

Climate Impact on 100-Year Foliage Chronologies of Scots Pine and Ponderosa Pine in the Northeast Lowlands of Brandenburg, Germany

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Due to differences in the high-frequency signal and mean sensitivity of needle parameters in Scots pine and Ponderosa pine revealed in previous investigations, variance caused by climate factors at a dry site in the northeast lowlands of Brandenburg was investigated. Although water is the general limiting factor for both tree species, there are evident differences in the climate-driven impact on individual needle parameters. Autumn precipitation of the previous year was equally important for Scots pine and Ponderosa pine, but summer precipitation was more significant for the needle parameters of Scots pine. In contrast to precipitation, temperature seems to have a minor impact on needle parameters. Although January temperatures are significant predictors for both species, intercorrelations between needle parameters and summer temperatures were found only for Ponderosa pine. Striking correlation was also found between sun activity and needle production in Ponderosa pine, but not Scots pine, indicating possible adaptation to solar radiation.

Keywords needle trace method, climate impact, foliage parameters, Scots pine, Ponderosa pine

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Symbols and Abbreviations

Symbol/abbreviation	Definition
AGE	Mean needle age
<i>b</i>	Bolt
C/N ratio	Quotient of carbon and nitrogen content of soil
DENS	Needle density
GLEV	Groundwater level
h	Hours
HEIGHT	Annual height increment
hPa	Hecto-pascal
<i>l</i>	length
LOSS	Absolute needle loss
MS	Mean sensitivity
NN	Number of attached needles along the whole stem
NTM	Needle Trace Method
<i>P</i>	Relative number of needle traces
pH _{KCL}	Negative decadal logarithm of proton concentration compared to potassic-chloride
PROD	Needle production along the entire annual shoot
<i>q</i>	Time in months spent from needle birth to senescence of needle
<i>r</i>	Year of investigation
RET	Annual needle retention in summer
<i>s</i>	Stem
SD	Standard deviation
<i>sh</i>	Shoot
SCL	Sun cycle length
<i>t</i>	Current year
<i>t</i> -1	Previous year
TOTAL	Absolute number of attached needles along the stem
<i>x</i>	Number of needle traces

1 Introduction

The foliage of trees is directly linked to wood formation dynamics (Liu et al. 1998) and subject to annual fluctuations caused by external and internal influences (Schmitt et al. 1998). Measuring the foliage of a tree, therefore, provides great potential for dendroecological investigations. The needle trace method (NTM), developed in the early 1990s (Kurkela and Jalkanen 1990), permits the foliage of conifers to be disclosed retrospectively throughout their entire lifetime in annual resolution. Initial investigations have shown that the needle parameters determined via this method

accurately mirror climate and environmental conditions (Jalkanen and Tuovinen 2001, Hicks et al. 2000, Jalkanen 2000). However, interest in trees grown under variable conditions has mainly focused on the species Scots pine. Regarding tree-ring and stem analysis, NTM seems to be a suitable tool for assessing the adaptation potential of different tree species for comparison at the same site. Study sites with one limiting climatic environmental factor are of special interest because growth reactions can be interpreted unambiguously – particularly dry locations have therefore proven to be very significant in the past (Schweingruber 1996).

In the northeast lowlands of Brandenburg, a series of trials involving native and exotic tree species was initiated in the 19th century. With regional precipitation sometimes below 400 mm, the sites can be classified as very dry. A very special part of the trials consists of a mixed stand of Scots pine (*Pinus sylvestris* L.) and Ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) Although both species have grown under almost identical climatic and edaphic conditions for more than a century, Ponderosa pine has shown increased forest yield parameters over the years (Insinna et al. 2006). The first tree-ring and stem analyses performed indicate that Ponderosa pine is better adapted to the dry conditions in Brandenburg than Scots pine due to its phylogenetically acquired adaptation to the natural habitat in North America. Previous investigations (Insinna et al. 2007) have also shown significant differences in the high-frequency signal (Hughes and Funkhouser 2004) and the mean sensitivity (Fritts 1976) of needle parameters for both species. These findings lead to the assumption that the foliage of Scots pine and Ponderosa pine are affected by different environmental factors. Thus, an extensive statistical analysis of the data set was carried out in this study. The multiple regression technique (bootstrapped response and correlation functions) was used to determine the climate variables, which have a significant impact on the foliage of both pine species. With it, needle chronologies of Scots pine were carried out for such a long growth period of more than 100 years for the first time. For Ponderosa pine it was the first time at all, that NTM was applied on trees grown in Europe. Thus a comparison of both pine species anyhow was possible.

2 Materials and Methods

2.1 Study Site

The study site is a 0.36 ha section of a field experiment with exotic tree species planted in 1889 in the northeast lowlands of Brandenburg, Germany (Schwappach 1891). The site is located near the village of Bralitz, 8 km west of the border between Germany and Poland (52°49'39" N, 14°00'51" E) at an elevation of 14 m a.s.l. The climate is

characterized by dry summers, cold winters, and sometimes spring frosts. The mean annual precipitation (1893–2001) was 510 mm and the mean annual temperature 8.4 °C. The soil is a sandy brown (forest) soil, partly underlain with clay, and is specified as a *Bodenseichener Sandbraunerde* (Schulze 1996) with a moderately moist moder (Insinna et al. 2006). The pH_{KCL} for the upper soil layers is 3.13, with a C/N ratio of 14.2.

2.2 Stand Description

The mean tree heights and mean diameters of the 112-year-old (2001) even-aged stand are 26.7 m and 41.0 cm with bark for Scots pine and 28.8 m and 50.2 cm for Ponderosa pine, respectively. Stand density (openness), calculated as the ratio between the actual basal area (m^2/ha) of all trees at breast height and the modelled basal area (m^2/ha) of a local forest yield table (Lembcke et al. 2000) for moderate thinning, is 0.8. Despite their advanced age, the trees show continuous stem axis (leaders), which is the basic prerequisite for applying dendrochronological methods. The whole stand is characterized by a dense black cherry (*Prunus serotina* Ehrh.) understory.

2.3 Sampling Strategy

In winter 2001/2002, we sampled five trees representative in terms of both dbh (diameter at breast height, i.e. 1.3 m) and tree height and applied the needle trace method (NTM) according to Aalto and Jalkanen (1998a). All trees were in a dominant position (Kraft 1 and 2) (Kraft 1884), healthy, and were not affected by being situated at the edge of the stand. A continuous stem axis simplified and optimized the subsequent steps.

2.4 Needle Trace Method

NTM enables the number of short shoots in conifers along the stem axis to be revealed retrospectively for the whole lifetime of a tree via traces of the vascular bundles (Jalkanen and Kurkela 1992). Since NTM is a destructive method, the sample trees had to be felled and segmented into

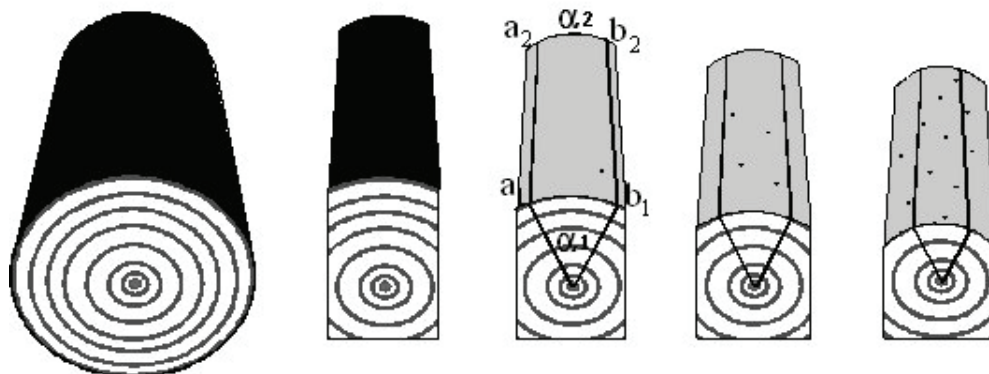


Fig. 1. Schematic process of NTM using arc-surface method for counting needle traces in annual rings (from Aalto and Jalkanen 1998).

pieces (bolts) 15–20 cm in length, representing the middle parts of the annual height increments of the stem (Aalto and Jalkanen 1998a). To reveal the tree-rings, the cross-sections were smoothed with sandpaper (P 80–400) and counted under a stereomicroscope.

Each bolt was treated with a knife and a plane on the east-facing side (Jalkanen et al. 2000) starting at the seventh or fifth innermost ring for Ponderosa pine and Scots pine, respectively. These values were set iteratively, representing the maximum age of short shoots for the two tree species at the study site. Planing down to the latewood of every consecutive tree-ring was performed using the arc surface method (Jalkanen et al. 2000), where needle traces were counted within a sector enclosed by an angle (α_1/α_2) of 70° (Fig. 1) until the needle pattern was complete. Below, the term “needle” is used as the generic term for short shoots.

The total number of needle traces in the first, i.e. innermost, tree-ring ($\alpha=360^\circ$) is used to convert the bolt-specific absolute number of needles into relative numbers of needle traces (Aalto and Jalkanen 1998a). The following formula performs this:

$$P_r = \frac{x_r}{x_1} 100 \tag{1}$$

where P_r is the relative number of needle traces, x_r is the number of needle traces x in year r , and

x_1 is the number of traces in the first annual ring. These relative numbers are then used to calculate the following parameters with the program NTMENG (Aalto and Jalkanen 1998b):

Annual needle retention in summer (RET):

$$\frac{\sum(P_b, P_{b+1}, \dots, P_{b+n})}{100} \tag{2}$$

Mean needle age (AGE):

$$\frac{\sum_{r=1}^n (P_r - P_{r+1}) \left(r - 1 + \frac{q}{12} \right)}{100} \tag{3}$$

where P_b is the relative number of needle traces in bolt b in the year in question, P_r =the relative number of needle traces, and q =time in months spent from needle birth to senescence of needles.

Besides the relative parameters, a series of absolute variables was computed:

Needle density (DENS, needles per cm along the stem axis):

$$\frac{360^\circ x}{\alpha * l_b} \tag{4}$$

where l_b is the length of the investigated bolt.

Needle production along the entire annual shoot (PROD):

$$\text{DENS} * l_{sh} \quad (5)$$

Total (absolute) number of attached needles along the whole stem (TOTAL):

$$\sum (\text{NN}_s, \text{NN}_{s+1}, \dots, \text{NN}_{s+n}) \quad (6)$$

Absolute needle loss in a given year (LOSS_r):

$$\text{TOTAL}_r - (\text{TOTAL}_{r+1} - \text{PROD}_{r+1}) \quad (7)$$

where x is the number of needle traces in a bolt's innermost ring, α = mean of the angles (here 70°), s = whole stem, l_{sh} = shoot length (=annual height increment, HEIGHT), and NN = number of attached needles along the stem.

Additionally, the annual height increments (HEIGHT) were measured to calculate PROD and to investigate the relationship between PROD and climate, similarly to Jalkanen and Tuovinen (2001).

Damage to terminal shoots continues to influence needle parameters even years after its occurrence and distorts the climate-driven needle patterns. Despite the careful selection of sample trees, some of them exhibited such damage, preventing a continuous time series for every tree. In this case, the raw-data chronologies were assembled using the cross-dating procedure for tree-ring analysis (Schweingruber 1983). Within the 5 sample trees of each species, only the unaffected tree(s) had a continuous time series. They were taken as a basis, to which the unaffected parts of the other tree series were added, omitting 3–6 years after the damage. For Scots pine 3 trees were completely unaffected and taken as a continuous time series. 2 of the sample trees had damages in terminal shoot in 1930 and 1960. Thus during the periods of 1930–1939 and 1960–1966 the needle chronology of Scots pine is reduced to 3 single curves. For most of the time all 5 trees are covering the chronology. Concerning Ponderosa pine only 1 tree had a completely unaffected time series. 3 trees had a damage in 1931, 1972 and 1993, 1 tree only in 1993. Thus the chronology of Ponderosa pine is remaining in 2 single curves

from 1931–1934 and 1972–1978. In the period of 1993–1995 the chronology is reduced to one single curve. For the other periods all 5 trees are covering the chronology.

2.5 Database

For the present investigations, data from Insinna et al. (2006, 2007) were taken as the basis for the statistical analysis. These were mean value (Mean), standard deviation (SD), mean sensitivity (MS), interserial correlation coefficients, and the asymptotic significance (two-tailed) for the Kolmogorov-Smirnov test (Table 1).

2.6 Climate Data

The Schiffmühle meteorological station (52°49'05" N, 14°03'05" E) near the study site has continuously recorded daily precipitation, temperature, and a number of other weather variables since 1950. All values have been checked for plausibility and were homogenized by the Potsdam Institute for Climate Impact Research. Transfer functions were deduced between Schiffmühle and the long-term (1893–2000) meteorological station at Potsdam (52°23'10" N, 13°04'05" E) for the common period of 1950–2000 in order to adapt the values for 1893–1950. For annual precipitation (mm), precipitation during the growing season (May–October), precipitation during the second half of the year (July–December), and insolation sum (h), mean monthly quotients between the series were used to fit the Potsdam values; for temperature (°C, mean, max, min), relative humidity (%), water vapor pressure (hPa), and air pressure (hPa), mean monthly differences were applied to generate the series.

In addition to the monthly climate data, a drought index was calculated by forest succession model 4C (Schaber et al. 1999), which considers not only temperature and precipitation but also the physiological characteristics of the soil and vegetation (Rizza et al. 2004). To describe sun activity, the length of sun cycles (SCL) was used for the correlation analysis (Friis-Christensen and Lassen 1991). The raw data, obtained from the Solar-Terrestrial Physics Division of the Danish

Table 1. Descriptive statistics, interserial correlations, and results of the Kolmogorov-Smirnov test, including all sample trees. SD=standard deviation, MS=mean sensitivity, ns=not significant, ** significant at the $p < 0.01$ level.

Needle parameter	Unit	Species	Mean	SD	MS	Interserial correl. coeff. (r)		Asymptotic significance (two-tailed) of K-S statistic
						Raw	Index	
RET	Short shoots	PS	2.6	0.35	0.11	0.02ns	0.28**	0.00
		PP	3.7	0.43	0.06			
AGE	Short shoots	PS	2.1	0.33	0.16	0.30**	0.46**	0.00
		PP	3.5	0.51	0.12			
TOTAL	Short shoots	PS	634	145	0.18	0.33**	0.42**	0.00
		PP	877	183	0.10			
PROD	Shorts shoots	PS	206	57.44	0.21	0.41**	0.20*	0.51
		PP	215	55.96	0.21			
LOSS	Short shoots	PS	202	97.5	0.38	0.37**	0.29**	0.68
		PP	196	87.8	0.55			
DENS	Short shoots	PS	6.8	1.15	0.15	0.60**	0.38**	0.00
		PP	7.8	2.17	0.17			
HEIGHT	cm	PS	28.1	9.4	0.21	0.52**	0.37**	0.00
		PP	30.4	8.1	0.20			

Gleichläufigkeit: a measure of the year-to-year agreement between the interval trends of two chronologies i.e. changes of needle values in the same direction, usually expressed as a percentage of cases agreement.

Meteorological Institute, were generated to a time series with annual resolution.

Data on groundwater levels (GLEV, m a.s.l.) near the study site were obtained from the Brandenburg Department of the Environment in Frankfurt/Oder (LUA 8/97, Bralitz No. 31502021) for the period of 1964–2001.

2.7 Statistical Analysis

To eliminate the low-frequency signal (standardization) due to endogenous factors and the high-frequency signal (indexing) due to exogenous factors (Fritts 1976) in raw needle data, a detrending process according to Cook and Peters (1981) was applied with the ITRDBL program ARSTAN, Version 6.04P (Cook and Holmes 1986, Holmes 1994). Depending on the variable, single or double detrending (1st detrending: linear regression or negative exponential curve; 2nd detrending: smoothing splines with 22- to 57-year stiffness and a 50% cut-off) was per-

formed (Insinna et al. 2007). These series, lacking trends and autoregression, were then used for statistical analysis (Riemer 1994). The effects of monthly climatic variables on needle parameters were tested by response and correlation functions using DENDROCLIM2002 (Biondi and Waikul 2004), which is commonly applied in dendrochronology but equally applicable for all kinds of indexed series. Only biologically plausible predictors (Sander 1997) were taken into account, because needle primordia are formed during the previous growing season; climate variables from April of the previous year to April of the current year (depending on the variable) were used for response and correlation functions. Using bootstrapped confidence intervals eliminates the underestimation of error estimates and ought to prevent coefficients from erroneously passing the significance test (Biondi and Waikul 2004). The response and correlation coefficients were tested for significance at the 0.05 level.

Mean sensitivity of the raw data (MS), as the mean percentage change from each measured

yearly value to the next (Douglass 1936), was calculated according to Fritts (1976):

$$MS = \frac{\sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|}{n-1} \tag{8}$$

where x_t is the value of the current year, x_{t+1} the value of the following year, and the vertical lines designate the absolute value of the term enclosed by them.

3 Results

3.1 Response and Correlation Functions for Monthly Temperature and Precipitation

Autumn precipitation of the previous year ($t-1$) significantly predicted the variables LOSS, TOTAL, and DENS of Scots pine (Table 2).

Response and correlation coefficients were positive for LOSS and negative for TOTAL and DENS. In Scots pine, April precipitation of the current year and May–June precipitation of the previous year had a significant influence on the HEIGHT of Scots pine. For needle production (PROD), only the June temperature (negative) of the previous year passed the significance test for response and correlation functions. LOSS (negative) and RET (positive) were significantly affected by the January temperatures of the current year. In Ponderosa pine, too, winter precipitation from the previous year significantly impacted RET, TOTAL, and HEIGHT (all negative). Spring and summer precipitation levels ($t-1$) were important factors for DENS (negative) and HEIGHT (positive). Response and correlation coefficients of actual January and February precipitation were significant for both AGE and DENS (negative). Temperatures played a minor role in Ponderosa pine but proved to be significant predictors for PROD, AGE (negative), DENS (positive) (previ-

Table 2. Results of bootstrapped response functions (multiple regression) for needle parameters of Scots pine (a) and Ponderosa pine (b), with climate predictors of precipitation (P) and temperature (T) in Brandenburg. Asterisks show verification of predictors by significant coefficients of correlation functions, R^2 =variance explained by climate. Level of significance: $p < 0.05$. Shaded areas mark the periods of used climate variables in the model, which are biologically plausible for each NTM parameter.

Variable	R^2	Year $t-1$								Year t					
		A	M	J	J	A	S	O	N	D	J	F	M	A	
a)															
PROD	0.18	-T*													
LOSS	0.31			P*						-T*					
RET	0.23	T*													
AGE	0.14			-P*											
TOTAL	0.33	-P*													
DENS	0.20	-P*													
HEIGHT	0.36	P*		P*								P*			
b)															
PROD	0.27	-T*													
LOSS	0.25			-T*											
RET	0.25	-P*													
AGE	0.43			-T*						-P*					
TOTAL	0.28	-P*								-P*					
DENS	0.46			-P*		T*						-P*			
HEIGHT	0.52	P*		P*		-P*									

ous year), and LOSS (current year).

The coefficients of determination (R^2) differed slightly for the two tree species: 18–36% for Scots pine and 5–52% for Ponderosa pine of the variance could be explained by climatic factors.

3.2 Cross-Correlations of Needle Parameter vs. Climatic Variables

Scots pine showed a significant ($p < 0.01$) negative correlation between DENS and the groundwater levels from January to August of the current year, from which the correlation coefficient of March was highest (Fig. 2a). DENS correlated with precipitation of the 2nd half of the previous year (Fig. 3). According to the results of the response functions, TOTAL of Scots pine correlated negatively with precipitation during the growing season (May–October) of the current

year (Fig. 2b), while annual height increment (HEIGHT) was positively related with precipitation during the growing season with a time lag of one year (Fig. 4).

In Ponderosa pine, needle retention (RET) correlated significantly with the temperature sum of the previous year (Fig. 5) and with GLEV from June ($r = -0.34^{**}$) and July (Fig. 2c) of the current year. Precipitation during the growing season (Fig. 4) and the drought index (Fig. 2d) correlated with HEIGHT with a one-year lag, and DENS ($r = -0.27^{**}$) showed linear correlation with precipitation of the second half of the previous year (Fig. 3).

Regarding the insolation sum of the previous year ($t-1$), significant correlations were found between HEIGHT ($r = -0.28^{**}$) and DENS ($r = 0.35^{**}$) for Ponderosa pine but not for Scots pine. Relative humidity ($t-1$) showed a linear correlation with HEIGHT ($r = 0.35^{**}$) and DENS

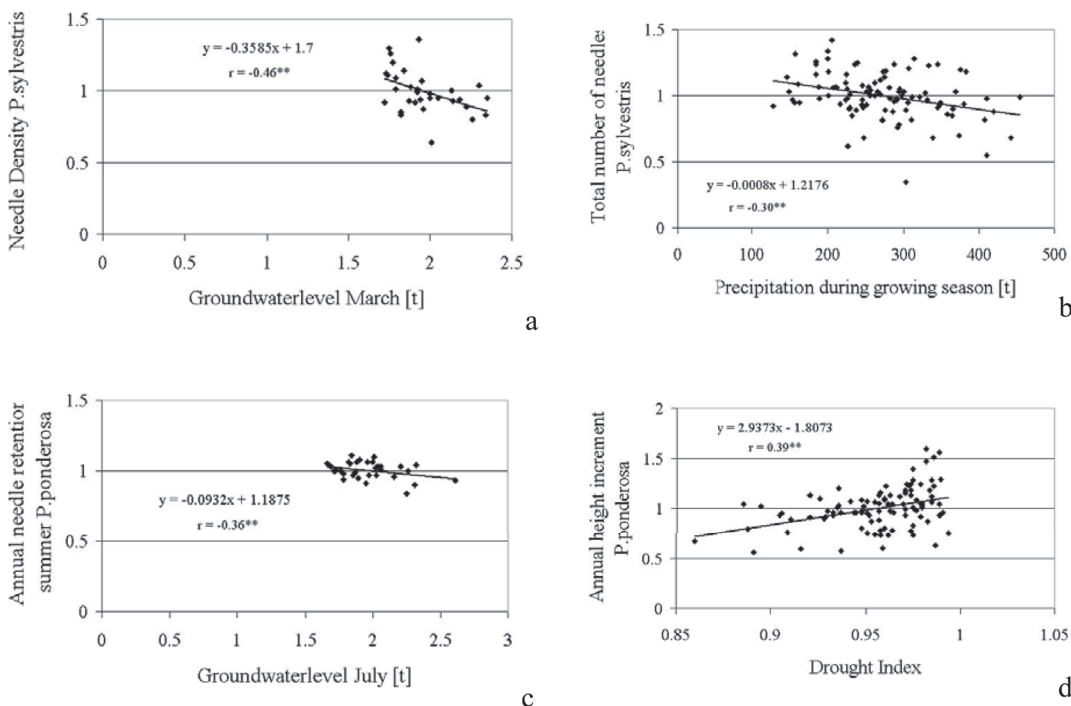


Fig. 2. Scatter plots of significant relationships between needle parameters and climate variables for Ponderosa pine and Scots pine. Asterisks (**) show the significance of the correlation coefficients at the $p < 0.01$ level; non-significant correlations are omitted.

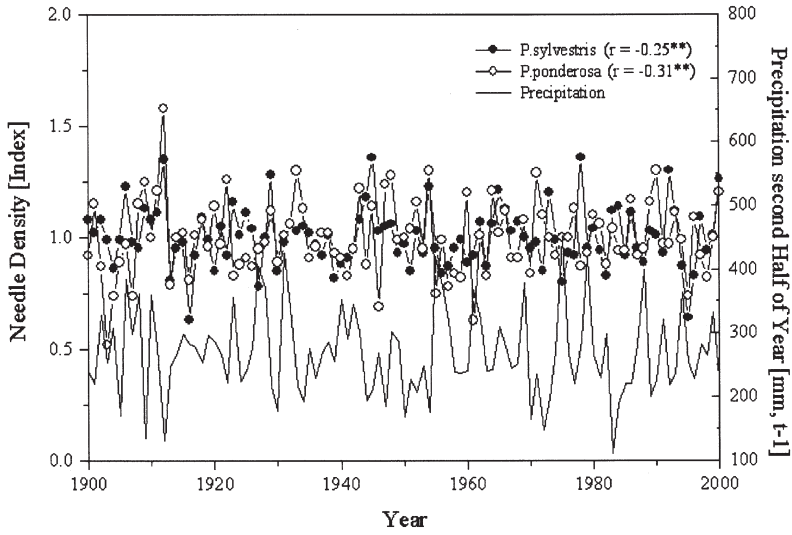


Fig. 3. Index values of needle density (DENS) for Scots pine and Ponderosa pine in combination with precipitation during the 2nd half of the previous year (July–December).

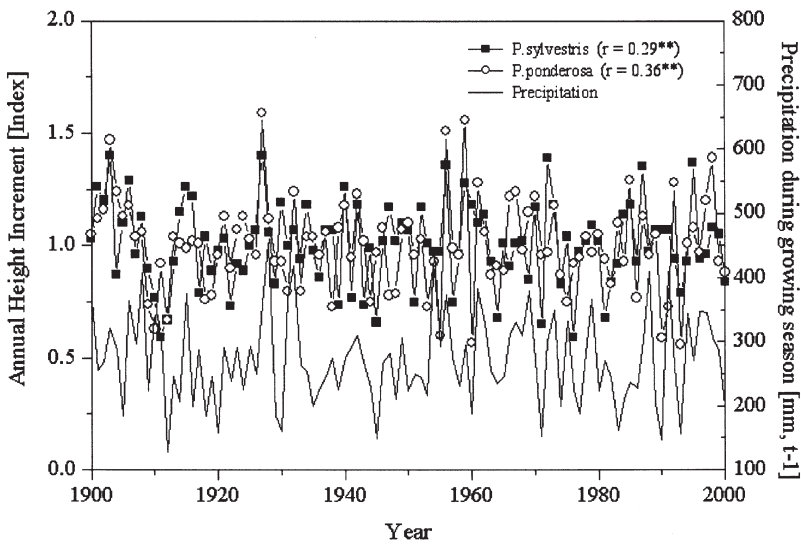


Fig. 4. Index values of annual height increment (HEIGHT) for Scots pine and Ponderosa pine in combination with precipitation during vegetation period (May–October) of the previous year.

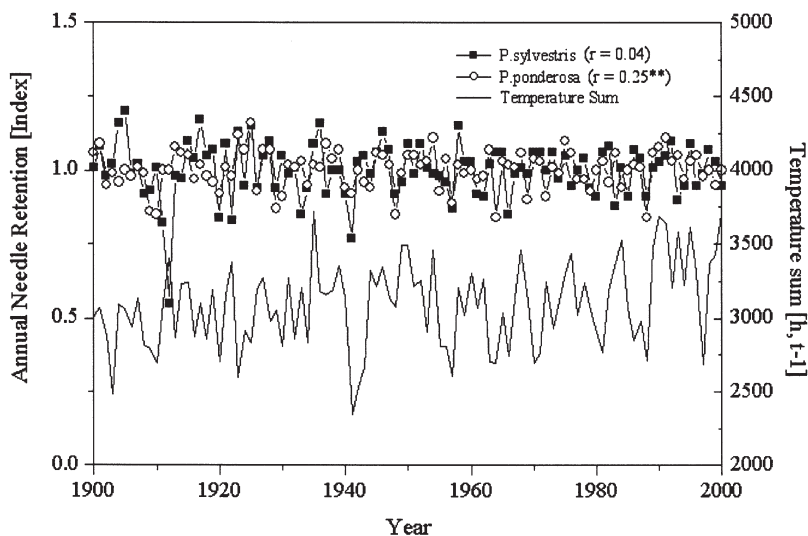


Fig. 5. Index values of needle retention (RET) for Scots pine and Ponderosa pine in combination with the temperature sums of the previous year.

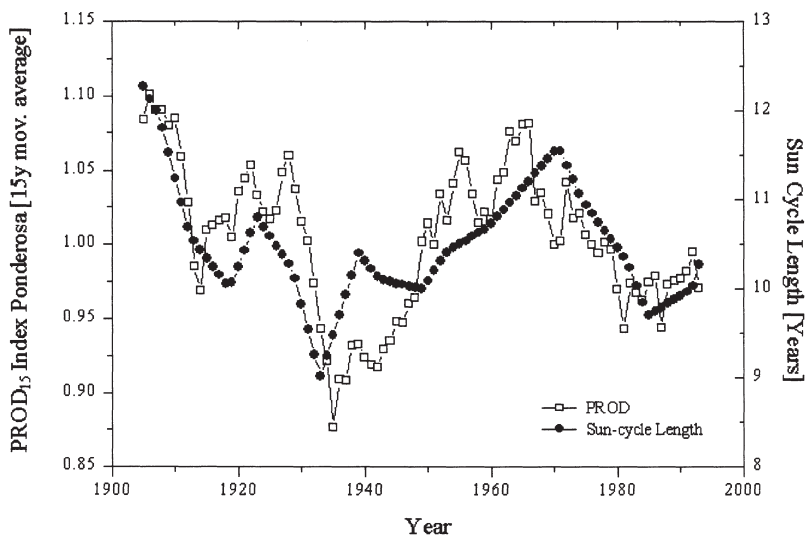


Fig. 6. 15-year moving average of needle production (PROD15) of Ponderosa pine vs. sun cycle length, obtained from the Solar-Terrestrial Physics Division of the Danish Meteorological Institute.

($r=-0.30^{**}$) of Ponderosa pine and TOTAL ($r=0.23^*$) of Scots pine. The maximum temperatures of the previous year significantly correlated with HEIGHT ($r=-0.25^{**}$), DENS ($r=0.23^*$), and RET ($r=0.22^*$) of Ponderosa pine; minimum temperatures ($t-1$) were correlated with PROD of Scots pine ($r=0.21^*$).

For mean temperatures, water vapor pressure, and air pressure, no significant relations were detected.

3.3 Sun Activity

Sun-cycle length (SCL) was used as a substitute for sun activity (Friis-Christensen and Lassen 1995). For Ponderosa pine, a correlation was detected between a 15-year moving average of the annual needle production (PROD₁₅) and SCL (Fig. 6). With $r=0.70^{**}$, the coherence between these two variables, which could not be confirmed for Scots pine ($r=0.08$), was quite strong.

4 Discussion

Investigations of forest yield for Scots pine and Ponderosa pine at the study site by Insinna et al. (2006) showed that the species had developed differently over the last 100 years under almost identical growing conditions. They demonstrated that Ponderosa pine clearly exceeds Scots pine in all growth parameters, culminating in over 60% bigger stem volume at the (sample) tree level. Additionally, crown dimensions were distinctively higher in Ponderosa pine than Scots pine (Insinna et al. 2006). Insinna et al. (2007) quantified a needle dry mass for Ponderosa pine double that of Scots pine. Foliage parameters have proven to be suitable bioindicators for environmental (exogenous) factors, especially when the needle trace method is applied (NTM, Kurkela and Jalkanen 1990). The results of this technique therefore provide important indications for comparing the growth behavior of two tree species by revealing differences in the climatic impact on needle parameters. The high-frequency signals of the NTM parameters determined by Insinna et al. (2007) are significantly different, indicating that

the needle parameters of both pines are influenced by diverse climate variables. Since the limiting factor (Schweingruber 1983) for the study site is water, primary attention was paid to its availability through precipitation and groundwater connection as well as indirectly through the temperature conditions influencing transpiration.

The results of the response and correlation functions show that for both Scots pine and Ponderosa pine, many distinct correlations exist between climate variables from the previous year and the needle parameters (Table 1). This is due to the fact that needle primordia are formed in the new buds during the previous growing season (Gruber 1987, 1991). Ponderosa pine is much more sensitive than Scots pine and shows distinctly more significant climate factors – a result already mentioned by Insinna et al. (2006) in connection with the analysis of tree-ring width. For this reason, Ponderosa pine seems to react much more complexly and flexibly to exogenous factors. The finding that after increased rainfall, the total (absolute) number of needles (TOTAL), annual needle retention in summer (RET), and mean needle age (AGE) all show a decreasing trend was unexpected (Insinna et al. 2007). Pensa and Jalkanen (2005) found the same relationship in Finland and Estonia, where temperature rather than precipitation is the limiting factor. Under improved growing conditions, i.e. in higher thermal sums at these sites in northern Europe (Fennoscandia), an increase in needle shed of older and unproductive needles in order to increase the proportion of productive needles was noted (Pensa and Jalkanen 2005). At the same time, TOTAL and RET are partly controlled by needle production. But as this information is already formed in the previous growing season, it appears plausible that the total number of needles is reduced, as PROD can no longer react to needle shed induced later in the year. However, for conditions similar to those in Brandenburg, Rebetez and Dobbertin (2004) recorded antithetical results for the dry inner-alpine valleys in Switzerland. With the aid of reference photographs, they assessed the defoliation of Scots pine over several years using the method specified by Müller and Stierlin (1990) and reported a clear decrease in foliation due to continuous warming. However, due to the resulting reduced vitality, the impact of drought has

also been identified as a precursor for nematodes and bark beetles (Rebetez and Dobbertin 2004). Therefore, the reasons for the decrease in needle retention observed are very complex and cannot be reduced to climatic factors alone.

Annual height increment (HEIGHT) and needle density (DENS) are partially interdependent and mainly determined by the spring and summer precipitation levels of the previous year (Insinna et al. 2007). DENS and especially HEIGHT react very strongly to precipitation and are therefore good indicators of water stress, as confirmed in the literature (Tingey et al. 2000, Dohrenbusch et al. 2002). As for the other needle parameters, more significant predictors were found for Ponderosa pine than for Scots pine, supporting the assumption that Ponderosa pine is more sensitive.

The cross-correlations support the results of the response function. In addition, the influence of groundwater level (GLEV) appears to be just as important for both tree species at the dry site of Bralitz as precipitation. For both Scots pine (Köstler et al. 1968, Skilling 2005) and Ponderosa pine (Ryan et al. 2000, Williams et al. 2001), taproot depths of up to 5–10 m are indicated. The groundwater, at a depth of approximately 12 m, is therefore not reached directly. Nonetheless, its indirect use through suction-based ascension is apparent, for example, from DENS, which is known to be sensitive to climatic variables, especially drought (Jalkanen and Levanic 2001, Salminen and Jalkanen 2004). Confirming the results of the response functions, Scots pine seems to profit more than Ponderosa pine from better water supply, i.e. higher groundwater levels. Further investigations focusing on the impact of GLEV are therefore suggested.

As shown, significant and biologically plausible relations between water availability and needle parameters can be detected by means of response functions and correlation analyses (Table 2). The correlation coefficients and the coefficient of determination (R^2) for the predictors of response functions are, however, much lower in comparison with other studies (Sander 1997). An explanation may be the number of sample trees aligned with much younger specimens in the investigations (Aalto and Jalkanen 1998a). Due to the appearance of trunk damage, which was not externally apparent when the trees were selected, the rep-

lication of individual chronology sections is in some cases reduced, i.e. not always covering five single curves (Insinna et al. 2007). In these ranges, the signal-to-noise ratio (SNR) can drop significantly, while the proportion of variance attributable to climatic factors (Fritts and Swetnam 1989) decreases, which can in turn impair the results of the calculations. Increasing the sample size with trees over 100 years old to a minimum of 8–10 per species is therefore suggested.

Nevertheless, it is astonishing – particularly for the important factor of needle production (PROD) – that the previous year's June temperature alone (indirectly indicating drought) was proven to be a significant predictor. This has prompted consideration of other exogenous factors. The influence of the sun on vegetation was investigated and confirmed long ago (Fabre 1905). In dendroecology, a link between the number of sunspots as a measure of solar activity (Eddy 1976) and the radial increment has been hotly debated (Douglass 1919, LaMarche and Fritts 1972, Mori 1981, Murphy and Veblen 1992), although the correlations have not been completely clarified. But as the data leading to the identification of such links mainly originate from dry sites, it is not surprising that correlations were found between “sunspot cycles” and the occurrence of drought periods (Currie and O'Brien 1988). At the study site, however, a correlation between radial growth and sun activity was not confirmed, even though Douglass (1919) described a synchronism for the Eberswalde region concerning the number of sunspots and radial increment.

As the short shoots of the leader axis are always exposed to direct sunlight, there is still a need to clarify whether sun activity explains needle production and possibly other needle parameters, such as TOTAL or RET. In fact, it appears that it is not the number of sunspots but the sun cycle length (SCL) that positively correlates with the needle production of current shoots (PROD) of Ponderosa pine (Fig. 6). This means that high solar activity (low SCL values) leads to the formation of fewer needles on dry sites. The extent to which the radiation energy itself has a decisive influence on PROD can only be speculated upon at this stage. It is, however, known from the literature that sun needles have a larger diameter than shade needles due to their greater mesophyll mass

and higher chlorophyll content (Lyr et al. 1992, Schulze et al. 2002). It is thus conceivable that under changed radiation conditions, sun needles could react by increasing chlorophyll content in order to reduce the total number of needles in the respective crown layers. This reduction would lower the transpiration surface and constitute an adjustment to dryer conditions.

The results therefore show that at the Bralitz site, water is the decisive control factor for most needle parameters; the type and temporal occurrence of individual factors partly differ significantly between the tree species. This clearly contrasts with the results from the northern/alpine tree line, where water is sufficiently available. At these sites, it is primarily temperature and temperature sum that have a decisive influence on radial increment (Schweingruber 1988, Briffa et al. 1990) as well as on needle parameters (McCarroll et al. 2003) or the height increment (Salminen and Jalkanen 2006). The initial hypothesis that differences exist in climate sensitivity between the tree species Scots pine and Ponderosa pine can therefore not be rejected. In fact, Ponderosa pine, while having a larger needle mass, reacts significantly more sensitively to existing environmental conditions than Scots pine, thereby underlining its high fitness at dry sites.

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