bare bedrock terrain occurs frequently. The topography is characterised by high relative altitudes, due to the unevenness of the bedrock and various glacial features.

Chronology building

All tree-ring chronologies were mainly based on samples from living trees, sampled with standard dendrochronological techniques. Ring widths of the samples were measured with a precision of 0.01 mm, and then cross-dated both manually and by computing cross-correlations between individual series using customary procedures (Holmes *et al.*, 1986; Aniol, 1989). In order to strengthen the common signal in the tree-ring data and to reduce unwanted “noise” (e.g. Fritts, 1976), the individual tree-ring series were standardised before averaging, by using procedures in the software ARSTAN (Holmes *et al.*, 1986; Cook *et al.*, 1990a). The use of negative exponential functions or regression lines (Cook *et al.*, 1990a), allowed for chronologies with inter annual-to-centennial scale properties to be built. Autocorrelation was removed from individual tree-ring series through autoregressive modelling (Cook *et al.*, 1990b), and the pooled autoregression model is reincorporated into the residual chronology to produce the arstan chronology. The arstan chronologies were used for correlation analyses and comparisons of long-term growth trends. Correlation analyses were computed for the period 1840-1993. The residual chronologies were used for analyses of growth-climate relationships, as they proved to yield more climate information than the arstan chronologies. It should be noted that due to low sample size in the end of the two Finnish chronologies (Figure 2), reduced analysis periods were used: 1840-1991 for F1 and 1840-1982 for F2. These reduced periods are consistent for all analyses. Generally, we anticipate for the analyses from 1840 to present that the reduced periods do not influence the analyses substantially. However, for growth-climate analyses the shortened period at F2 are expected to have an influence on the result, especially for the temporal analyses (see below).

Dendroclimatic analysis

Response function analysis (Fritts, 1976; Briffa and Cook, 1990) is a form of multiple regression analysis where the predictor variables are replaced by principal components, as climatic parameters are often intercorrelated (Guiot *et al.*, 1982). Principal components do not correlate with each other and can thus be used to express the real, independent relationships between tree growth and climate (e.g. Briffa and Cook, 1990). In our investigation we used a

12-month analysis period, extending from September of the year preceding growth to August of the growth year, with the residual tree-ring chronologies as predictand and monthly mean temperature and monthly total precipitation values as predictors. Response function analyses were performed with software PRECON, version 5.17b (Fritts *et al.*, 1991).

A regional temperature and precipitation index for central Norway was representative for climate in Norway as well as westernmost Sweden (S1). This record dates back to 1896 (Hanssen-Bauer and Førland, 1998; Hanssen-Bauer and Nordli, 1998). For S2 and S3, we used homogenised data from Östersund and Härnösand, respectively. These data cover the period 1860 to present and were obtained from the Swedish Meteorological and Hydrological Institute. Finnish climate series were modelled by a method based on the work of Ojansuu and Henttonen (1983). This method produces unbiased estimates of local values from observations made by the Finnish Meteorological Office (1880-1993). Growth-climate responses were analysed for a period where both meteorological and tree-ring data were available for all sites: 1897-1993 (note the shorter periods for the Finnish chronologies as described above). To determine whether the growth-climate relationship was stable through the 20th century, additional analyses were performed in 2 sub-periods (1897-1944 and 1945-1993). By doing so, we were able to discover changes in growth sensitivity to climate. Finally, to detect possible signals of the NAO in the ring-width patterns, residual chronology indices were compared to monthly indices of the NAO (Jones *et al.*, 1997) for the period 1897-1993 and two sub-periods in the same manner as for the temperature and precipitation data.

Results

Growth variance and long-term growth patterns

Chronology statistics, which summarise the quality of the chronologies, are shown in Table 2. All series surpassed expressed population signal > 0.85 (Figure 2, Table 2) within the period 1840-1993 and so showed inherent qualities making the chronologies applicable for growth-climate analyses (Briffa and Jones, 1990). Correlation analyses showed a strong coherent growth pattern among the sites west of the Scandinavian Mountains, including S1 and N4 (henceforth referred to as the western sites) (N1-N4; $r^{\text{mean}}=0.52$, Table 3). East of the Scandinavian Mountains (henceforth referred to as the eastern sites), F1 was fairly well

correlated to F2 and S3, but F2, S2 and S3 were not well correlated. Instead, there was a gradual transition where tree growth in the transition zone between oceanic and sub-continental areas (N4 and S2) was positively correlated to both western and eastern sites. Generally, the high covariance among the western sites gave evidence for common growth forcing environmental factors (Table 3).

The low-frequency growth patterns along the west-east gradient were characterised by relatively high variance at the western sites and considerably lower variance at the eastern sites (Figure 2). There were no periods where a common growth pattern with above or below average growth occurred simultaneously at all sites in central Fennoscandia. At the western sites, common periods of above average growth were found around 1820, 1880, 1950 and 1970, where the periods around 1880 and 1970 were unique for the three westernmost sites (N1-N3). Common below average growth was found around 1900-1910 for all sites, and around 1925 for the three westernmost sites. The low variance in the low-frequency growth patterns at the eastern sites did not indicate any clear common decadal growth trends. One exception is a period of above average growth in the 1920's. The S2 and S3 sites showed some similar characteristics with the western sites with above average growth around 1820 for S2 and around 1950 for both sites. The S2 site showed an individual and characteristic pattern between 1810-1880, where the below average growth from 1835 to 1845 was unique. Below average growth in the 1930's was seen at F2, and to some degree S3, coinciding with the temperature maximum for the 20th century.

Growth-climate relationships

The most distinct significant growth response to climate was a positive response to summer temperature at all Norwegian sites, S1, S2, and F2, while F1 had a negative response to summer (June) temperature (Figure 3). At the three westernmost sites, the main response was in June while at the other sites in July. A negative response to summer precipitation was found at N1, N3 and S1. At the most oceanic site (N1), where precipitation is very high, the negative response to precipitation seemed to be stronger than the positive response to temperature. Furthermore, all western sites, except N3, had positive growth responses to spring precipitation. Trees at the western sites and S2 showed positive responses to previous autumn/early winter temperature. At the remaining eastern sites, pine growth showed positive responses to June precipitation. Also, all eastern sites displayed negative growth responses to previous autumn precipitation. Additionally, F1 showed a negative response to January

precipitation. Pines close to the Baltic Sea in Sweden (S3) had few and weak significant growth responses to climate, and the lowest R^2 value of all sites (Figure 3).

At all western sites except N4, there was a marked decrease in sensitivity to climate in the last sub-period (1945-1993) (Table 4). The most prominent change in growth response to climate in the last sub-period is the lack of significant negative responses to precipitation at the western sites. The response to temperature, however, turned out to be quite similar between the two analysed sub-periods along the entire west-east transect. The eastern sites and N4 showed a slight increase in growth sensitivity to climate in the last sub-period, especially at S2 where R^2 became highest of both western and eastern sites (Table 4). At N4 and S2 there was an increase in significant responses to temperature.

Generally, tree growth in central Fennoscandia was less correlated to monthly indices of the NAO compared to temperature and precipitation (Figures 3 and 4). The strongest growth response to NAO was found at the west coast of Norway (N1 and N3) and in south-eastern Finland (F1) (Figure 4). At the west coast of Norway, there was a negative response to both January and July NAO, while in south-eastern Finland there was a positive response to winter NAO (December- March). A positive relationship between radial tree growth and one winter month NAO (December or January) was also present at N4, S2 and S3. Only at three sites did the importance of the NAO increase in 1945-1993, where R^2 -values at N1, N4 and F2 reached around 0.3 (Table 5). At the remaining sites R^2 -values decreased in 1945-1993, except at N3 where there was no change. The most prominent reductions in growth responses to the NAO were seen at N2 and S1, where responses were more or less halved.

Discussion

This study revealed higher growth variance and stronger responses to climate in the oceanic area west of the Scandinavian Mountains compared to the flatter and more continental area east of the mountains. Several of the decadal growth variations for the last 150 years are held in common by the sites from Norway to central Sweden (N1-S2), but also with other pine tree-ring series from northern and central Fennoscandia (Lindholm, 1996; Kalela-Brundin, 1999; Kirchhefer, 2001; Linderholm, 2002). On the other hand, the low decadal growth variations for the three most eastern sites (S3-F2) indicate a different climate forcing

on radial tree growth. The eastern sites share common decadal growth variations with radial tree growth from central and southern Finland, especially the period with increased growth around 1925 (Lindholm *et al.*, 2000). Increased growth from 1930 to 1950 at the western sites coincides with the highest summer temperature recorded since 1770 from the Trondheim meteorological station (Kalela-Brundin, 1999). On the contrary, the eastern sites have tendencies for reduced growth in the 1930's, which is also found in continental mountain valleys in northern Norway (Kirchhefer, 1999). Our results do not give evidence for a well-defined border between sites with oceanic or continental growth patterns. Instead, there is a gradual change in growth patterns and climate responses from oceanic western Norway to the more continental climate of eastern Finland, where a couple of the central sites (N4 and S2) have positive correlations to both western and eastern sites.

The differences in pine growth along the Fennoscandian transect are ultimately caused by differences in climate. The dominance of Atlantic air masses and proximity to the North Atlantic current in western Fennoscandia results in relatively mild winters and cool summers. In the more continental parts of Fennoscandia, air masses from the interior of Asia have a stronger influence on climate, resulting in colder winters and warmer/drier summers. Furthermore, during summer cool maritime air masses are heated and dried out as they subside on the leeward side of the Scandinavian Mountains (Wallén, 1970). High air temperatures are therefore a rather usual phenomenon in summer in eastern Norway, Sweden and Finland, even for the westerly type of circulation. Cool summers in western Fennoscandia give response patterns with positive responses to summer temperature, while warm and dry summers in the east cause pine to respond positively to summer precipitation. This is especially convincing at the southernmost eastern site (F1), where pine had an additional negative response to June temperature. It is well known that when going from north (cold) to south (warmer) trees shift their response to climate from being temperature limited to be precipitation limited (Fritts, 1976; Lindholm *et al.*, 2000). In this west-east gradient, there is probably the same effect because the eastern sites are under influence from warmer and drier air masses during the summer season.

Generally, trees are more sensitive to temperature close to the tree line than at lower altitudes (Fritts, 1976). This contributes to the stronger emphasise on temperature in the western sites, and to more distinct decadal growth variations. Furthermore, in the west, the sampled pines grew close to their western distribution limit while in the east they grew in a more central part of the distribution area of the species (Nikolov and Helmisaari, 1992). It is expected that species close to the distribution limit will be more sensitive to climate compared

to the situation in more central parts of the distribution area, and this will potentially influence on the sensitivity to climate for pines at the different sites along the west-east transect.

Kirchhefer (1999) showed that Scots pine along a transect across the Scandinavian Mountains of 10° longitude in northern Norway (69°N), displayed a strong and coherent growth pattern and growth response to climate (PC1: $R^2 \sim 0.70$, positive responses to July temperatures at all sites). Consequently, despite the large climate variability across the mountains, pine at all eight sites shared strong common growth variability (Kirchhefer, 1999). The strong common variability along the northern Norway transect is probably caused by its northerly position with a short growing season along the entire transect. The larger dissimilarities along the central Fennoscandian transect may have several explanations. First, the west-east transect in the central area extend over 20° in longitude compared to 10° in the north. Second, the Scandinavian Mountains are higher and more massive in the central area, which has implications for the distribution and dominance of different large-scale air masses, which strongly influence climate (Wallén 1970; Hanssen-Bauer and Førland, 2000). Consequently, our results showed that it is not possible to combine tree-ring width chronologies from eastern and western parts of central Fennoscandia expecting them to yield a common climate signal.

The negative relationship between radial tree growth and summer NAO is an exclusive pattern for the three westernmost sites, indicating that the NAO influences climate also in summer in this area. Thus, during high NAO index summers, high precipitation combined with relatively low temperatures will have a negative influence on radial growth. This supports the positive/negative correlation between summer temperature/precipitation and radial growth in the west. The lack of a negative correlation between summer NAO and radial tree growth further east suggests that the NAO index is an inadequate measure of the atmospheric circulation over the more continental parts of central Fennoscandia during summer (Slonosky *et al.*, 2001). This is in agreement with the findings of Chen and Hellström (1999), that there is only a weak relationship between summer temperatures and the NAO. During winter, the NAO has a considerable influence on Fennoscandian climate, and influences tree growth over a large area despite pines being dormant during winter (D'Arrigo *et al.*, 1993; Lindholm *et al.*, 2001). In the oceanic part of west central Scandinavia, there are indications for a negative relationship between NAO for both pine and spruce radial tree growth (see Solberg *et al.*, 2002). Periods of high winter temperatures at oceanic sites, associated with high NAO index, may potentially represent a stress factor for pine (Kirchhefer, 2001). Also, high NAO index in oceanic environments during winter, results in

unstable weather with possible increases in freeze-thaw cycles and more unfavourable soil conditions (Kramer and Kozlowski, 1979). Mild spells in winter with precipitation falling as rain instead of snow would increase snow free periods, particularly at low elevations (Mysterud *et al.*, 2000), and further expose the ground to frost in coming cold periods (Kramer *et al.*, 2000). This could lead to a prolongation of ground frost in spring, but also to winter desiccation (Tranquilini, 1979). In the areas with a more continental climate character (N4-F2), there are positive relationships between winter NAO and radial growth (D'Arrigo *et al.*, 1993; Lindholm *et al.*, 2001), and negative tree growth departures were found in low NAO index winters when conditions are unusually cold in Scandinavia. Evidently, the influence on radial tree growth in central Fennoscandia of the NAO is dependent on habitat, local climate and exposure to the North Atlantic Ocean.

Reduced tree growth sensitivity to climate has been reported from large areas in the Northern Hemisphere during the last 30-50 years of the 20th century (e.g. Briffa *et al.*, 1998). Furthermore, in dry, continental areas in North America, reduced radial tree growth has been associated with increased drought stress caused by increased temperatures during the last decades (Jacoby and D'Arrigo, 1995; Barber *et al.*, 2000; Biondi, 2000; Lloyd and Fastie, 2002). In the central Fennoscandian tree-ring data, reduced climate sensitivity in the last half of the 20th century was only present west of the Scandinavian Mountains, while at the remaining sites climate sensitivity increased. The reduced climate sensitivity at the western sites is likely an effect of increasing temperatures. However, positive effects on tree growth of increased temperatures were only seen at the two Norwegian inland sites (N2, N3). As precipitation (annually as well as in summer) in western Fennoscandia has increased in the 20th century, causing increased oceanic conditions (Hanssen-Bauer and Førland, 1998; Tuomenvirta *et al.*, 2000), we suggest that increased precipitation has counteracted the positive effects of increased temperatures at the remaining western sites. This can be seen in the N4 and S1 chronologies, where the growth optimum around 1950 is followed by a slightly declining growth trend. However, the effect of increased oceanic conditions is most evident at S2, which is the only central Fennoscandian chronology displaying a clear negative growth trend in the 20th century contemporary with an increase in tree growth sensitivity to climate. We suggest that just east of the Scandinavian Mountains, the wetting and warming in the 20th century has altered the climate regime from sub-continental (due to the sheltering effect of the mountains) to be more sub-oceanic, causing decreased growth of the trees at the S2 site. The increased response to temperatures at S2 in 1945-1991, together with decreasing growth trend, implies that the change in climate regime in this area caused the trees to suffer from

increased oceanic conditions. As there was no evidence for increased growth stress at either the oceanic, western, sites or the more continental, eastern sites, we suggest that presently the 20th century climate change has only had a negative effect on Scots pine in areas where a marked change in climate regime occurs, e.g. from sub-continental to sub-oceanic. Consequently, provided that future increases in temperature are accompanied by increases in precipitation, Scots pine in central Fennoscandia are unlikely to be subjected to drought stress similar to that of North American trees.

Conclusion

Our main conclusions from this investigation were:

1. Growth variability, as well as correlation among sites, was higher in the western, oceanic, area of central Fennoscandia, compared to the eastern, more continental, areas. However, there was a gradual transition between western and eastern sites.
2. Trees in western Fennoscandia showed a stronger response to climate, mainly to summer temperatures, than those in the eastern parts, which mainly responded to summer precipitation.
3. The relationship between pine growth and the NAO was generally low. Pines at western sites responded both to summer and winter NAO, while the eastern sites only responded to winter NAO.
4. Reduced growth sensitivity to climate in the second half of the 20th century was found in the western parts, while the opposite was the situation in the east. Only at one site just east of the Scandinavian Mountains, evidence of growth stress was found.

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Table 1. Site description.

Site	Country	Length of chronology	Elevation (m a.s.l.)	Lat. (N)	Long. (E)	No trees	Temp. Jan.*	Temp. Jul.*	Precip. Year*
N1	Norway	1655-1997	250	64°19'	10°55'	41	-2.4	13.3	1565
N2	Norway	1500-2000	425	63°15'	10°37'	26	-4.0	13.0	1260
N3	Norway	1754-1997	350	64°09'	12°33'	48	-6.3	12.9	934
S1	Sweden	1472-1998	700	63°07'	13°20'	38	-7.7	10.8	902
N4	Norway	1635-1997	470	64°27'	13°58'	49	-10.4	11.8	630
S2	Sweden	1471-1999	270	63°59'	16°32'	34	-8.6	13.4	483
S3	Sweden	1452-1998	250	62°20'	18°29'	36	-7.0	15.5	703
F1	Finland	1794-1993	90	61°80'	28°50'	87	-8.5	16.0	589
F2	Finland	1413-1991	170	63°16'	30°40'	52	-10.4	15.0	536

* 1961-1990; Temperature in °C and precipitation in mm

Table 2. Chronology statistics for the arstan chronologies with 1840-1993 as common period.

	Common period	MS	SD	IPC%	SNR	EPS	Mean corr. between trees	No trees*
N1	1840-1993	0.17	0.26	34.5	8.5	0.90	0.30	20/41
N2	1840-1993	0.14	0.18	47.7	12.2	0.92	0.43	16/26
N3	1840-1993	0.15	0.22	38.5	21.9	0.96	0.35	40/48
S1	1840-1993	0.15	0.21	36.4	17.1	0.95	0.32	36/38
N4	1840-1993	0.14	0.19	32.3	13.2	0.93	0.29	33/49
S2	1840-1993	0.13	0.23	54.8	33.8	0.97	0.52	31/34
S3	1840-1993	0.13	0.17	33.8	14.7	0.94	0.30	34/36
F1	1840-1991	0.16	0.19	41.9	9.1	0.90	0.36	16/87
F2	1840-1982	0.14	0.19	40.3	25.8	0.96	0.37	44/52

* number of trees included in the common period divided by number of total trees in the chronology

MS = Mean Sensitivity, a measure of the relative change in ring-widths from one year to the next

SD = Standard Deviation

IPC% = The percentage of variation explained by the first principal component expresses the variation held in common among the trees included in the chronology

SNR = Signal to Noise Ratio, measurement of the degree to which the chronology signal is expressed when tree-ring series are averaged

EPS = Expressed Population Signal

Table 3. Correlations among the arstan chronologies for the common period 1840-1993. The common period are adjusted for the Finnish chronologies due to low sample size (Figure 2) in some periods. $R > 0.4$ in bold. * sign. at $p=0.05$, ** sign. at $p=0.01$

	N1	N2	N3	S1	N4	S2	S3	F1 [§]	F2 [!]
N1	1								
N2	0.56**	1							
N3	0.58**	0.76**	1						
S1	0.45**	0.42**	0.56**	1					
N4	0.42**	0.37**	0.42**	0.67**	1				
S2	0.31**	-0.04	-0.15	0.29**	0.46**	1			
S3	0.08	0.08	0.13	0.27**	0.29**	0.20*	1		
F1 [§]	-0.17*	-0.10	-0.16	-0.05	0.11	0.19*	0.33**	1	
F2 [!]	0.07	0.12	0.13	-0.01	0.22**	0.17*	0.26**	0.36**	1

[§] 1840-1991

[!] 1840-1982

Table 4. The course of R^2 and number of significant response variables for the residual chronologies and climate variables between the two sub-periods 1897-1944 and 1945-1993. For the F1 and F2 chronology is the last sub-period ended in 1982 and 1991, respectively.

	N1	N2	N3	S1	N4	S2	S3	F1	F2
R^2 1897-1944	0.59	0.66	0.63	0.75	0.53	0.49	0.34	0.50	0.41
R^2 1945-1993	0.50	0.39	0.53	0.51	0.58	0.67	0.41	0.50	0.66*
# SIGN. RESP. P 1897-1944	3	4	3	2	2	1	0	1	1
# SIGN. RESP. P 1945-1993	1	1	0	0	0	2	1	1	0
# SIGN. RESP. T 1897-1944	0	2	2	4	0	1	0	1	0
# SIGN. RESP. T 1945-1993	0	0	2	3	2	2	0	1	0

* This figure is not comparable with the other R^2 values because the regression equation contains considerable fewer years.

P=precipitation

T=temperature

Table 5. The course of R^2 and number of significant response variables for the residual chronologies and the NAO between the two sub-periods 1897-1944 and 1945-1993. For the F1 and F2 chronology is the last sub-period ended in 1982 and 1991, respectively.

	N1	N2	N3	S1	N4	S2	S3	F1	F2
R^2 1897-1944	0.25	0.24	0.29	0.31	0.25	0.36	0.16	0.31	0.17
R^2 1945-1993	0.31	0.10	0.28	0.16	0.29	0.26	0.11	0.25	0.31*
# SIGN. RESP. 1897-1944	1	1	2	1	0	2	1	2	0
# SIGN. RESP. 1945-1993	1	0	0	0	1	0	0	0	1

* This figure is not comparable with the other R^2 values because the regression equation contains considerable fewer years.

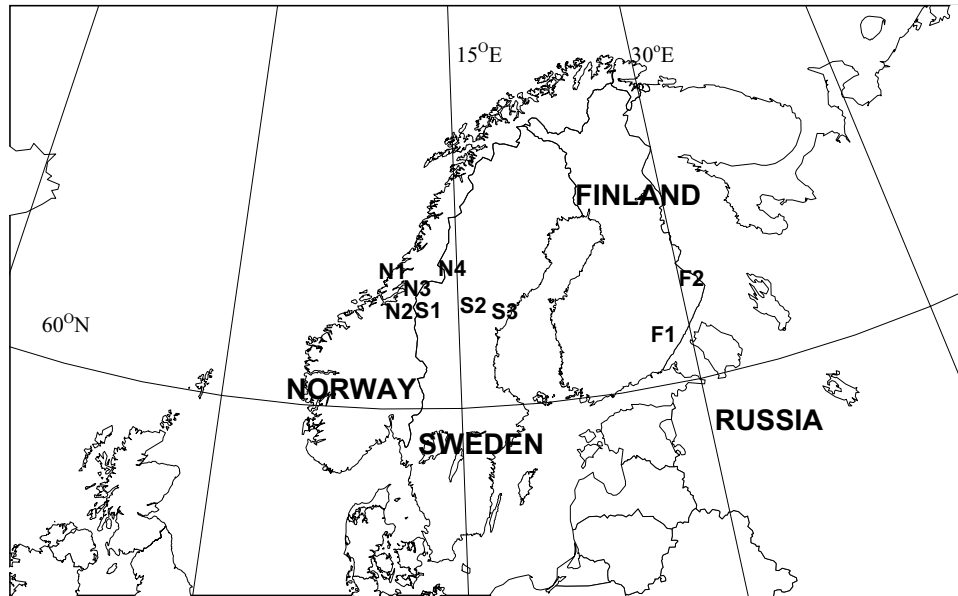


Figure 1. Map of Fennoscandia, showing locations of sampled sites. Further details are given in Table 1.

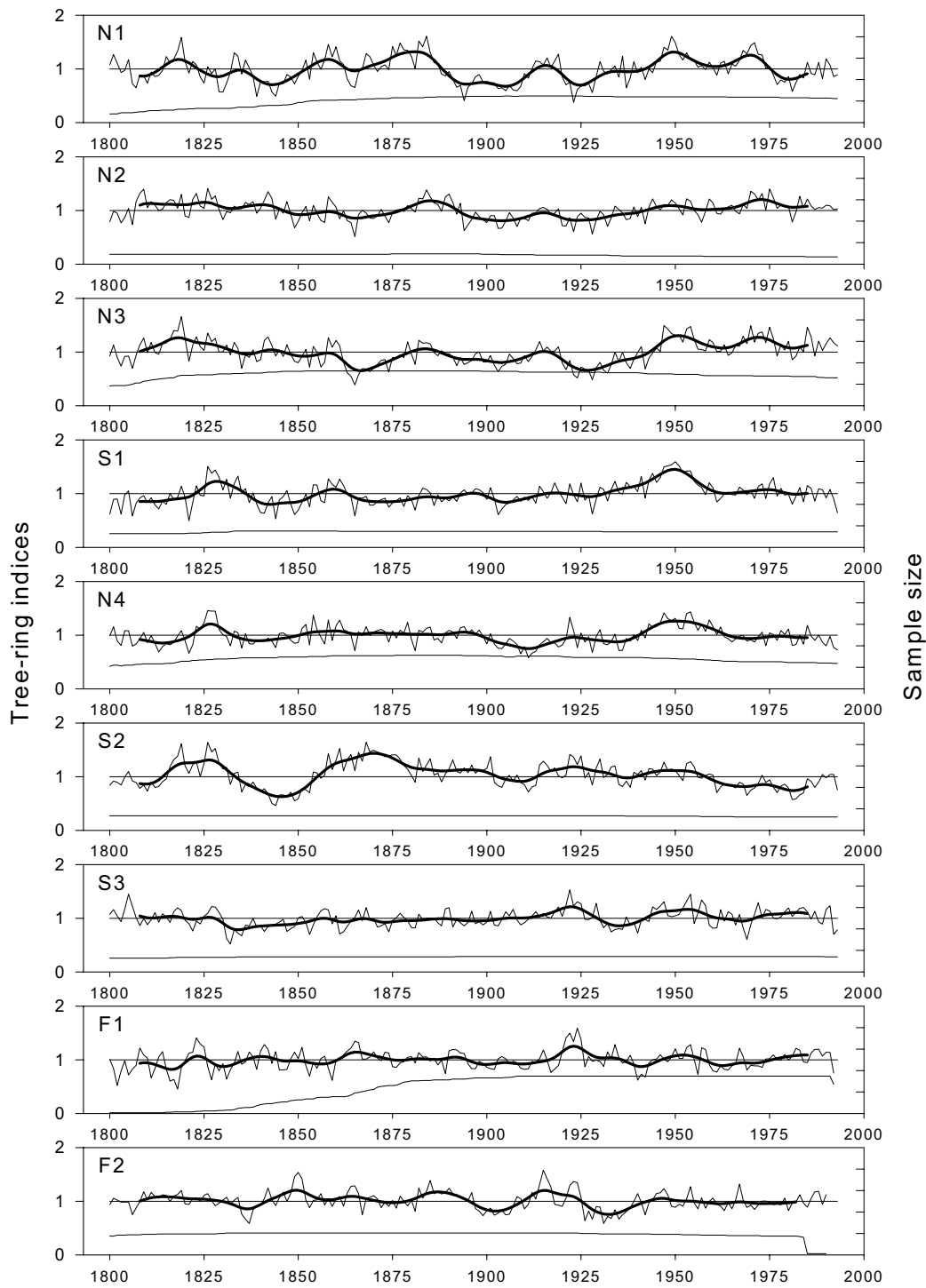


Figure 2. Standardised Scots pine tree-ring width chronologies (arstan version, thin lines), smoothed with a Gaussian filter with $\delta=3$ corresponding to a 10-year running mean (thick lines). Lower lines indicate sample size over time (right y-axis) with a scale of 50.

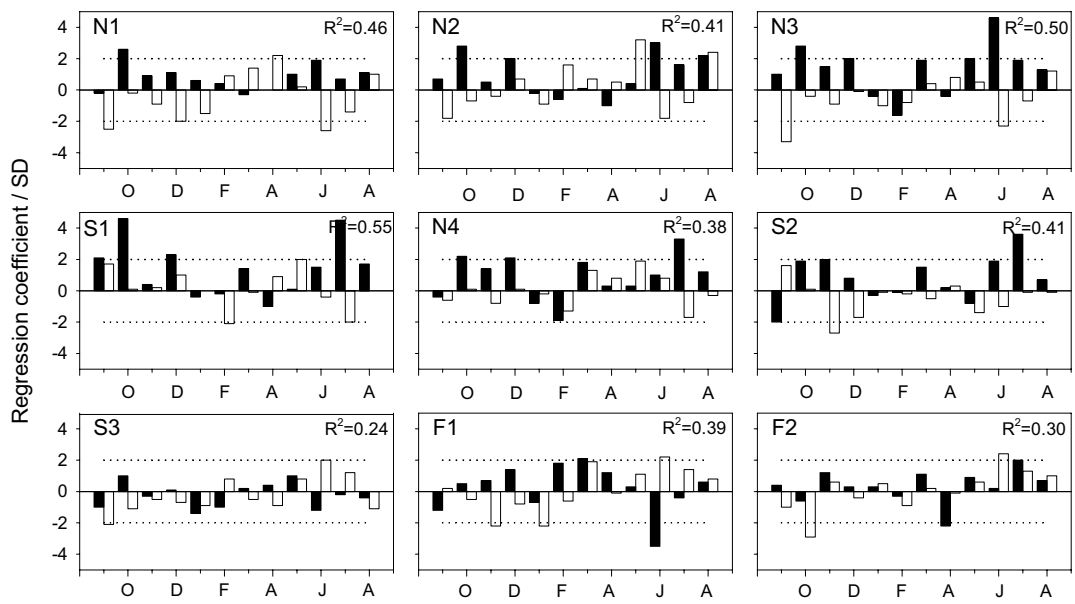


Figure 3. Effect of temperature (black bars) and precipitation (white bars) on ring width indices shown by the regression coefficients divided by its standard deviation for the period 1901-90. Dotted horizontal lines indicate significance level ($p < 0.05$) above and below mean.

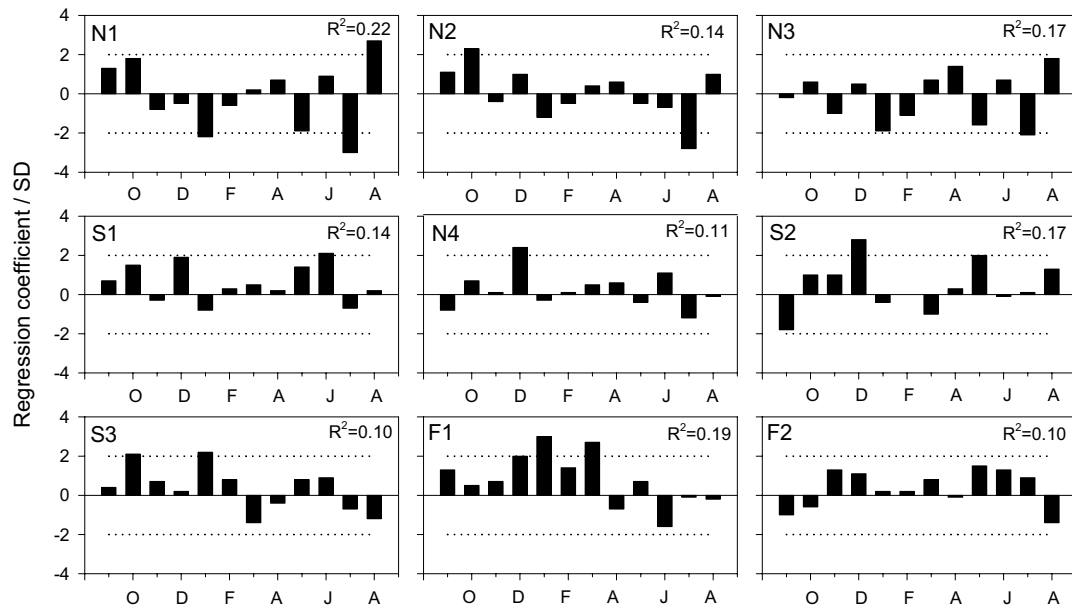


Figure 4. Effect of the NAO on ring width indices shown by the regression coefficients divided by its standard deviation for the period 1901-90. Dotted horizontal lines indicate significance level ($p < 0.05$) above and below mean.

Paper IV

Manuscript

**Tree growth and decadal climate oscillations in western Scandinavia:
species specific and general responses**

by
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**Tree growth and decadal climate oscillations in western Scandinavia:
species specific and general responses**

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Abstract: The relationships between monthly mean temperature, monthly precipitation and large scale climate indexes (North Atlantic Oscillation (NAO), Arctic oscillation (AO), Zonal Index (ZI) and Meridional Index (MI)), and radial growth of *Picea abies* and *Pinus sylvestris* are analysed with dendroecological methods along a coast-inland gradient in central Norway. Both species are mainly temperature limited and show a dominating response to summer climate but with different timing in most important growth period, i.e. late spring to early summer for spruce and mid- to late summer for pine. During two temperature optima in the 20th century both species responded positively to the first optimum in the 1930's. This was characterised by increased summer temperatures and decreased NAO index. None of the species reacted to the second optimum in the 1990's, which was mainly caused by increased winter temperatures and increased NAO index. Generally, the correlation between radial tree growth and tested climate indexes were low, but ZI showed most significant relations and significant impact by winter climate on tree growth was demonstrated. The response was species specific and varied along the gradient with pine showing a limited positive response to early winter temperatures above average in the inland. Spruce showed significant negative response to increased zonal weather pattern (i.e. increased oceanicity) during winter along the entire gradient. In addition to differences in species response the response shifted through time. Short and long-term changes in the degree of oceanicity are thus impacting on growth, vitality and species abundance in the boreal forest. Consequently, species specific responses to temporal changes in oceanicity in specific areas and along natural environmental gradients has to be given increased consideration in analyses of tree growth responses and in predictions of forest growth responses to future climate changes.

Keywords: oceanicity, large-scale climate, boreal forest, tree growth, environmental gradients

Introduction

The climate in western Scandinavia is characterised by a zonal weather pattern dominated by moist Atlantic air masses from the west (Wallen 1970; Hanssen-Bauer & Førland 2000). Periodically, a quasi-meridional circulation replaces the zonal flow of air over the North Atlantic and adjacent terrestrial areas (e.g. Norway), and drier air masses from the north and/or east influence the region. Throughout most of Norway the dominating influence from the westerly circulation leads to generally mild, wet winters and cool, moist summers (Hanssen-Bauer & Førland 2000). This oceanic type of climate is less expressed during periods with meridional types of circulation. The frequency and intensity of zonal vs. meridional atmospheric circulation pattern changes throughout the year, between years and periods of years (Wallen 1970; Slonosky et al. 2001). Such change in climate pattern alters the prerequisites for tree growth through time and impacts on vegetation distribution and structure (Bryson 1966; Krebs & Barry 1970; Larsen 1971). These temporal alterations of terrestrial ecosystems have received increased scientific interest during the last decade (Hofgaard et al. 1999; Post & Stenseth 1999; Chimielewski & Rötzer 2001; Solberg et al. 2002). Throughout the Holocene changes in climate have triggered changes in vegetation composition, and species distribution and abundance (Huntley 1990; Payette & Lavoie 1994; Bradshaw et al. 2000; Hofgaard & Wilmann 2002). On a century to millennial scale, the Arctic front position during winter and summer have largely determined the northern and southern limit of the boreal forest (Bryson 1966; Krebs & Barry 1970; Scott et al. 1988). On shorter and more recent time scales are treeline fluctuations (Scott et al. 1988; Jacoby & D'Arrigo 1995; Kullman 2001), disturbance regimes (Bergeron & Archambault 1993; Engelmark et al. 1994), vitality of forest ecosystems (Hofgaard et al. 1991; Lavoie & Payette 1994; Kullman 1996) and radial tree growth (Hofgaard et al. 1999; Allen et al. 2001; Peterson & Peterson 2001) related to changes of the climate pattern.

A proportion of the variation in radial tree growth is caused by other factors than climate variation but the climate-growth relation is strengthened towards distribution limits of the tree species. At polar and altitudinal distribution limits a positive correlation with summer temperatures is prevailing (Briffa et al. 1990; Villalba et al. 1997; Jacoby et al. 2000) but less evident correlation with other temperature and precipitation variables may be present (Jacoby & D'Arrigo 1995; Solberg et al. 2002). Further, radial tree growth are related to large scale atmosphere-ocean circulation like El Nino/Southern Oscillation (Stahle et al. 1998; Villalba &

Veblen 1998) and the North Atlantic Oscillation (NAO) (D'Arrigo et al. 1993; Piovesan & Schirone 2000; Lindholm et al. 2001). However, the correspondence with different variables shows a considerable temporal variation (Hofgaard et al. 1999). Climate-growth signals from tree-ring chronologies at individual sites may have applicability to wider geographical areas (Fritts 1976; Briffa et al. 2001), but the reliability of the climate information is strongly improved when chronologies along environmental gradients, and latitudinal and elevation species ranges are used (Peterson & Peterson 2001).

In central Norway and adjacent areas, radial tree growth of the main species, Norway spruce (*Picea abies* (L) Karst.) and Scots pine (*Pinus sylvestris* L), is strongest correlated with summer temperatures but with some variation in seasonal timing (Linderholm 2002; Solberg et al. 2002). Both species are common to vast areas of northern Eurasia and dominate the boreal forest in Fennoscandia (Nikolov & Helmisaari 1992). Their area of distribution overlap at the regional scale but show important differences in habitat requirements (Nikolov & Helmisaari 1992). Spruce is generally favoured by a humid climate and is thus locally found on slightly deeper soil with better moisture conditions compared to pine which is found in more xeric habitats. As a consequence of this difference in preferred sites *P. abies* has generally been favoured through time by weak seasonality, i.e. cool humid summers and snow rich winters, and *P. sylvestris* by pronounced seasonality, i.e. warm, dry summers and thin snow cover during winter (Nikolov & Helmisaari 1992). Consequently, temporal changes in vitality and growth of these species disclose in a detailed way past and present changes of climatic variables. When in addition, analysed along gradients of oceanicity and altitude, spatiotemporal variation in the response to changes in prevailing climate can be disclosed.

In this study we analyse the radial growth response of *P. sylvestris* and *P. abies* to climate variables (all seasons) and the correlation with and the applicability of different commonly used climate indexes. Three main questions are addressed: 1. How has radial tree growth of two ecologically different species responded to temperature and precipitation changes along a coast-inland gradient during the 20th century? 2. To what degree are changes in large-scale circulation pattern of air masses registered in regional tree growth? 3. Can growth correlation with seasonal large-scale climate indexes be used to demonstrate temporal shifts in the climate-growth response?

Material and Methods

STUDY AREA

The study area in central Norway, 64°N 10°-14° E, covers a 200 km long coast-inland gradient from the west to the east (Figure 1). The area is dominated by North Atlantic air masses with decreasing impact with distance from the coast (Chen & Hellström 1999; Slonosky et al. 2001). This causes predominately mild winters, especially at the coast. Along the coast-inland gradient spruce and pine are sampled in three climatically different areas (A, B and C) reflecting a total yearly precipitation of 1500, 900 and 600 mm, respectively (Førland 1993). The mean annual temperature in the west is 5.0°C (20 m a.s.l.) and in the east 0.9°C (433 m a.s.l.) (Aune 1993). The mean temperature in the west and east for January is –2.4°C and –10.4°C, and for July 13.3°C and 11.8°C, respectively (Aune 1993). The standard period 1961-90 is used for all climate data.

In each area along the coast-inland gradient, 3-4 sites (a-d) were sampled along altitudinal gradients from lowland forests to the forest lines. The sampling was performed at sites with westerly expositions, gentle slopes, moraine deposits and relatively dry habitats (Table 1). The coastal landscape surrounding area A is characterised by steep hills, deep valleys and small summits where the local tree line is reached (Table 1). Area B is situated 100 km inland from area A. Site Ba is at the valley bottom on glacial-fluvial deposits while Bb and Bc is on the same mountain side on moraine deposits. Area C is situated close to the Swedish border in a landscape characterised by wide valleys and gentle slopes up to the treeline. All sites in area C were on the north to northwesterly slope of the Hestkjølen mountain massif (1300 m a.s.l.), but site Cb had a southerly exposition due to its position on a small hill.

LARGE SCALE AND REGIONAL CLIMATE INDEXES

During the last years there has been an increased focus on the relationship between NAO and conifer tree growth in Fennoscandia (Lindholm et al. 2001; Linderholm 2002; Solberg et al. 2002). In this paper we include three additional large-scale climate indexes in the analyses (presented below). These four indexes are tested against regional temperature and precipitation data and against radial growth data for spruce and pine. The NAO index (<http://www.cru.uea.ac.uk/cru/data/nao.htm>; Hurrell 1995) reflects the pressure differences between Iceland in the north and the Azores in the south. A high index value indicate that mild and

moist air masses are influencing the climate in northern Europe including the study area, while a low index value indicate lessened influence of moist North Atlantic air masses (Hurrell 1995). During the winter the NAO index is positively correlated to both temperature and precipitation along the West Coast of Norway (Hurrell 1995; Hanssen-Bauer & Førland 2000). In the last decades, there has been a major increase in the NAO index (Hurrell 1995) and the winters have been predominantly mild and wet in central Norway.

An other commonly used climate index for the Northern Hemisphere is the Arctic Oscillation (AO) index (http://www.atmos.colostate.edu/ao/Data/ao_index.html) also named Northern Hemisphere “annular mode” (NAM; Thompson & Wallace 1998; Wallace 2000). AO reflects the mean deviation from the average sea level pressure measured throughout the Northern Hemisphere at longitudes poleward of 20°N. AO resembles NAO in many respects, but its primary centre of action covers more of the Arctic than NAO. NAO have been referred to as the signature of AO in the Atlantic sector, and the two are strongly correlated (Thompson & Wallace 1998; Overland & Adams 2001).

The Zonal Index (ZI) and Meridional Index (MI) are regional climate indexes that are valid to a somewhat smaller geographical area (Frich et al. 1996; Tuomenvirta et al. 2000). These indexes are determined from the difference in monthly mean sea level pressure between Hammerodde (Denmark) – Bodø (Norway) and Helsinki (Finland) – Bergen (Norway), respectively. The ZI resemble the NAO and AO in that it expresses the zonal influence of air masses, but the MI expresses the meridional influence of air masses flowing over Fennoscandia, and thus represents a different weather pattern than the zonal indexes.

CHRONOLOGY CONSTRUCTION

10 spruce and 9 pine ring-width chronologies are used in the study. At each site, minimum 30 trees per species were sampled with two cores from opposite sides (0.5-1.3 m above ground) extracted from each tree. The cores were mounted, sanded, crossdated and measured in the laboratory according to standard procedures. The ring width were measured to the nearest 0.01 mm using LINTAB measuring equipment and the software Time Series Analysis and Presentation (TSAP) version 2.4 (Rinn 1996). The crossdating was performed both manually and with correlation coefficients (Holmes 1994). By using approaches in the TSAP (Rinn 1996) and the COFECHA (Holmes 1994) computer programs, dating or measurement errors were tested and corrected when possible. Cores showing low correlation values ($r < 0.5$) with the mean site chronology were excluded from further analyses.

Generally, tree-ring width decrease with increasing age of the tree (Fritts & Swetnam 1989) and together with variation in microhabitat inside the sampled stand individual growth trends are produced. Through standardisation this individual growth trends were removed before the tree-ring series were averaged together to form STANDARD chronologies per species and site (Cook et al. 1990a). All series were detrended by a negative exponential curve or, if failed, a regression line, by using procedures in the software packages ARSTAN (Holmes 1994). During this detrending procedure the ring width were divided by the value of the modelled curve to express ring width as an index (Cook et al. 1990a). The mean of the index is expected to be 1 and the variance is generally stationary through time. Further, autocorrelation were removed from the individual series through autoregressive modelling (Cook et al. 1990b). In the resulting RESIDUAL chronologies, non-climatic variation is minimised and high-frequency climatic signals maximised. As a consequence of the standardisation procedure long-term climate variation is eliminated (cf. Cook et al. 1990b). The RESIDUAL chronologies are used to construct composite chronologies per species and area (in total 6 chronologies). These chronologies are used to decipher regional climate influence on tree growth, and to analyse differences and similarities between the species through time and along the coast-inland gradient.

STATISTICAL ANALYSES

Standard chronology statistics provided in ARSTAN were used to judge the quality of the different chronologies. The mean correlation technique (Briffa & Jones 1990), the expressed population signal and the signal to noise ratio (Wigley et al. 1984) were applied to estimate measures of common signal between trees in each RESIDUAL chronology (n=19). The expressed population signal was used to define the reliable part of the chronologies, and the threshold expressed population signal = 0.85 is used for this purpose (Briffa & Jones 1990).

Correlations between the six composite chronologies were analysed by using principal component analysis (PCA; Peters et al. 1981) and Pearson's correlation analysis. The common period 1873-1997 was used in both analyses. Additionally, the data set was split in 50-years sub-periods with an overlap of 25 years, and both PCA and correlation analyses were carried out for all sub-periods. In the correlation matrix years were used as variables and RESIDUAL chronologies as observations.

Climate-growth relationships between the composite chronologies and climate variables for the period 1901-1990 (i.e. the period in common between all tree-ring chronologies and climate data) were analysed with correlation analyses. The climate variables

used were: homogenised and standardised regional monthly mean temperatures and monthly totals precipitation values (Norwegian Meteorological Institute; Hanssen-Bauer & Nordli 1998; Hanssen-Bauer & Førland 1998), NAO index (Hurrell 1995), AO index (Thompson & Wallace 1998), ZI (Frich et al. 1996; Tuomenvirta et al. 2000), and MI (Frich et al. 1996; Tuomenvirta et al. 2000). The climate-growth relationships were analysed in a sequence of 12 months from September the year prior to growth to August the year of growth.

Additionally, response function analyses (Fritts et al. 1991) between ZI and radial tree growth were analysed in nine 10-year windows from 1901 to 1990. Ring width indexes from the six composite chronologies were used as predictands and seasonal ZI (winter=December-February; spring=March-May; summer=June-August; autumn=September-November) as predictors, and each season was analysed separately. One hundred bootstrap iterations were computed to assess statistical significance of the results (Guiot 1990).

Results

CHRONOLOGY STATISTICS

Spruce chronologies included slightly more climatic information than pine. The signal to noise ratio is generally high for spruce indicating a strong climatic signal, while there are more noise in the pine chronologies (Table 2). The expressed population signal is only slightly higher for spruce than for pine, but the mean number of trees required to pass the critical expressed population signal value is considerable lower for spruce compared to pine (mean 6.7 for spruce and 9.6 for pine). The spruce chronologies contain more high frequent variation than the pine chronologies reflected by a generally higher mean sensitivity (Table 2). Altogether, all sampled chronologies are reliable and can with confidence be used in dendroclimatic analyses covering the period 1873-1997. Within individual areas, the species specific chronologies are strongly correlated along altitude gradients (Figure 2). However, there is a clear difference between the two species. Based on this pattern in chronology positions, site chronologies are averaged together to form one chronology per species and area. This resulted in six composite chronologies in total.

SPATIOTEMPORAL GROWTH PATTERN

The first four principal components (PC) from the PCA of the six composite chronologies explained 95% of the total variance, with major contribution from PC 1 and 2 (57 and 25 %) and only minor contribution from PC 3 and 4 (8 and 5%). Scores along the first axis describe main environmental conditions specific to differences between the species, shown by positive loading for spruce chronologies and negative for pine chronologies (Figure 3). The second axis show the sum of variables describing the coast-inland gradient, where the coastal area have lowest loadings and the inland area have the highest loadings for both species. PC 3 and 4 did not seem to display interpretable patterns of chronology positions in the environmental space, and are therefore not included in the interpretation of the results.

Temporal changes in chronology positions are identified by ordination based on four 50-year intervals (Figure 4). Generally, for both species the environmental distance between studied areas showed an initial increase up to mid 20th century along both axes 1 and 2. Thereafter these distances decreased to a minimum for the entire period during the last part of the century, resulting in restricted species specific positions along the first axis. The overall pattern thus shows a transition towards a fairly homogenous environmental space for both species along the coast-inland gradient during the end of the 20th century.

The correlation analyses showed high within-species correlations, while the between-species correlations were lower and more variable. Spruce showed higher within-species correlations than pine, which is indicative of a more homogenous environment and radial growth pattern for spruce. Further, both species showed decreasing correlations with increasing distance between areas along the coast-inland gradient (Table 3). Generally, the temporal pattern shown by the correlation analyses resemble that of PCA for both species, i.e. a trend towards higher correlation between areas in the last sub-period (Figure 4, Table 3).

REGIONAL TREE GROWTH AND CLIMATE

Both spruce and pine show positive correlation to summer temperature and a negative correlation to summer precipitation the year of growth (Figure 5). For spruce the earlier part of the summer (May – June) is emphasised and for pine somewhat later during summer (June – August). Along the coast-inland gradient there is a change in the most important species specific response periods towards later season for both species (Figure 5). Additionally, there is a general positive correlation between radial tree growth and October_{t-1} - December_{t-1} temperatures. This pattern is consistent for both species and all chronologies except for spruce

at the coast. Temperatures above average in September_{t-1} and February_t have negative impact on spruce growth at the inland area (C) but this is not evident at other areas or for pine.

RELATIONSHIP BETWEEN REGIONAL TEMPERATURE AND PRECIPITATION DATA AND LARGE-SCALE CLIMATE OSCILLATION INDEXES

All tested large-scale climate indexes (NAO, AO, ZI, MI) showed significant correlations with temperature and/or precipitation for the period 1901-1990, but the relationships varied in strength with season and index (Table 4). The regional indexes, ZI and MI, were strongest correlated to precipitation, while the more large-scale indexes, NAO and AO, were stronger correlated to temperature. The regional indexes differed in that the ZI showed positive correlations with precipitation (all seasons) and winter temperature, while the MI showed negative correlations with precipitation in all seasons. The NAO and the AO indexes differed in that AO showed positive correlations with both temperature and precipitation in winter and spring, while NAO showed positive correlations with winter temperature and considerable weaker with spring temperature and precipitation (all seasons). Furthermore, all three zonal indexes, NAO, AO and ZI, were positively correlated ($p < 0.001$) between 1901-90; NAO-AO $r = 0.59$; NAO-ZI $r = 0.49$; AO-ZI $r = 0.75$. MI, on the other hand was not correlated to the zonal indexes, except for a weak negative correlation ($r = -0.22$, $p = 0.034$) between the MI and the AO.

TREE GROWTH AND LARGE-SCALE CLIMATE OSCILLATION INDEXES

The three zonal indexes share some common characteristics in respect to correlation between radial tree growth and individual indexes (Figure 5). The most evident common pattern is a negative correlation between spruce growth and January – February indices of NAO, AO and ZI. This pattern is not seen for pine or MI. For ZI, which show most significant correlations of the four tested indexes, negative correlations between May-June and spruce growth are most apparent. Additionally, pine growth is positively correlated to the ZI during April along the entire coast inland gradient and negatively during May-July with different emphasis depending on distance from the coast. In general, the MI showed few significant correlations between tested months and regional growth of both species. However, October for the coastal pine chronology and November for all other chronologies stands out as important periods. Overall, pine show fewer significant correlations with tested climate index values compared to spruce.

The ZI showed both the strongest correlations with regional temperature and precipitation data of the four climate indexes (Table 4) and most relevance for tree growth (Figure 5), and were thus chosen for the analyses of temporal changes in the relationship between large-scale climate pattern and regional tree growth. These analyses visualised a few trends and episodes with evident change in zonal climatic impact for both spruce and pine (Figure 6). The most distinct trend for pine is that a negative correspondence to summer indices up to the 1940's is changed to a positive correspondence towards the end of the 20th century. Additionally, for pine there is an indication of a general change in the regional zonal climate impact during the beginning of the 20th century and during the 1960's. There is a strong agreement between areas along the coast-inland gradient although the central area seems to have responded stronger to the changes during the beginning of the analysed period. For spruce there are marked change in correspondence to the spring indices during the beginning of the century and to the winter indices during the 1960's (Figure 6). There is no apparent long-term trend in the spruce data but a short-term trend of increasing values during autumn from the 1950's to 1970's. The different seasonal timing of radial growth for pine and spruce (Figure 5) and the definition of the summer season to June – August (cf. Methods) more or less hides sequences with significant correspondence between summer ZI and spruce radial growth. When analysed for the more relevant spruce-summer period (i.e. May-June) the correspondence between ZI and growth show two apparent periods with negative correspondence during the 1930's and 1960's (Figure 7). The period in the 1930's, particularly emphasised in the eastern area, is not at all shown when analysed for the pine-summer period (i.e. June-August) (Figure 6).

Discussion

The temperature development in central Norway during the 20th century is characterised by two maxima, one during the 1930's and a second around 1990 (Hanssen-Bauer & Nordli 1998). During the 1930's, mainly above average summer temperatures caused the maximum, while around 1990 above average winter temperatures dominated. Additionally, the 1930's were characterised by decreasing NAO intensity for northernmost Europe and around 1990 by increasing NAO intensity (Hurrell 1995). The growth of both

species traced the temperature increase in the 1930's but not around 1990. This general pattern in regional tree growth for the 20th century is in accordance with previously published data (Kalela-Brundin 1999; Linderholm 2002; Solberg et al. 2002).

There was a general good agreement in the response pattern to climate for spruce and pine. The prevailing pattern for both species was a positive response to summer temperatures above average and a negative response to summer precipitation above average in accordance with general boreal tree growth responses (Briffa et al. 1990, 2001; Schweingruber et al. 1993; MacDonald et al. 1998; Jacoby et al. 2000). This opposite response pattern to temperature and precipitation show the importance of a temperature-moisture balance during the growth period (Szeicz & MacDonald 1996). Due to species specific initiation periods for annual diameter growth (Ladefoged 1952; Kozłowski 1971), the timing in spruce and pine growth was however slightly different with late spring to early summer response for spruce and mid to late summer for pine. This division in most important diameter growth periods will consequently produce species specific response signals to changes in the climate both in the long and short term. In addition to this direct climate effect, the competition between the tree species and their distribution pattern is altered indirectly through climate mediated changes in disturbance regimes (Bradshaw & Zachrisson 1990; Sykes et al. 1996; Bradshaw et al. 2000; Niklasson & Drakenberg 2001). Accordingly, vitality and abundance of individual tree species in the boreal forest will be affected.

The variability and dynamics of an increasing number of terrestrial ecosystem components have been related to changes in the NAO during the last decade (cf. review by Mysterud et al. 2002). For example a dominating positive relationship between the winter NAO and pine radial growth is shown (D'Arrigo et al. 1993, Lindholm et al. 2001). Pine growth in the western Scandinavia (this study) does not support this positive influence by winter climate. Only very limited significant correlations with the three tested zonal indexes were shown during winter along the studied gradient. Spruce on the other hand showed significant negative growth response to mean temperatures above average during winter (see also Solberg et al. 2002). Mild winters in the studied region are generally caused by increased impact of Atlantic air masses which increases the frequency of freeze-thaw cycles, especially in lowland and coastal areas, and might thus produce stressful conditions to growth (Isard & Schaetzel 1998, cited from Venäläinen et al. 2001; Kramer et al. 2000; Mysterud et al. 2000; Venäläinen et al. 2001). In the future predicted climate characterised by warmer winters (IPCC 2001), occasional periods without insulating snow cover and formation of deep frost would increase. Thus, the probability of frost damage would also increase as a result of

warming (Kramer et al. 2000; Venäläinen et al. 2001). Increased oceanicity in western Scandinavia (i.e. warmer winters with increased proportion of rain at the coast and increased snow cover in inland and upland areas) will thus alter the competition between pine and spruce and change their dominance relation. In presently more continental parts of the region, an increase in oceanic impact might however initially be positive to both species due to reduced period with ground frost in late autumn and early winter as indicated by the positive response to December climate (ZI correlation) for the eastern area. In an oceanic climate involving prolonged periods during winter without an insulating snow cover, pine will be favoured in front of spruce (Nikolov & Helmisaari 1992).

Effect of winter climate on radial tree growth in the region might be better captured by zonal climate indexes than by temperature and precipitation variables, as they reflect both temperature and precipitation and the zonal climate impact is strongest during the winter season (Chen & Hellström 1999). The ZI is correlated to both summer and winter climate, while significant correlation between the NAO and the AO, and temperature and precipitation data are more or less limited to the winter season. Further, the ZI is stronger correlated to radial tree growth than the other tested circulation indexes. This implies that ZI is better representing weather pattern important to radial tree growth in central Norway, and consequently should be more considered to gain insight into large-scale climate variation using tree-rings as proxy data. Furthermore, the deviating climate signals for spruce and pine chronologies indicate the need for a stronger emphasise on more than one species in dendroclimatological studies (Graumlich 1993, Hofgaard et al. 1999) both at single sites and along environmental gradients.

Tree-ring data from Scandinavia have been used in reconstruction of the NAO index (Cook et al. 1998, 2002). However, this study has shown that there are reasons to be cautious in the interpretation of the causal relationship between NAO and radial tree growth from the Scandinavian region. The strength in the correlation between radial tree growth (both species) and large-scale climate oscillation indexes are generally relatively weak (Lindholm et al. 2001; Linderholm 2002; Solberg et al. 2002) and varies through time (Solberg et al. 2002). Further, the relationship between temperature, precipitation and the NAO varies between regions (Dickson et al. 2000) and through time (Slonosky et al 2001). Therefore, the shifting value of the NAO index as a predictor for ecosystem component variability has to be given more emphasis in studies of specific areas, environmental gradients, species and time periods (Myerud et al. 2000, 2002; Solberg et al. 2002).

Reconstructions of climate are generally based on a linear relationship between growth and the warmest summer month, which means July for most boreal forest regions (Fritts 1976; Briffa et al. 1990, 2001). Reconstructions using this constant relationship through time will not be well suited for regions where the oceanic impact varies periodically. For example, depending on position along the oceanicity-continentality continuum, an increase in oceanicity under a hypothetical constant temperature regime will change from mainly negative responses on tree growth in coastal areas to mainly positive in continental areas (D'Arrigo et al. 1993; Lindholm et al. 2001). However, independent temperature reconstructions from these areas would show different temporal trends. In analyses of previous responses and constructions of predictions for forest growth responses to a changing climate, increased consideration has to be given to natural environmental gradients of the region in focus, to shifts in the degree of oceanicity characterising the region through time, and to the non-linear relationship between growth and climate variables. Studies with increased focus on these issues would be desirable and would provide deepened understanding of the complexity of the growth-climate relationship.

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Table 1. Site description including location, altitude above sea level, aspect and oceanicity according to vegetation (c.f. Moen 1999), O2: oceanic, O1: sub-oceanic, OC: oceanic-continental transition zone. A-C indicates study areas from coast to inland, and a-d individual sites from lowland forests to forest line within each area.

Site	Locality name	Lat. N	Long. E	m a.s.l	Aspect	Slope in °	Oceani- city	Vege- tation
Aa	Drossavikhaugen	64°22'	10°50'	75	NV	15-20	O2	A4-A3
Ab	Sørsætra	64°19'	10°56'	200	SV	10-13	O2	A3-A4
Ac	Salahalsen	64°19'	10°55'	290	S	15-20	O2	A3-A4
Ba	Kjenstad	64°10'	12°21'	150	NV	--	O1/O2	A4
Bb	Kjenstadlia 1	64°09'	12°33'	310	V	6-9	O1/O2	A3-A4
Bc	Kjenstadlia 2	64°09'	12°34'	410	V	6-9	O1/O2	A3-A4
Ca	Murusjøen	64°28'	14°01'	330	N	4	OC	A4-(A5)
Cb	Skograudberget	64°27'	13°57'	410	S	10-20	OC	A3(1)-A4
Cc	Middagshaugen	64°27'	14°00'	520	NV	5-7	OC	A3-A4
Cd	Storbekken	64°26'	13°56'	620	V	5-8	OC/O1	A4-A3

A1 = boreal forest dominated by *Pinus sylvestris*, dwarf-shrub species and lichens

A3 = boreal forest dominated by *Pinus sylvestris* with elements of *Picea abies*, *Calluna vulgaris*, *Cornus suecica*

A4 = boreal forest dominated by *Picea abies*, *Pinus sylvestris*, *Betula pubescens*, *Vaccinium myrtillus*, grasses and herbs. A4 represents moister and more nutrient-rich soil than A3

A5 = quite similar to A4, but on moister and more nutrient-rich soil than A4

Table 2. Chronology statistics from residual site chronologies. Common period 1873-1997. SNR is Signal to Noise Ratio, EPS is Expressed Population Signal, SD is Standard deviation. S=Spruce and P=Pin. A-C indicates study areas from coast to inland, and a-d individual sites from lowland forests to forest line within each area.

	SAa	SAb	SAc	SBa	SBb	SBc	Sea	SCb	SCc	SCd	PAa [§]	PAb	PAc	PBa	PBb	PBc	PCa	PCb	PCc
Number of trees	23	28	25	27	27	26	22	24	25	16	15	18	13	21	21	18	15	19	15
(cores)	(36)	(51)	(42)	(48)	(46)	(47)	(37)	(43)	(48)	(27)	(24)	(32)	(18)	(38)	(32)	(32)	(27)	(32)	(25)
Autocorrelation*	0.25	0.33	0.50	0.48	0.54	0.39	0.41	0.48	0.44	0.42	0.52	0.62	0.64	0.60	0.53	0.63	0.39	0.49	0.53
Autoregression order*	1	1	1	2	1	1	1	1	1	1	4	2	1	1	1	1	1	2	1
SNR	14.5	29.5	21.6	25.1	20.1	21.7	26.7	24.6	33.5	13.9	9.1	10.2	8.8	15.9	12.8	10.9	12.2	10.7	8.1
EPS	0.94	0.97	0.96	0.96	0.95	0.96	0.96	0.96	0.97	0.93	0.90	0.91	0.90	0.94	0.93	0.92	0.92	0.91	0.89
EPS > 85% since	1843	1803	1816	1747	1761	1799	1864	1773	1751	1800	1876	1812	1809	1722	1791	1797	1865	1794	1737
No trees EPS=85%	9	6	7	7	8	7	5	6	5	7	10	10	9	8	10	10	7	11	11
Variation PCI	41.1	53.0	48.6	50.0	44.8	47.4	56.2	52.6	58.9	49.5	41.7	39.6	45.0	45.6	40.7	40.7	48.0	38.8	38.9
Mean sensitivity	0.26	0.26	0.25	0.21	0.24	0.22	0.20	0.21	0.23	0.26	0.18	0.23	0.24	0.19	0.18	0.21	0.15	0.18	0.18
SD	0.21	0.22	0.22	0.18	0.21	0.19	0.17	0.18	0.20	0.23	0.15	0.20	0.21	0.18	0.16	0.18	0.14	0.16	0.16
Mean correlation																			
Between trees	0.39	0.51	0.46	0.48	0.43	0.46	0.54	0.51	0.57	0.46	0.38	0.36	0.40	0.43	0.38	0.38	0.45	0.36	0.35
Within trees	0.54	0.70	0.67	0.66	0.58	0.64	0.69	0.70	0.73	0.72	0.65	0.63	0.57	0.65	0.58	0.56	0.64	0.53	0.56

* Refers to statistic from the STANDARD chronologies

§ Common period 1910-1997 because of too few samples between 1873-1910

Table 3. Correlations between all composite chronologies for the period 1873-1997, and 50 years sub-periods. Numbers in bold indicate the sub-period with highest correlation coefficient and numbers underscored indicate the sub-period with lowest correlation coefficient. P=Pine, S=Spruce, and A-C indicate study areas from coast to inland.

	1873-1997	1873-1922	1898-1947	1923-1972	1948-1997
PA-PB	0.700**	0.694**	0.717**	<u>0.687**</u>	0.693**
PA-PC	0.414**	0.350*	<u>0.315*</u>	0.388**	0.511**
PB-PC	0.707**	0.688**	<u>0.660**</u>	0.690**	0.758**
PA-SA	0.445**	<u>0.368**</u>	0.497**	0.540**	0.419**
PA-SB	0.304**	<u>0.249^{ns}</u>	0.318*	0.335*	0.311*
PA-SC	0.260**	<u>0.080^{ns}</u>	0.320*	0.380**	0.279*
PB-SA	0.443**	0.433**	0.537**	0.492**	<u>0.344*</u>
PB-SB	0.473**	<u>0.421**</u>	0.560**	0.517**	0.436**
PB-SC	0.453**	0.462**	0.558**	0.482**	<u>0.365**</u>
PC-SA	0.124 ^{ns}	0.072 ^{ns}	0.066 ^{ns}	<u>0.063^{ns}</u>	0.223^{ns}
PC-SB	0.231*	<u>0.091^{ns}</u>	0.214 ^{ns}	0.224 ^{ns}	0.346*
PC-SC	0.373**	0.371**	0.399**	<u>0.288*</u>	0.394**
SA-SB	0.855**	<u>0.813**</u>	0.865**	0.869**	0.879**
SA-SC	0.719**	<u>0.668**</u>	0.683**	0.727**	0.775**
SB-SC	0.833**	<u>0.779**</u>	0.809**	0.847**	0.886**

* = p<0.05

** = p<0.01

^{ns} = not significant

Table 4. Correlation functions between precipitation/temperature and large scale climate indexes. Only significant ($p < 0.05$) correlations are shown. P=precipitation; T=temperature; ZI=Zonal index; MI=Meridional index; AO=Arctic Oscillation index; NAO=North Atlantic Oscillation index.

1901-1990	P_winter	P_spring	P_summer	P_autumn	T_winter	T_spring	T_summer	T_autumn
ZI_winter	0.662				0.628			
ZI_spring		0.793				0.334		
ZI_summer			0.769				-0.482	
ZI_autumn				0.731				0.264
MI_winter	-0.706							
MI_spring		-0.509						
MI_summer	-0.283		-0.24		-0.228		0.409	
MI_autumn				-0.641				0.361
AO_winter	0.659				0.685	0.274		
AO_spring		0.523				0.49		
AO_summer			0.288				0.267	
AO_autumn				0.466				0.376
NAO_winter	0.382	0.222			0.581	0.28		
NAO_spring		0.266				0.296		
NAO_summer					0.231			
NAO_autumn								0.253

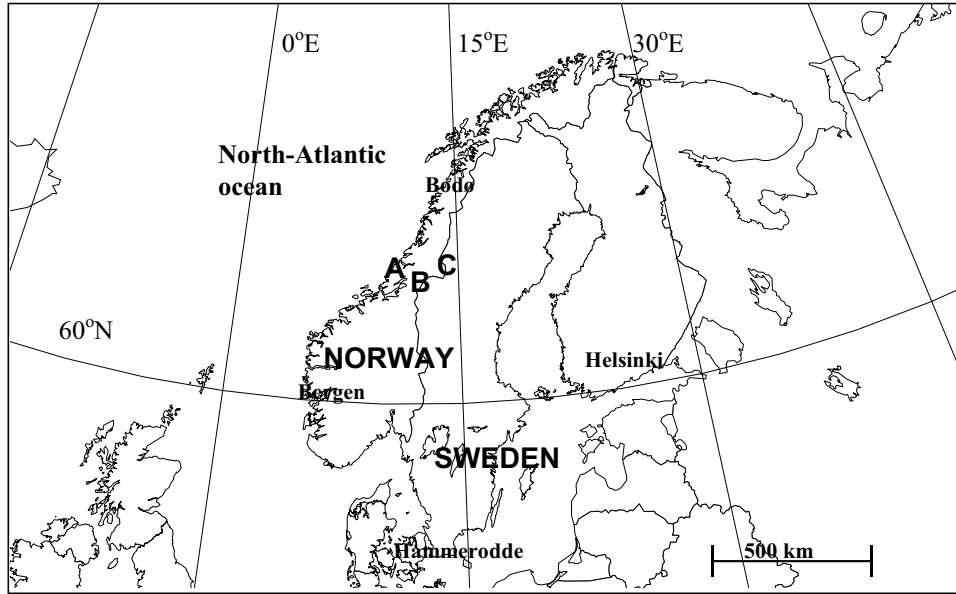


Figure 1. Study area.

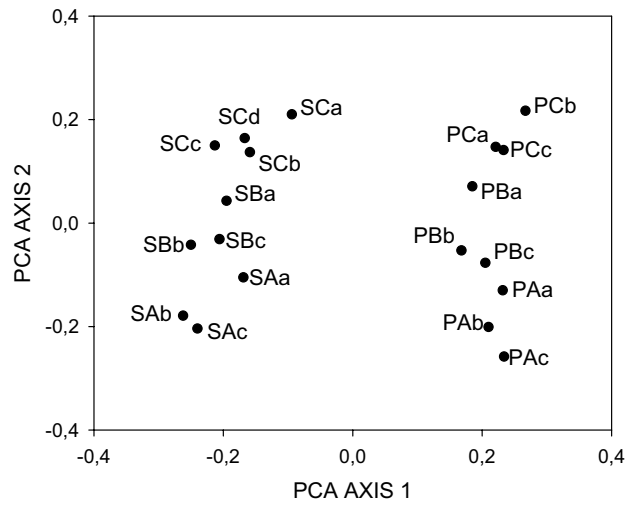


Figure 2. Principal component score positions for spruce (S) and pine (P) residual chronologies (N=19) along the coast-inland gradient (A-C) and altitude gradients (a-d), 1873-1997.

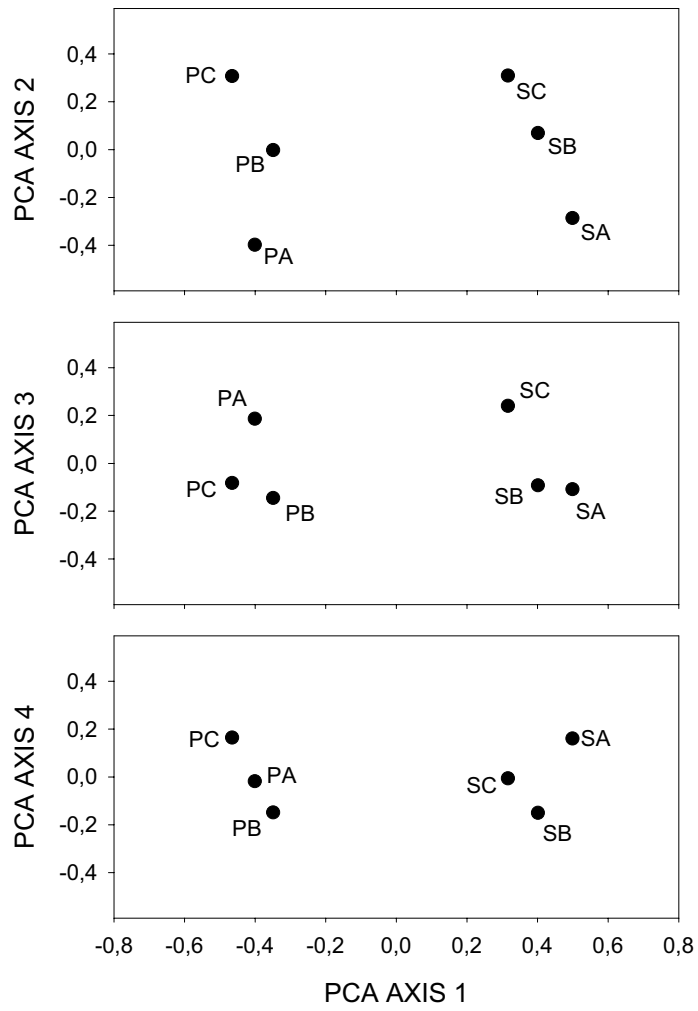


Figure 3. Principal component score positions for spruce (S) and pine (P) composite chronologies along the coast-inland gradient (A-C), 1873-1997.

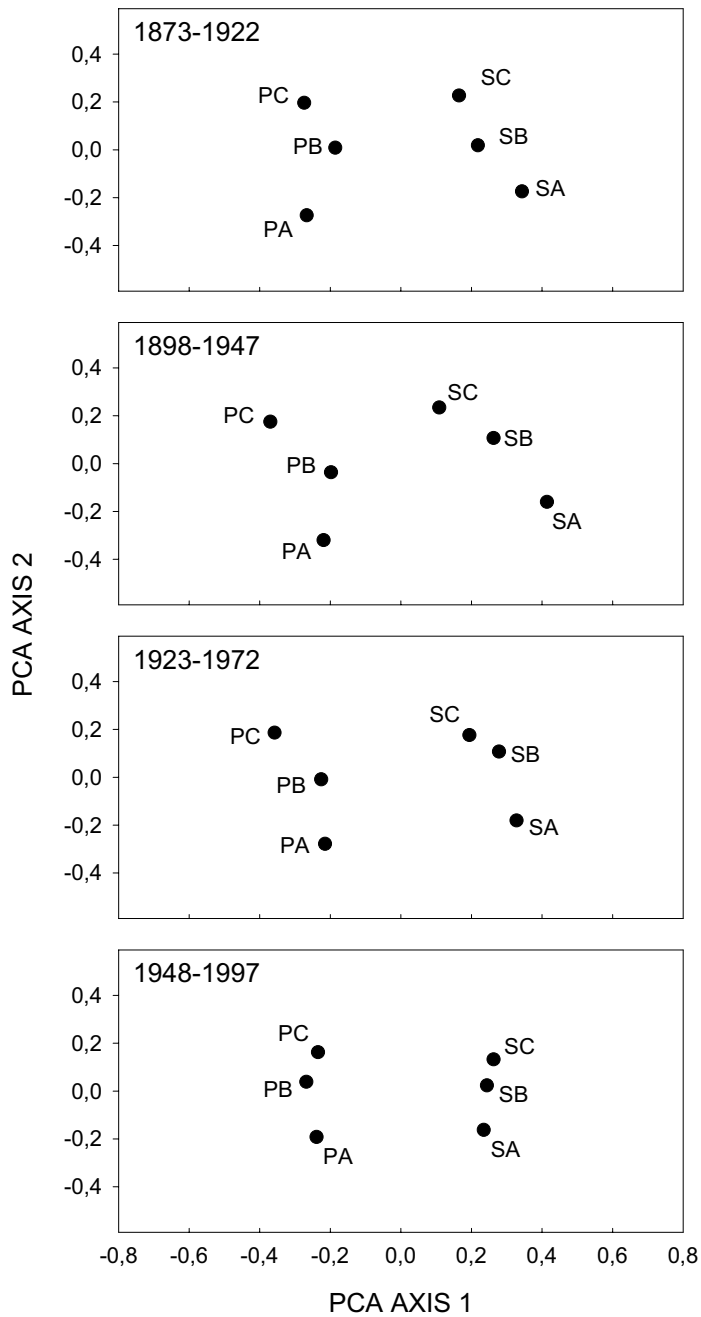


Figure 4. Principal component score positions for spruce (S) and pine (P) composite chronologies along the coast-inland gradient (A-C) for four successive 50-years periods from 1873 to 1997.

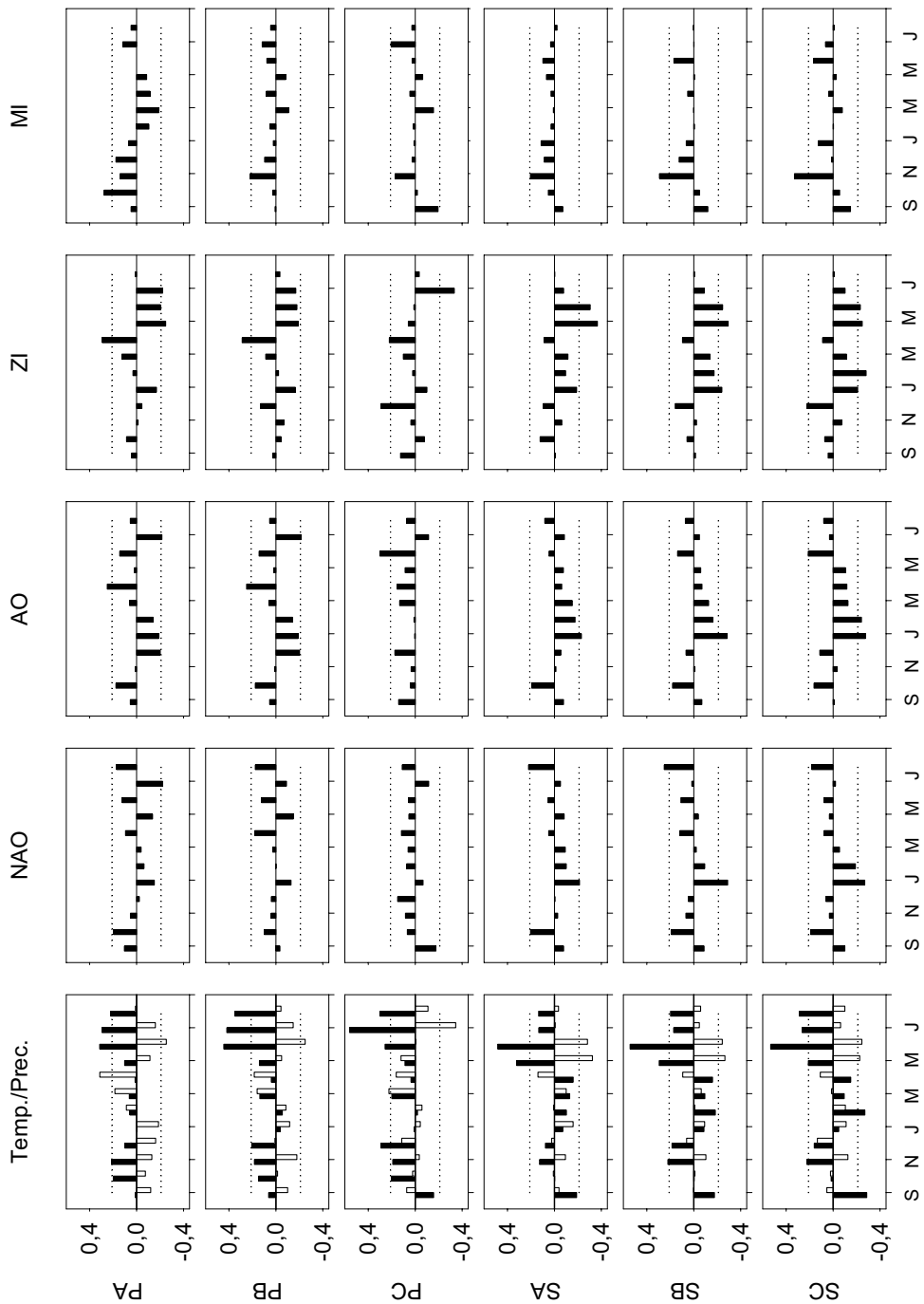


Figure 5. Correlation function between composite chronologies and temperature/precipitation, North Atlantic Oscillation (NAO), Arctic Oscillation (AO), Zonal Index (ZI) and Meridional Index (MI) for the period 1901-1990. In the left colon, filled bars are temperature and open bars are precipitation. A bar that passes the dotted horizontal lines indicate significant correlations ($p < 0.05$). P = pine, S = spruce, and A-C are areas along the coast-inland gradient.

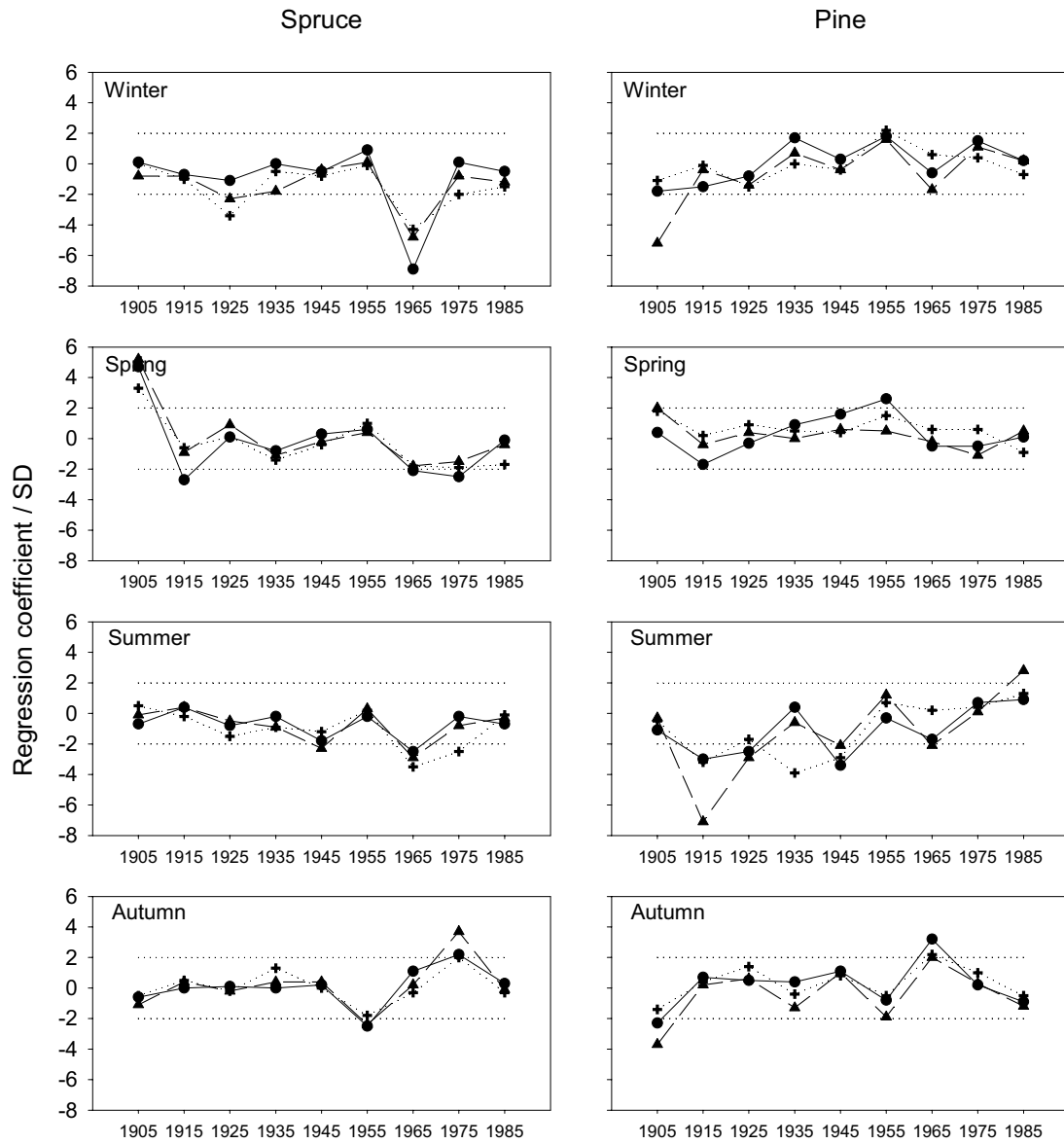


Figure 6. Correspondence between the Zonal Index (ZI) for all seasons and the composite chronologies shown by response function analyses for 10-years sub-periods (1901-10; 1911-20;;1981-90). Area A is indicated by filled circles and solid lines, area B by filled triangles and dashed lines, and area C by crosshairs and dotted lines. Dotted horizontal lines indicate significance level $p < 0.05$ above and below the mean.

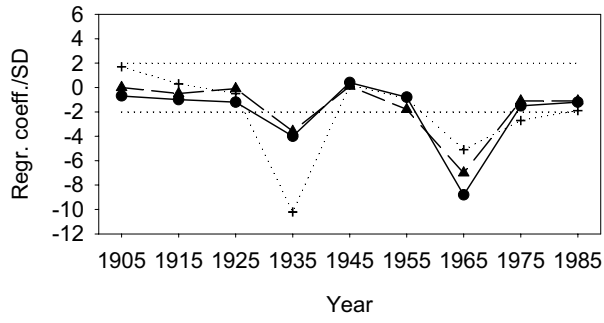


Figure 7. Correspondence between the Zonal Index (ZI) during May and June, and the spruce composite chronologies. For explanations: see Figure 6.