ADAPTABILITY OF RADIAL GROWTH OF NORWAY SPRUCE TO CLIMATE VARIATIONS: RESULTS OF A SITE-SPECIFIC DENDROECOLOGICAL STUDY IN HIGH ELEVATIONS OF THE BLACK FOREST (GERMANY)

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ABSTRACT. We quantify the effects of climate variations on radial growth of Norway spruce (*Picea abies* (L.) Karst.) and interactions between growth and site conditions. Radial growth data are derived from cross-section analysis. The sampling sites were selected pairwise to compare extremes in the available moisture capacity of the soil. A network of long-term synoptic meteorological data has been assembled from climatic stations of the German Weather Service. Cross-correlation analysis of unwhitened and prewhitened chronologies is used for selection of influential variables and for identification of transfer function models. The general transfer function model is incorporated into time varying coefficient models that are calculated with Van Deusen's DYNACLIM (1992) software. Material from all sites shows close inverse correlations with potential evapotranspiration from April to June and close direct correlations with the climatic water balance during July and August of preceding years. This was unexpected because, on average, precipitation is high and air temperature is relatively low in the study sites. Persistence in growth responses is more pronounced in chronologies of older than of younger trees. We interpret the lagged growth response to climatic inputs in terms of phenological adaptation by successive partial adjustment of tree vitality to changing environmental conditions.

INTRODUCTION

In addition to fundamental interest in tree growth–climate relations, unfavorable climatic conditions have periodically triggered waves of case studies involving growth and climate. At the end of the 1970s, regional and larger-scale growth declines of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.) were observed predominantly in higher elevations of mountainous areas such as the Black Forest. Research on this "new forest decline" syndrome produced a multitude of hypotheses that have been partially successful in explaining some potential causes of the observed decline symptoms, but that also gave rise to a number of controversies concerning its causes and the question of its lack of precedence (Landmann 1989). We realize now that interpretations based on short-term observations remain unreliable, and that deeper insight into the underlying mechanisms cannot be expected until there is a long-term basis for calibrating the findings. In order to represent characteristic timescales of tree growth dynamics, investigations have to consider at least several decades.

The Dendroecological Approach

Taking the place of monitoring needle-loss status of trees, dendroecological studies are proving to be objective and efficient tools for long-term retrospective analysis of tree vitality and tree growth responses to changing environmental conditions. Earlier studies have shown that drought can induce several years of reduced growth in silver fir and Norway spruce, even at elevations where precipitation sums are high and air temperatures are relatively low on average during the vegetative period (Becker 1989; Spiecker 1986, 1987, 1990, 1991c). Besides meteorological factors that cause drought stress, site characteristics, in particular available moisture-storing capacity (AWC) of the soil, have to be taken into account when investigating tree growth responses to drought. To study the effects of drought on radial increment with respect to the AWC of the soil, we selected study sites with large differences in AWC in high elevations of the Black Forest.

Retrospective dendroecological studies over long timescales are restricted to comparative rather than (manipulative) experimental strategies. However, the dendroecological comparison of sample

Tree Rings, Environment and Humanity, edited by
J. S. Dean, D. M. Meko and T. W. Swetnam. RADIOCARBON 1996, pp. 785–801

trees from different site types can be regarded as a quasi-experimental approach in environmental research (Cook and Campbell 1979).

The Model-Based Approach

Instead of being steady, site and growth conditions change constantly with time (Spiecker 1986, 1987, 1991a, 1991b, 1992). Visser (1986), Van Deusen (1987a, 1987b, 1989, 1991) and Visser and Molenaar (1988, 1992) helped to establish methodological prerequisites for quantitative analyses by introducing time-varying coefficient models. Several subsequent tree-ring studies based on Kalman filter techniques (Cook and Johnson 1989; Innes and Cook 1989; LeBlanc 1993; Spiecker 1992; Stolte *et al.* 1992) reflect the interest of the scientific community in adopting these instruments.

However, there is an ongoing critical discussion of both the formal (Eriksson 1989) and conceptual (Innes and Cook 1989) appropriateness of these models in tree-ring research, and alternative model formulations have been suggested (Yue 1993). The conceptual criticism is especially directed at the lack of basic ecophysiological knowledge able to explain and interpret time-varying tree growth environment relationships on process-based levels (Arbaugh and Peterson 1989; Mayer and Schmidt 1991).

Fundamental characteristics of the system under investigation (tree growth in the environment) can be expressed in terms of complex adaptive systems theory (Ford and Milne 1981; Holland 1992; Kaufmann 1990):

- Phenological adaptation – trees evolve through time in order to improve their ability to survive environmental stresses. Adaptive processes cover a continuous range of different timescales. In the context of drought-induced responses of radial growth, modificative phenological adaptation is of primary interest. Modificative adaptation is medium-term and mainly structural, in contrast to short-term modulative, mainly physiological acclimatization and long-term evolutionary, genetic adaptation (Larcher 1980).
- Aggregate behavior – behavior of the whole system is not simply derived from the actions of the metabolic, structural or functional units. In experimental studies, Bloom, Chapin and Mooney (1985) found that plants are plastic in their allocation pattern, and that the degree of flexibility depends on resource availability. Plants from resource-rich environments generally show highly plastic allocation patterns, whereas those from resource-poor environments show less flexible ones. Most frequently the interactions of the plant parts are thought to seek optimality. But it is uncertain whether optimality for the whole can be defined at all (Kaufmann 1990; Ulrich 1991).

One of the most important reasons for the use of model-based approaches in plant growth research is that models establish formal statements about the hypothetical mechanisms underlying the system under consideration. Therefore they should be consistent with *a priori* knowledge, explain observations, and identify fields in which sufficient knowledge is lacking and improvement is needed (Landsberg 1981). Statistical models permit the comparison of alternative models and model building approaches and serve for parametrization of model equations.

DESCRIPTIVE BACKGROUND

Study Area and Sampling Design

Study sites were selected in the southern Black Forest at elevations between 800 and 1160 m above sea level (m asl). Underlying geology is composed of periglacial solifluction deposits predominantly of gneissanatexites. Typical soil type is "Braunerde" (Inceptisol Umprept). Because of medium to poor soil cation saturation, suboptimal needle Ca and Mg nutrition is widespread in this area (Buberl, von Wilpert and Hildebrand 1994; Ferraz 1985). According to Müller and Oberdorfer (1974), the potential natural vegetation type (hypothetical plant society without anthropogeneous disturbances) is small-scale mixed ***Luzulo-Fagetum*** with ***Abies alba*** and ***Abieti-Fagetum***, and in elevations above 1100 m asl, ***Luzulo-Fagetum*** with ***Picea abies***. Today Norway spruce occupies about 50% of the public forest land in the Black Forest.

In order to minimize variability in growth due to silvicultural treatment and mesoclimate, one study site pair in each of eight ecologically similar forest stands (silvicultural treatment units), consisting of one study site with higher AWC (site type HAWC) and one study site with lower AWC (site type LAWC) were selected. On each of these site types, groups of five dominant trees without visible stem and crown injuries or anomalies were sampled in a next-nearest-neighbor process, for a total of 75 sample trees (from one stand only site type HAWC was selected). Table 1 presents descriptive statistics for the sample trees.

TABLE 1. Descriptive Statistics for the Sample Trees Stratified in Two Site Types According To Available Soil Moisture Storing Capacity

Site type*	Statistic	Age (yr)	Height h_{A50}† (m)	Diameter d_{A50}† (cm)	h/d_{A50}‡
LAWC	Min	54	12.3	12.6	48
	Max	148	28.5	37.6	98
	Mean	99	18.3	24.1	77
	s	29.4	4.4	5.9	12.1
	n§	35	34	35	34
HAWC	Min	54	14.9	15.2	53
	Max	166	28.7	44.1	99
	Mean	99	21.1	29	74
	s	28.9	3.9	6.9	10.5
	n§	40	38	40	38

*Sample trees from sites with lower (LAWC) and with higher available moisture storing capacity (HAWC)

†Dimension at reference age of 50 yr

‡Height-diameter-ratio, indicating tree social status

§Number of observations

The study forest stands are uneven aged (with respect to the species), vertically structured, single tree to groupwise mixed spruce forests with *Abies alba* Mill. and *Fagus sylvatica* L. as the main associated species. The stands were managed in a group-selection system.

AWC was determined in a relative classification scheme using the standard, regionally based, site mapping method applied in the public forests of Baden-Württemberg on a microsite, single-tree level. On the local level the method is mainly based on the mapping of (in order of importance):

- the type of soil substrate
- the maximum mechanical soil penetrating depth of a soil boring tool (measured in decimeters),
- the type of herbaceous vegetation (categorial scale),
- the type of humus layer (categorial scale).

The qualitative AWC classes range from medium dry (LAWC) to medium moist and moist (HAWC). For one site pair (two trees from LAWC and two trees from HAWC sites) quantitative determination of AWC was conducted based on field methods described in Arbeitskreis Standortskartierung (1980) (Fig. 1). Marked differences between the two strata are indicated, amounting to *ca.* 100 mm of moisture storing capacity. The history of the study stands (*e.g.*, stand establishment, volume yield by thinning, mortality (in terms of damaged wood volume) caused by storms and snow damage) was traced back based on recent and old office records.

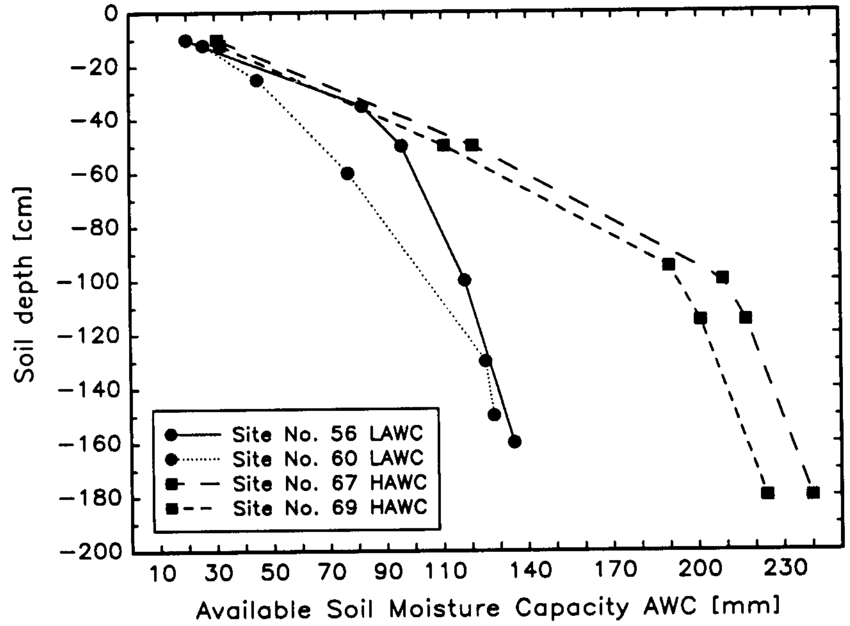

Fig. 1. Available soil moisture storing capacity (*AWC*) in the rooting zone. Determination of AWC was based on field methods, and is presented for four sites (corresponding to four sample trees), representing the two site strata (lower (*LAWC*) and higher (*HAWC*) available moisture storing capacity, respectively). Marked differences between the two strata are indicated, which amount to *ca.* 100 mm of moisture storing capacity.

Tree-Ring Measurement, Crossdating and Standardization

Trees were selected in summer and autumn of 1991. Cross-sections (thickness *ca.* 5 cm) of felled trees were collected at a height of 1.3 m, air-dried and sanded. Tree rings were visually crossdated using marker rings and annual radial increment (IR) was measured with a semiautomated device to the nearest 10^{-2} mm along eight radii, oriented according to the azimuth, on each cross-section. Crossdating was verified by analyzing cross-correlations between-radii (with lags of ±2 yr) of shifted 50-yr periods (in 25-yr steps), in first differences of log-transformed annual IRs (Van Deusen 1987a), using Van Deusen's XCHECK software (1992). Indicated dating errors (95% level) were checked visually on the cross-sections. Two radius measurements had to be verified by remeasurement. Some partially missing (on some radii on a cross-section) but no totally missing rings were found.

The measurements of the eight radii were averaged using the biweight robust mean (Cook 1985; Mosteller and Tukey 1977) to obtain a mean radial increment sequence, called tree chronology.

In order to reduce low- and medium-frequency variations in the tree chronologies due to age and dimension related growth trends as well as those due to changing competitive status and (probably) changing site conditions, the tree chronologies were detrended on an individual tree basis prior to the dendroclimatic analysis using the stochastic trend model discussed in Visser and Molenaar (1990) and Van Deusen (1991). Estimation is based on prediction error decomposition using the Kalman filter technique. An example is shown in Figure 2.

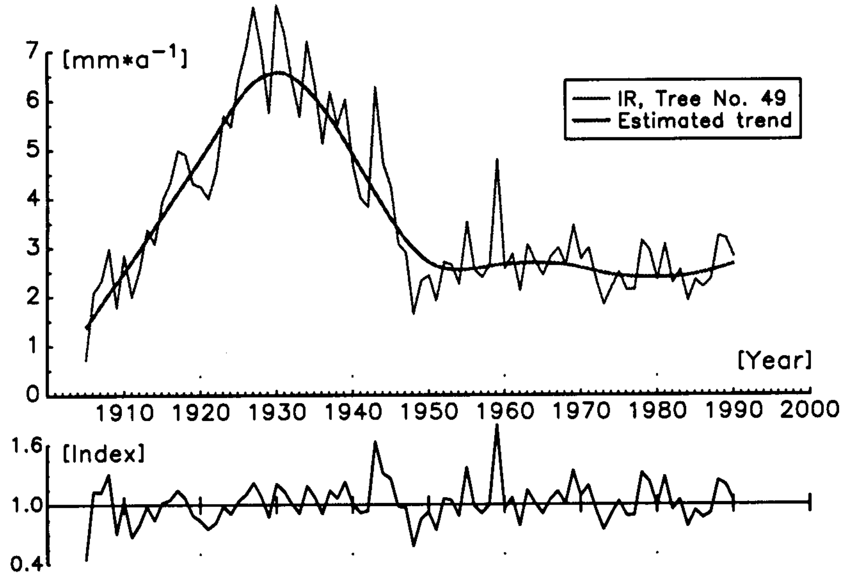

Fig. 2. Detrending with the "stochastic trend model". The stochastic trend model produces rather flexible trend estimates (Fig. 2, upper graph). Radial increment indices were calculated as ratios between observed and estimated values (Fig. 2, lower graph).

The stochastic trend model produces rather flexible trend estimates that may eventually absorb some of the low-frequency climatic signals (Fig. 2, upper graph). Its advantages, however, lie in its objective and data-adaptive control of the flexibility of the estimated trend, being high when common signal is low and *vice versa*.

Radial increment indices were calculated by dividing the observed and estimated values, and pooled to obtain mean index chronologies, which serve as response variables in the dendroclimatic regression analyses. Chronology sequences were stratified according to the AWC into a chronology consisting of trees from sites with lower AWC (*LAWC-C*) and into a chronology consisting of trees from sites with higher AWC (*HAWC-C*). Based on the hypothesis that even after detrending remaining age-related differences in growth responses could be detected, an additional stratification was undertaken with regard to tree age at sampling date, with those trees ≤80 yr in age forming strata *Y* (young trees; $n_{LAWC\text{-}Y} = 10$, $n_{HAWC\text{-}Y} = 10$ sample trees), those between 80 and 120 yr forming strata *M* (medium aged trees; $n_{LAWC\text{-}M} = 15$, $n_{HAWC\text{-}M} = 21$ sample trees), and those older than 120 yr forming strata *O* (old trees; $n_{LAWC\text{-}O} = 10$, $n_{HAWC\text{-}O} = 9$ sample trees). *E.g.*, stratum *HAWC-CM* represents the mean index chronology formed by 80–120-yr-old trees from HAWC sites.

Analysis of Intra-Tree Variation in Radial Increments

Since stem inflections caused by storms initiate development of reaction wood (*e.g.*, compression wood; Timell 1986a, 1986b), we hypothesized that part of the inter-radii variation of the IR-series may be due to the occurrence of reaction wood and therefore may reflect storm events in the past. The directional asymmetry of the annual radial increments is expressed in terms of the IR_{max}-ratio, which is defined as the percentage of the maximum radial increment among the eight measured radii in a given year to the mean radial increment of all the eight radii in this year.

Climate Data Preparation

Monthly data of air temperatures and precipitation sums at climate stations located within a radius of 50 km around the center of the study sites in the southern Black Forest were obtained from the German Weather Service (18 climate stations for air temperature data and 27 stations for precipitation data). In order to obtain homogeneous and local specified climate data, the data had to be preprocessed in a two-step procedure that included homogenization and spatial interpolation. The test of homogeneity and adjustment of inconsistencies in the data series was based on standard climatological methods (Buishand 1982; Chang and Lee 1974; Craddock 1979), whereas the "Karlsruhe" and "Freudenstadt" (Rhine Valley and Black Forest, respectively) series were used as basic reference stations (Schönwiese, Malcher and Hartmann 1990). Monthly data of each series that had missing observations within the observation period from 1900 to 1990 were "reduced" in a stepwise procedure using regression analysis on maximum overlap periods (Paesler 1983).

Single-station climate data may reflect site specific conditions. Pooling the data may reduce this location bias, but extrapolation to remote, high-elevation forest stands is still a critical task, especially because of forest stand and topographic position effects (König and Mayer 1990). Therefore spatial interpolation was calculated based on second-order polynomial trend surface analysis (Ojansuu and Henttonen 1983; Ripley 1981) using the stations' location data (longitudinal, latitudinal and elevational coordinates) as input data.

In order to derive physiologically more meaningful variables, the monthly climate data are transformed into potential evapotranspiration (ETP) and climatic water balance (WBP), which are calculated based on Thornthwaite's formulae (Thornthwaite and Mather 1955). These climate variables are used as predictor variables in the dendroclimatic regression analyses (Arbaugh and Peterson 1989; Mayer and Schmidt 1991). The ETP-variable was included because transpiration of trees can be reduced when ETP is high, even when soil water supply is not constrained (Gross and Pham-Nguyen 1987). Figure 3 shows the courses of WBP for the vegetative period (May–September; Fig. 3, upper graph) and for the period from July to August (Fig. 3, lower graph).

Dendroclimatic Analyses

Selection of Influential Climate Variables

Cross-correlation analysis was used for selection of influential climate variables. Because contemporaneous as well as lagged correlation coefficients were inflated through autocorrelation in the univariate time series, serial correlation has to be taken into consideration. In order to minimize pitfalls of spurious correlations in screening for influential climate variables, the individual univariate series of climate as well as tree-ring variables were transformed into white-noise processes (prewhitened) based on Box and Jenkins (1970) autoregressive moving average (ARMA) models using the ARMA procedure of Aptech Systems GAUSS™ (1994) (Ans 1976; Guiot 1986; Guiot, Berger and Munaut 1982; Henttonnen 1984; Monserud 1986; Yamaguchi 1986). The cross-correlation function

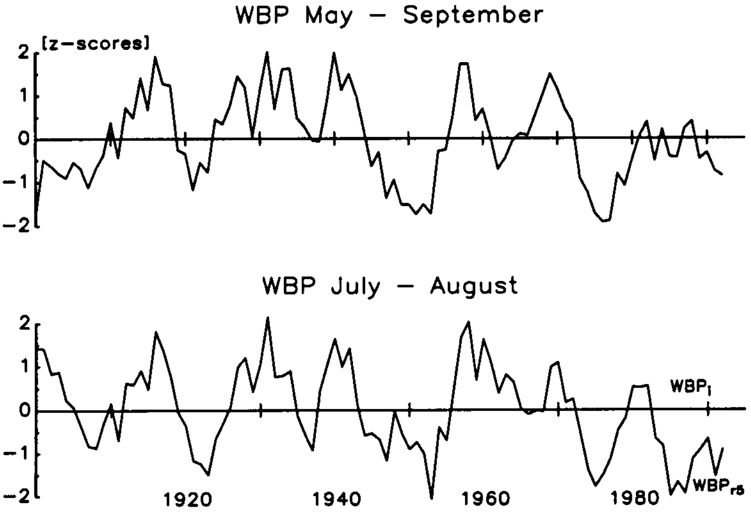

Fig. 3. Courses of climatic water balances (WBP). The solid lines represent annual (*WBP$_i$*), the dotted lines smoothed (*WBP$_{r5}$*) values of *WBP* as average values of the vegetative period (upper graph) and of July–August (lower graph). A causal five-year running average has been used as smoothing function. This filter is not zero-phase, but exclusive consideration of past observations is physiologically more meaningful. Data were standardized to a mean of 0 and a standard deviation of 1 (z-scores). The severe water deficiencies in the early 1920s and during the period 1944–1955 were interrupted by several years lasting positively balanced periods. On the other hand, the dry period during 1973–1980 was immediately followed, without major relaxation, by the most extreme moisture deficiencies since the beginning of this century starting in 1983.

was calculated with the prewhitened mean residual chronologies and with prewhitened bimonthly averages of ETP and WBP of the period April to September including lags up to four years. Subsets of the best correlated climate variables were selected for subsequent modeling of the dynamic association of bivariate time series based on transfer function analysis.

Model Specification

The bivariate time series (tree variables with each of the selected climate variables) possess a triangular relationship, implying that the tree data depend on their own past (autoregressive component) and on the present and past of the climatic input. The long-term, growth trend–related part of the autoregressive structure in the tree data has been removed through detrending. The remaining autocorrelation in the indices is therefore thought to be predominantly controlled by exogeneous driving forces, like delayed responses to climatic inputs. In order to represent growth-climate relationships in the "final" or "distributed lag" form (without using lagged growth data as predictor variables; *e.g.*, Harvey 1981), the contemporaneous and time-delayed associations of unwhitened bivariate time series was used to determine the length and the shape of the impulse response function (the number and weights of the causal running average filter to be applied to the climate data) (Bennett and Chorley 1978; Box and Jenkins 1970).

Kalman Filter Analyses

Regression models with time-varying regression coefficients were calculated using Van Deusen's DYNACLIM software (1992). For a full discussion of the Kalman filter theory see Harvey (1984,

1989) and, including a description of the algorithms used in this study, Van Deusen (1991). Some aspects deserve brief mention here. The Kalman filter is a recursive procedure for calculating the optimum (minimum mean square error) estimator of the state space vector at time *t*, using information up to time *t*. The filtering problem is solved via prediction error decomposition. Once all observations have become available, optimal estimates of unobserved components can be made by smoothing, which yields an estimation of the evolutive paths of the varying parameters through time. The hyperparameters (those controlling the temporal evolution of the varying parameters) follow stochastic processes. Because of the desired discounting of past observations, the parameter variations were modeled as random walk plus noise processes, which are therefore allowed to drift through time and, in contrast to random coefficients time paths, may behave in a nonstationary maner.

RESULTS

Analysis of Intra-Tree Variation

Figure 4 shows the courses of the IR_{max}-ratio (percentage of the maximum radial increment among the eight measured radii in a given year to the mean radial increment of all the eight radii in this year) and the mortality in terms of volume of damaged wood in the study stands caused by storms (DW_{storm}). In order to become stationary, the IR_{max}-values had to be detrended using a regression line (the IR_{max}-indices are the residuals thereof). Both curves are significantly correlated ($r = 0.637$ ($p > |t| = 0.0000$), so that the IR_{max}-values can be regarded as indicators for storm stresses of the sample

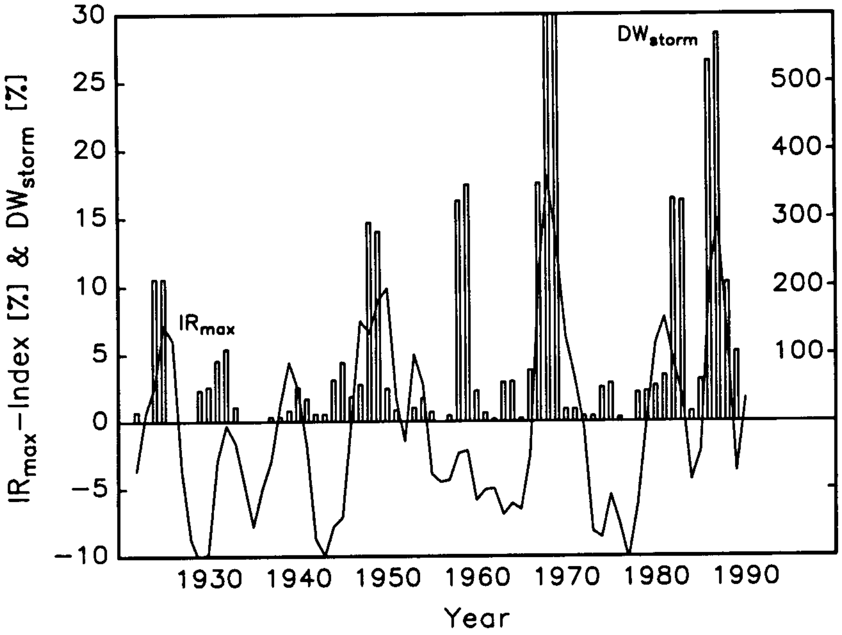

Fig. 4. Asymmetry of the annual radial increments on cross sections compared to the mortality caused by storms. The mean of the IR_{max}-indices of all sample trees ($n = 75$) is compared with the amount of damaged wood caused by storms (DW_{storm}, in units of volume of damaged wood in the study stands in % of the average amount during the period 1922–1990). Both curves are smoothed using a second-order running average filter. They are significantly correlated with $r = 0.637$ ($p > |t| = 0.0000$).

trees. Discrepancies between the IR_{max}- and DW_{storm}-curves in the late 1950s are possibly due to inaccurate records of the damage causes, because heavy snow-breakage damages were observed in the close neighborhood in the years 1957/58 and 1958/59 (Eisenkolb 1963; Volk 1968).

The development of the *IR* along the eight radii is strongly dependent on the azimuthal direction of the radii on the cross-sections. In the period from 1922 to 1990, 75% of the maximum *IR* values were found on the north-east, and 23% on the east-oriented radius. This reflects very well the major storm directions in this area. The comparison of annual maximum and minimum *IR* values on the cross-sections revealed that the differences between these two quantities linearly increase with increasing radial stem dimension. During the period from 1825 to 1990, maximum and minimum *IR* values were inversely correlated (in the average of all 75 increment series with $r = -0.577, p > |r| = 0.0000$).

Dendroclimatic Analyses

Results of Cross-Correlation Analyses

Figure 5 and 6 present results of cross-correlation analyses of prewhitened series.

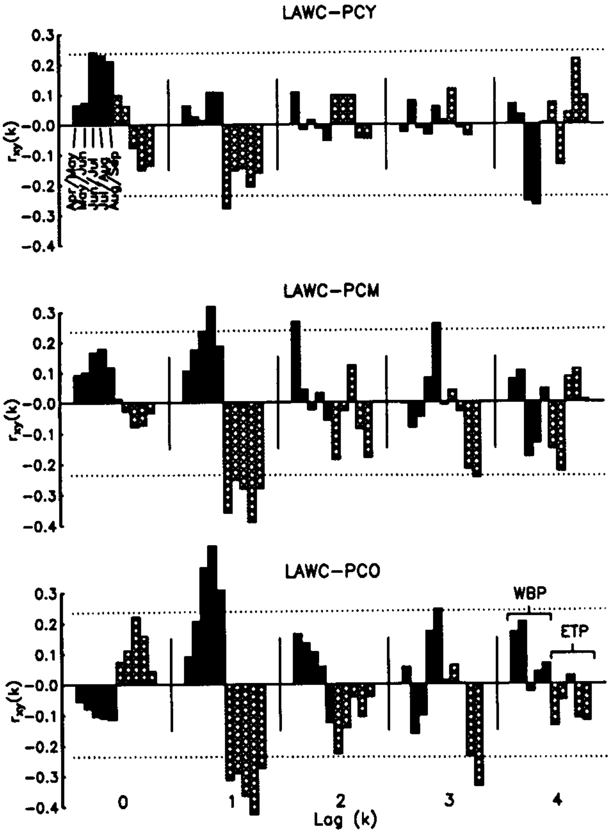

Fig. 5. Cross-correlation analyses between climate variables (water balance *WBP* and potential evapotranspiration *ETP*) and mean index chronologies of trees from sites with lower moisture storing capacity (prewhitened chronologies, *LAWC-PC*), stratified by age classes. Cross-correlation coefficients ($r_{xy}(k)$) for lags (k) from $k = 0$ to 4 yr between prewhitened WBP and ETP (as two-monthly means) and prewhitened LAWC chronologies stratified in three age classes (young Y: n = 10 sample trees, age range: 54–80, mean: 67 yr; medium aged M: n = 15, age range: 82–114, mean: 96 yr; old O: n = 10, age range 128–148, mean: 137 yr) are shown related to the period 1915 + k to 1990 (maximum common overlap period). The dotted lines represent 0.05 significance thresholds. Significant contemporaneous correlations are found between the chronology of young trees (*LAWC-PCY*) and WBP during June and July. Lagged correlations are found for the older strata, positive between WBP and negative between ETP. ETP from April to June and WBP during July and August, both lagged one year, perform best.

The chronology of young trees from sites with lower soil moisture storage capacity is directly correlated with contemporaneous WBP during June and July (Fig. 5). On the other hand, the chronologies of medium-aged and old trees are significantly correlated with one-year lagged WBP (directly;

primarily with that of July and August) and lagged ETP. The finding that lagged correlations were more pronounced in the older chronologies is confirmed through the results represented in Figure 6.

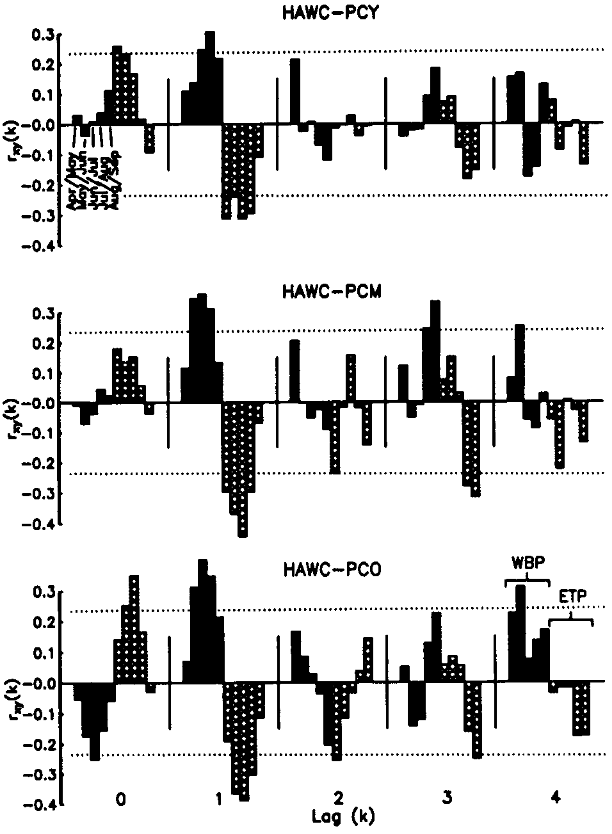

Fig. 6. Cross-correlation analysis between climate variables (water balance *WBP* and potential evapotranspiration *ETP*) and mean index chronologies of trees from sites with higher moisture storing capacity (prewhitened chronologies, *HAWC-PC*), stratified by age classes. Cross-correlation coefficients ($r_{xy}(k)$) for lags (k) from $k = 0$ to 4 yr between prewhitened WBP and ETP (as two-monthly means) and prewhitened HAWC chronologies stratified in three age classes (young Y: n = 10 sample trees, age range 54–76, mean: 67 yr; medium aged M: n = 21, age range: 85–118, mean: 96 yr; old O: n = 9, age range: 122–166, mean: 143 yr) are shown related to the period 1915 + k to 1990. Dotted lines represent 0.05 significance thresholds. Positive contemporaneous correlations are found between the chronologies and ETP during April to July (not significant with *HAWC-PCM*). Lagged correlations are more pronounced with the older collectives. ETP from April to June and WBP during July and August, both lagged one year, perform best.

Comparison of the results for the two site strata (Fig. 5 and Fig. 6) yields several noteworthy points:

- The chronologies of young and old trees from sites with higher moisture storage capacity show significant positive correlations with contemporaneous ETP from April to June and May to July, respectively, whereas those from the other site type do not.
- Significant correlations for WBP and ETP variables lagged up to four years can be found.
- The older the trees, the higher the similarity in the cross-correlative structure between the site strata.

Overall, ETP from April to June (*ETP46*) and WBP during July and August (*WBP78*), both lagged one year, perform best, and show the most consistent associations among the strata.

Dendroclimatic Regression Analyses

From the results of the cross-correlation analyses it was concluded that:

1. The strong lagged associations may reflect adaptive behavior in the trees' responses to climatic inputs. Since prewhitening implies filtering out the dynamic structure of the chronologies (and

therefore makes cross- correlative structures more transparent), modelling of adaptive behavior has to be based on unwhitened series.

2. The growth-climate model can be based on two candidate variables, one covering the early, and the other covering the late vegetative period.

Therefore, the variables *ETP46* and *WBP78* were selected for subsequent specification of the impulse response function based on unwhitened series (Fig.7).

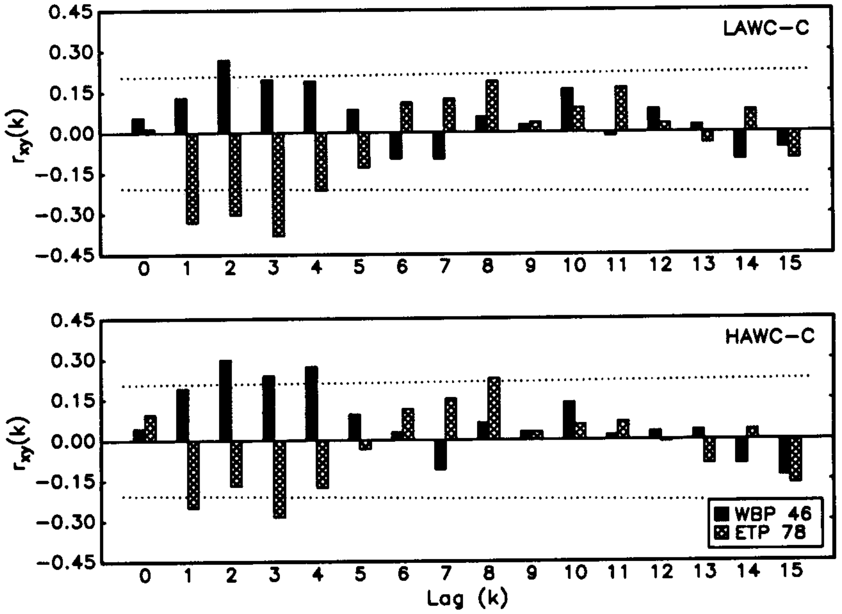

Fig. 7. Specification of lag structure. Cross-correlation analysis between unwhitened site chronologies (*LAWC-C* upper graph; *HAWC-C* lower graph) and unwhitened series of climate variables (water balance from April to June (*WBP46*) and potential evapotranspiration during July and August (*ETP78*)) is performed for specification of the impulse response function (shape and number of lag weights). Lags are in years. Dotted lines represent 0.05 significance thresholds. Analyses are based on the maximum common overlap period 1915 + *k* to 1990.

High values of cross-correlation coefficients can be found for both climate variables in the lag range from 1 to 4 yr. In the range from lag 1 to 5, no sign reverse can be observed. The association between the bivariate series decreases with increasing time delay. This is mainly due to autocorrelation in the chronology series, and the shape of exponentially decreasing correlation coefficients is in fact expected in the presence of a positive *AR*(*1*) process. As will be discussed later, this finding is consistent with the assumption of adaptive behavior of the system under consideration.

For the subsequent dendroclimatic regression analyses, distributed fifth-order lag models with similar geometric lag structures for both input variables (*ETP46* and *WBP78*) and for all site- and age-strata were formulated. Results of the Kalman filter analyses are shown in Figures 8 and 9. The model values not only follow major growth depressions but also increase, when growth accelerates (Fig. 8). The analyses indicate that temporal variation is present for the climate variable *WBP78* (Fig. 9) but not for the variable *ETP46* (not shown). The time-varying coefficients show synchronously increasing trends, with the longer series since the beginning of the century.

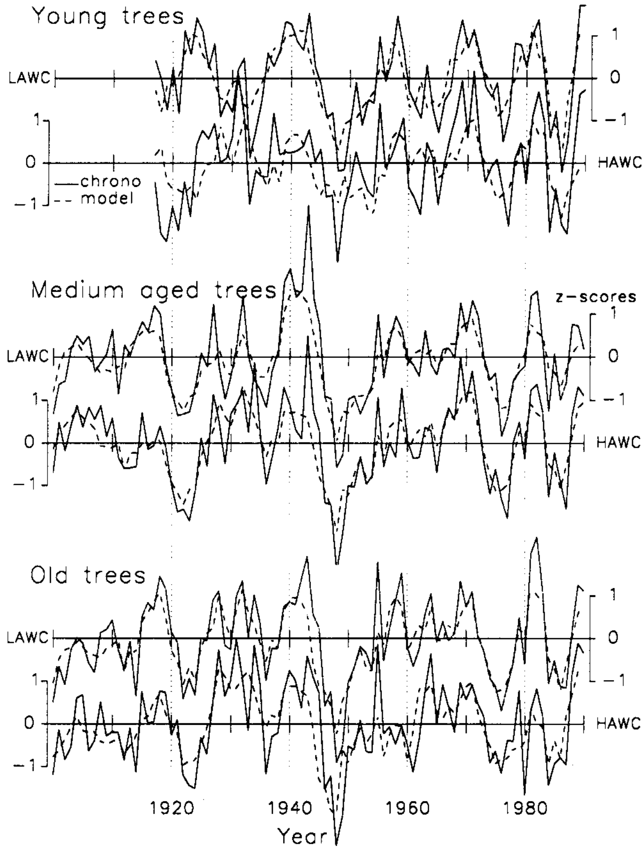

Fig. 8. Growth-climate models. The overall two-variable growth-climate models (dashed lines) (including lagged potential evapotranspiration from April to June (*ETP46*) and water balance during July and August (*WBP78*)) are shown together with the radial growth chronologies (solid lines; *LAWC* resp. *HAWC*: chronologies of trees from sites with lower resp. higher water storing capacity). Data are standardized to a mean of 0 and a standard deviation of 1 (z-scores; this standardization was done before model estimation).

Some goodness-of-fit statistics for the time varying growth-climate models fit to the tree-ring data are given in Table 2. The modified Von Neumann Ratio is only in one case slightly below the 95% limit (*HAWC-Y*), which suggests positive correlation in the prediction errors (Harvey 1989; Van Deusen 1990). The C^* test shows no significant trend as judged by $P(C^*)$, which gives the probability of obtaining a larger absolute value of C^* under the null hypothesis of no trend. The R^2 values are all highly significant. Apart form the exception mentioned above, the fit statistics indicate no particular lack-of-fit problem with the growth-climate models.

DISCUSSION

Time-Delayed Responses of Radial Tree Growth to Climatic Inputs

Lagged radial growth responses of Norway spruces to climatic inputs have been observed frequently, especially following severe droughts (*e.g.*, Krauss 1948; Wiedemann 1925). Quantitative assessment of drought-induced growth depressions with regard to delayed effects was investigated early (Weck 1948), but has virtually been neglected for several years. Bernhart (1963) and Spiecker (1986) referred to Weck's work and confirmed his findings (see also Henttonen 1984; Münster-Swendsen 1984). The phenomenon of lagged growth responses has gained much interest in the dendroecological literature (*e.g.*, Fritts 1976: 193). We here discuss two aspects, 1) its quantitative assessment and 2) its ecophysiological interpretation.

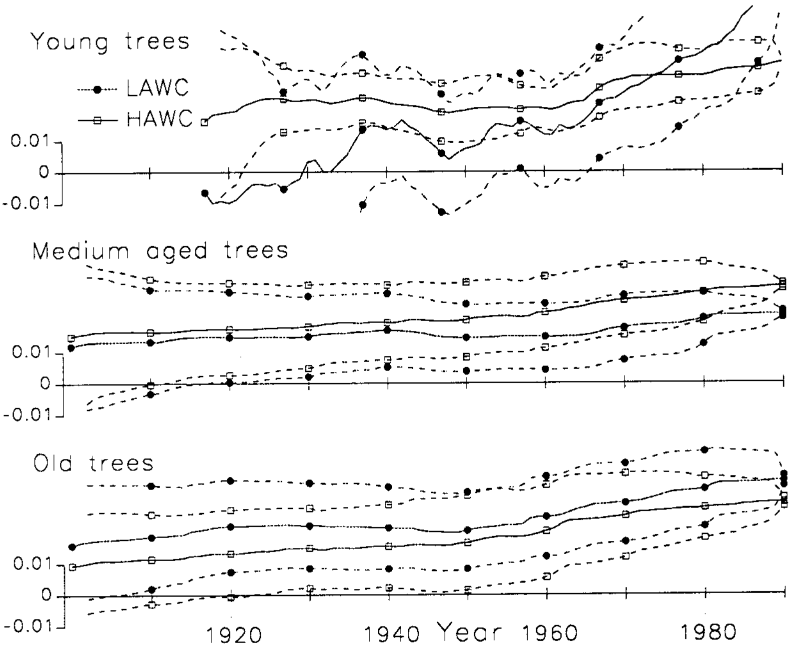

Fig. 9. Time varying model coefficients. The curves of the model coefficients corresponding to the climatic water balance during July and August of the five preceding years (*WBP78*) for the site-/age-stratified chronologies (*LAWC* resp. *HAWC*: chronologies of trees from sites with lower and higher water storing capacity, respectively) are shown, together with the 95%-confidence intervals (dashed lines).

TABLE 2. Goodness of Fit Statistics for the Time Varying Growth-Climate Models Fit to the Tree-Ring Data

Data set*		MVNR†	MVNR 95% interval		C^*‡	$P(C)$	R^2§	DF#
LAWC	Y	1.606	1.525	2.475	0.986	0.328	0.65	70
	M	1.690	1.574	2.426	0.496	0.621	0.71	87
	O	1.824	1.574	2.426	0.664	0.508	0.73	87
	Y	1.385	1.525	2.475	0.537	0.593	0.29	70
HAWC	M	1.801	1.574	2.426	0.134	0.893	0.69	87
	O	2.047	1.574	2.426	1.105	0.272	0.55	87

*LAWC / HAWC: chronologies of trees from sites with lower and higher available moisture storing capacity, respectively; Y = young trees; M = medium-aged trees; O = old trees.

†Modified Von Neumann Ratio (Harvey 1989; Van Deusen 1990). The 95% MVNR confidence interval gives the limits within which model fit is acceptable

‡The C^* test is based on the sum of the standardized prediction errors and indicates misspecification of the model if the probability of a greater absolute value of C^*, $P(C^*)$, is small.

§The R^2 statistic is an analogy to the usual OLS value (Harvey 1989: 268; Van Deusen 1991), but it is possible that adding a variable will reduce R^2.

#Degrees of freedom.

Quantitative Assessment of Lagged Radial Growth Responses

Most tree-ring series exhibit significant autocorrelation, even after major sources of serial correlation have been removed through detrending (*e.g.*, Monserud 1986). Different strategies have been suggested to handle its statistical implications (for more extensive discussions, see Cook 1987; Briffa, Wigley and Jones 1987; Guiot 1986), *e.g.*:

- including lagged dependent variables as predictors, as implemented in Fritts's response function analysis (Fritts *et al.* 1971).
  This procedure fails to clarify responses lagged more than one year. Including lagged dependent variables can mask time delayed responses to climatic inputs and therefore may confuse the interpretations (Blasing, Solomon and Duvick 1984; Guiot, Berger and Munaut 1982).
- prewhitening the dependent (and independent) variable (*e.g.*, Monserud 1986).
  The estimation gained from this procedure is incomplete because it prevents adaptation to be part of the modelled process (Van Deusen 1989).
- prewhitening and recoloring/reddening as suggested by Cook (1985) and Guiot (1986).
  These are very sophisticated methods, but there are still some weaknesses involved, *e.g.*, some kind of subjectivity in determining the "reference period" for specification of reddening coefficients.

With the models described in this study we mainly tried to reduce this complex subject to its main determinants based on well-developed methods in econometric literature. However, the method described here is also affected by some weak points, *e.g.*,

- The cross-correlation analysis reduces the selection of influential variables to the bivariate case without temporal variation, which is a strong simplification of the real underlying mechanisms.
- The relationships between climate variables and growth responses are handled as if they were linear, but it is more likely that they are nonlinear.
- There is some subjectivity in the specification of the impulse response function (its order and shape).

Ecophysiological Interpretation of Lagged Radial Growth Responses

Persistence in tree-ring data has been interpreted extensively by Fritts (1976: 186, 188, 193), and some of its causes may be summarized under physiological preconditioning, which is defined by Fritts (1976: 541) as "the induction of internal metabolic conditions which can influence the biochemical reactions and other processes of a plant during later stages in its life cycle". The external forces inducing these metabolic alterations may either serve as energy sources for the induced processes or may function as signals which trigger certain metabolic mechanisms without being matter or energy sources. Both aspects can well be integrated in an interpretation based on adaptive mechanisms. Therefore the lagged growth responses to variations in air temperature and precipitation regimes may be interpreted as modificative phenological adaptations to changing environmental conditions. Inertia of tree growth response to climatic inputs only allows for partial adjustment to new conditions and therefore results in the long-memory behavior indicated in the presented study.

Temporal Variation of Climate Indices

The time-varying coefficients of the climatic water balance during July and August of the five preceding years show synchronously increasing trends since the beginning of the century (Fig. 9). The following aspects should be considered when explanation of this phenomenon is assessed. Possible causes for the indicated structural changes may be:

1. general or partial misspecification of the growth-climate model, *e.g.*, due to omitted variables,
2. structural changes in the selected input variables themselves, or in their interactions and interrelations,
3. changes in sensitivity of radial growth to variations in climate.

Diagnostic checking of the models revealed that general misspecification is unlikely to be the cause of the observed structural change. However, it remains possible that new exogeneous variables, especially increased atmospheric nitrogen input, may cause higher sensitivity of radial growth to moisture deficits in late summer (Spiecker 1987). In addition, it cannot be excluded that part of the increase in the model coefficients is due to aging effects that are probably not completely filtered out through the standardization process. The unprecedented high frequency of years with extremely warm and dry late summer months (July and August) during the recent decades as indicated in Figure 3 seems to be the most likely cause for the observed structural changes.

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