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Age-related growth trends in ancient Norway spruce trees and potential effects on long term growth patterns

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Introduction

A long-term increase in radial tree growth has been reported in tropical (Lloyd & Farquhar 2008), temperate (Spiecker 1996, Voelker et al. 2006), alpine (Rolland et al. 1998) and boreal forests (Hofgaard et al. 1999) over the last decades. Variations in forest growth patterns have been ascribed to different causes, such as longer growing seasons due to climate warming (Hu et al. 2010), changes in land management practices (Hunter & Shuck, 2002), nitrogen deposition (Magnani et al. 2007), and atmospheric CO_2 enhancement (Voelker et al. 2006).

Tree-ring analyses provide detailed information on the past growth of forests. In order to assess the effect of climate change on forest growth, non-climatic variation should be removed from tree-ring series. The effect of endogenous (inter-tree competition) and exogenous (insects attacks, fires, storms, human influence, etc.) disturbances on tree-ring series can be detected and reduced by considering trees from different sites. Furthermore, as tree-ring width generally decreases as trees grow older and larger, age-related growth trend should be removed, to preserve climatic low-frequency variability of chronologies. Different detrending methods used to remove non-climatic variations need to be adapted to the objectives of a particular study.

A universally suitable estimation of the age-related growth trend cannot be developed (Briffa et al. 1996), as individual trees differ in growth rates along their life-span due to differences in environmental factors, stand dynamics, disturbances, etc. (Fritts 1976, Nicault et al. 2010). One of the more used methods in dendrochronology is the Regional Curve Standardisation (RCS) (Esper et al. 2003, Mitchell 1967). In this method, tree-ring series are aligned by cambial age, providing an expected age-growth Regional Curve (RC). The RCS method assumes that this curve describes the age-related growth trend of a population, and departures from the curve can be attributed to climate or other factors common to all trees (Esper et al. 2003). Several authors indicate that this method has specific limitations, mostly related to sample selection (Biondi & Qeadan 2008, Linderholm et al. 2010, Melvin 2004, Nicault et al. 2010). A necessary precondition for the application of RCS is to employ trees belonging to the same "biological growth" population, i.e. a group of trees with similar age-related growth trend (Esper et al. 2003). When fast and slow-growing trees are not equally distributed through time, significant biases can limit the interpretation of tree-ring chronologies (Biondi & Qeadan 2008, Briffa & Melvin 2011, Esper et al. 2003, Linderholm et al. 2010, Nicault et al. 2010). A few recent studies demonstrate an inverse relationship between growth rate and longevity (Bigler & Velben 2009, Black et al. 2008). This relationship should be considered, as it can affect long term growth trends, especially in chronologies composed of only living trees (Melvin 2004, Nicault et al. 2010).

In the present work we examined the radial growth of Norway spruce with respect to cambial age and calendar years. Increment cores from ancient and adult trees were collected close to the altitudinal forest limit in Trillemarka Nature Reserve, southern Norway. Dendrochronological analyses have been conducted (1) to evaluate growth trends along lifespan of different age trees and (2) to determine possible biases on long term growth trends using different age living trees. To achieve the second goal, we employed the RCS method. RCS assumes that Regional Curve describes the common age-related growth trend. However, if different age trees have different growth rates, unequal distribution of fast and slow-growing trees through time occur. Such pattern could affect long-term trends in index chronologies and, consequently, interpretation of growth patterns.

Material and Methods

The study area was located in Trillemarka Nature Reserve (60° 05' N, 9° 10' E), a protected area in southern Norway, between the valleys of Numedal and Sigdal, representing one of the last large and relatively undisturbed forested areas in southern Fennoscandia. The Reserve was established in 2002 and enlarged in 2008, today covering 147 km^2.

In order to sample the oldest Norway spruce trees in the forest, in 2003-2009 repetitive field surveys were conducted in old-growth Norway spruce stands close to the altitudinal forest limit (700-850 m a.s.l.), in an area extending 8 x 15 km. One or two (three) cores per tree were taken at 50-130 cm above ground level. Increment cores were shaved with a scalpel and treated with zinc paste to enhance tree-ring borders. Ring width was measured with a micrometer to the nearest 0.01 mm. Raw ring-width series were visually and quantitatively cross-dated against an existing site chronology (Storaunet, unpublished data) using TSAP (Rinntech, Heidelberg, Germany) and Cofecha (Holmes 1983) programs. 4 cores not reliably cross-dated were excluded from further analyses. For cores that did not include the pith, pith offset was estimated with a pith locator (Applequist 1958). The mean width of 10 innermost rings was used to estimate the number of missing rings (Groven et al. 2002). 9 cores with an estimated distance to pith >30 mm were excluded from further analyses. In order to calculate the total age of trees it was necessary to take into account the time to reach coring height. As cores were taken at different height above ground, estimated time varied between trees. Based on studies in similar forests (Storaunet, unpublished data), we estimated 2 years for each 10 cm of height. If two cores per tree were available, the core with more rings was used to estimate the age, while the core taken at breast height, or with less estimated distance to pith, was used for the analyses (Bigler & Veblen 2009).

93 individual tree-ring series were grouped in three classes according to estimated tree age: adult (130-230 years), old (230-350 years), and ancient (>350 years). We employed the RCS method to assess radial growth along cambial age and calendar years. As the pith offset may influence RCS (Linderholm et al. 2010), the number of years estimated to the pith and to sample height was added to the series, with a maximum of 59 and a minimum of 14 years. We calculated the Regional Curve (RC) as the arithmetic mean of ring widths for each cambial year for each age class, and for all series together. The RC was then smoothed using a cubic spline with a 50% frequency cutoff at 67% of the segment length (Leonelli et al. 2008). Index series were derived by calculating ratios between the measured ring width series and the RC. Mean index chronologies (IC) were calculated using the bi-weight robust mean, and were truncated at a replication of $n < 6$ series. ICs were smoothed with a 20-year cubic spline function to emphasize low frequency variations. Analyses were performed using Arstan (Cook & Holmes 1986).

Results and Discussion

Regional curves (RC)

Regional Curves of the three age classes show common age-related trends in ring width. However, growth rates appear to be different between the age classes, as the rings of adult trees were wider than those of old and ancient trees (Fig. 1). Recent studies show that trees have to grow slowly to reach very old age, particularly when competition scarcely affects growth (Bigler & Velben 2009, Black et al. 2008, Castagneri et al. unpublished). In our dataset, slow growth of ancient trees could be due to inverse relationship between growth rate and longevity. Indeed, juvenile growth rates of ancient trees were lower than those of old trees, even if these trees were established in the XVII and XVIII centuries, long before global warming. However, changing environmental influences cannot be excluded as a reason for these differences.

The all-RC is produced from the mean ring width of all chronologies aligned by tree age. However, adult trees only contribute to the young part of the all-RC, while the old part of the all-RC is formed only by ancient trees (Fig. 2). Therefore, the all-RC curvature is biased and produced not only by the age-related ring widths, but also by the differing growth rate of adult and ancient trees.

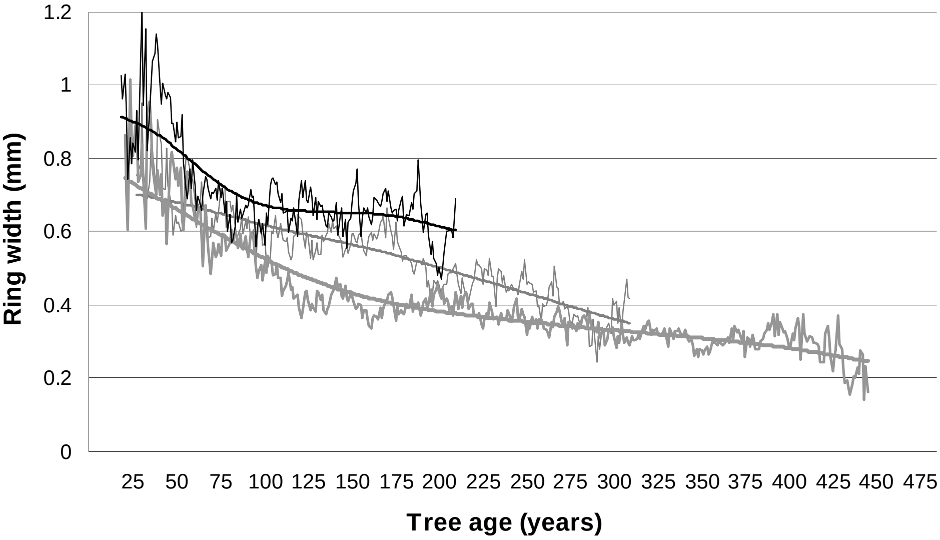

Figure 1: Regional Curves of adult (black), old (grey), and ancient (grey, bold) classes.

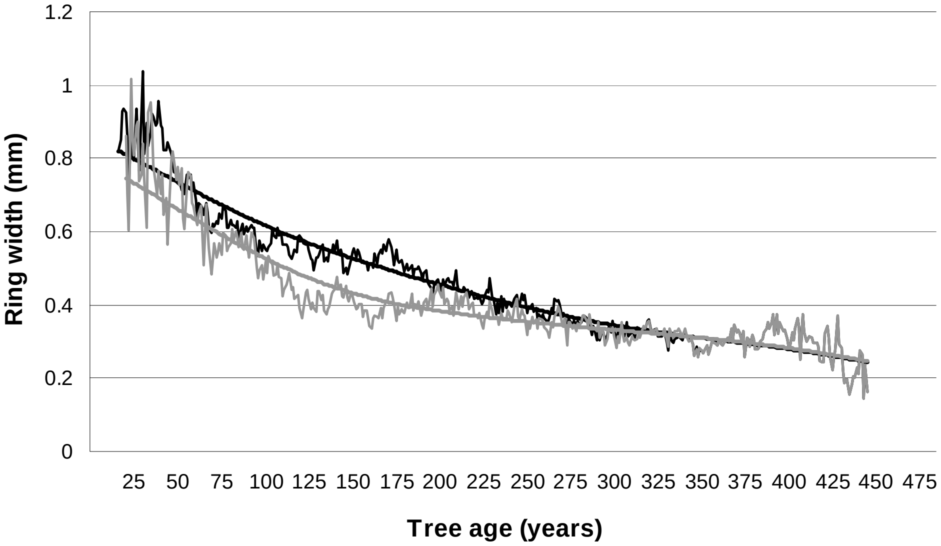

Figure 2: Ancient (grey, bold) and all (black, bold) Regional Curves.

Index chronologies (IC)

The Index Chronologies (IC) of the three age classes (adult, old, ancient) show multi-decadal variations, but no general increasing or decreasing trends (Fig. 3, 4). However, there is a positive long-term trend in the all-IC (Fig. 4), as ring width indices are mostly <1 before 1820 and >1 in the last century. Such trend results from an unequal distribution through time of slow and fast-growing trees. The early part of the all-IC derives from the ratio between the juvenile part of slow-growing ancient trees RW (which were young in 1600-1700, other trees were not yet alive) and the juvenile part of the all-RC, resulting in index values mostly <1. The recent part of the all-IC is influenced by the ratio between the juvenile part of fast-growing adult trees RW and the juvenile part of the all-RC, resulting in index values mostly >1.

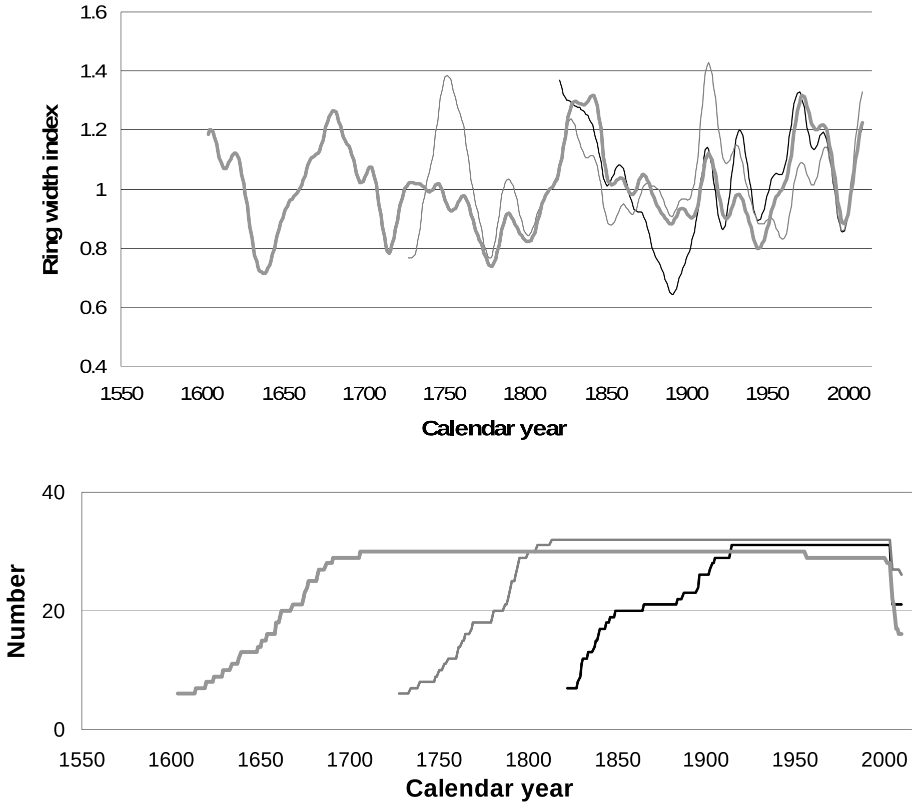

Figure 3: Index Chronologies (ICs) of adult (black), old (grey) and ancient (grey, bold) classes and sample size along calendar years. Series were smoothed with a 20-year cubic spline to emphasize low frequency variations.

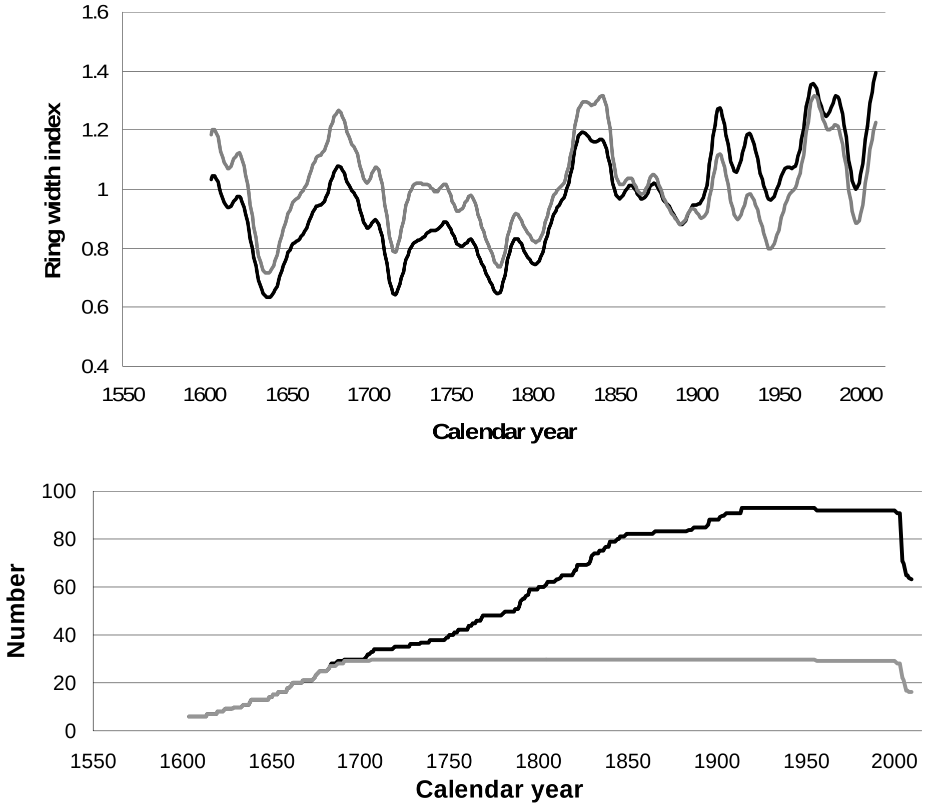

Figure 4: Ancient (grey, bold) and all (black, bold) Index Chronologies (ICs), and sample size along calendar years. Series were smoothed with a 20-year cubic spline to emphasize low frequency variations.

Conclusion

Regional Curves show that the oldest Norway spruce trees had lower growth rates than younger trees close to the altitudinal forest limit in Trillemarka forest. As sampled trees were established long before the global warming, influence of climate change on growth rates cannot be the only reason for observed patterns. A few studies suggest that such patterns are related to higher longevity of slow-growing trees (Bigler & Veblen 2009, Black et al. 2008, Briffa & Melvin 2011).

Applying RCS method to all series together, we obtained an Index Chronology with an increasing trend. Such trend was, at least partially, not related to climate change effect on tree growth. Fast-growing trees had low probability to reach old age, thus they could not survive long enough to be included in the early part of the chronology (Briffa & Melvin 2011, Melvin 2004). Therefore, this part was composed only by the oldest trees, which tend to grow slowly. The apparent increase in long term growth pattern resulted from associating growth rates of slow-growing ancient and fast-growing young trees. Indeed, Index Chronology composed solely by ancient trees did not show such trend.

Tree rings provide quantitative information on past forest growth. Radial growth trends have been widely investigated to assess long-term growth trends. However, while climatic reconstruction of past centuries use chronologies composed of living and dead material (Büntgen et al. 2005), many studies on forest growth trends have been conducted only on live trees (Bontemps et al. 2010, Rolland et al. 1998). Differently than short-term (annual) and medium-term (decadal) growth variations, long-term trends can be severely affected by age-related growth trends. Sub-fossil material in long-term records reduces biases, as young trees series can be included in the early part of the chronology. Further research is needed on that issue, and new methods (Melvin 2004, Melvin & Briffa 2008, Nicault et al. 2008) should be tested using different datasets.

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