Recent growth of conifer species of western North America: assessing spatial patterns of radial growth trends

Donald McKenzie, Amy E. Hessl, and David L. Peterson

Abstract: We explored spatial patterns of low-frequency variability in radial tree growth among western North American conifer species and identified predictors of the variability in these patterns. Using 185 sites from the International Tree-Ring Data Bank, each of which contained 10–60 raw ring-width series, we rebuilt two chronologies for each site, using two conservative methods designed to retain any low-frequency variability associated with recent environmental change. We used factor analysis to identify regional low-frequency patterns in site chronologies and estimated the slope of the growth trend since 1850 at each site from a combination of linear regression and time-series techniques. This slope was the response variable in a regression-tree model to predict the effects of environmental gradients and species-level differences on growth trends. Growth patterns at 27 sites from the American Southwest were consistent with quasi-periodic patterns of drought. Either 12 or 32 of the 185 sites demonstrated patterns of increasing growth between 1850 and 1980 A.D., depending on the standardization technique used. Pronounced growth increases were associated with high-elevation sites (above 3000 m) and high-latitude sites in maritime climates. Future research focused on these high-elevation and high-latitude sites should address the precise mechanisms responsible for increased 20th century growth.

Résumé : Nous avons étudié la distribution spatiale des variations à faible occurrence dans la croissance radiale des espèces de conifères de l'ouest de l'Amérique du Nord et nous avons identifié des indicateurs de la variation dans ces patrons. À l'aide de 185 sites de la Banque internationale de données dendrochronologiques, chacun contenant 10–60 séries brutes de largeurs de cernes, nous avons reconstruit deux chronologies pour chaque site en utilisant deux méthodes conservatrices conçues pour conserver toute variation à faible occurrence associée à des changements environnementaux récents. Nous avons utilisé l'analyse factorielle pour identifier les patrons régionaux à faible occurrence dans les chronologies des sites et nous avons estimé la pente associée à la tendance de la croissance depuis 1850 dans chacun des sites, à partir d'une combinaison de techniques de régression linéaire et de séries temporelles. Cette pente constitue la variable de réponse dans une équation de régression qui modélise la réaction de l'arbre pour prédire les effets des gradients environnementaux et des différences entre les espèces sur les tendances de la croissance. Les patrons de croissance dans 27 sites du sud-ouest américain sont consistants avec les patrons quasi périodiques de sécheresse. Selon la technique de standardisation utilisée, 12 ou 32 des 185 sites sont caractérisés par une augmentation de croissance entre 1850 et 1980 A.D. De fortes augmentations de croissance sont associées aux sites situés à haute altitude (au-dessus de 3000 m) et aux sites dont la latitude est élevée en présence d'un climat maritime. Les travaux futurs devraient chercher à préciser les mécanismes responsables de l'augmentation de la croissance au 20e siècle en se concentrant sur les sites situés à haute altitude et les sites dont la latitude est élevée.

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Introduction

Given predictions of climatic variability and projected emissions of greenhouse gases (Houghton et al. 1995; Schlesinger 1997), understanding the spatial and temporal patterns of tree growth in relation to changing environmental

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conditions is crucial for improved estimates of future productivity and species distributions. Recent dendroecological evidence indicates that radial tree growth at many high-elevation and high-latitude sites in the Northern Hemisphere has been increasing since about 1850 (LaMarche et al. 1984; Parker 1987; Briffa 1990; Peterson et al. 1990; Graumlich 1991; Innes 1991; D'Arrigo and Jacoby 1993; Peterson 1994; but see Briffa et al. 1998*a*, 1988*b*). Temperature increases, elevated atmospheric carbon dioxide (CO_2), and nitrogen (N) fertilization in N-limited ecosystems have all been suggested as explanations for increased growth (Innes 1991; Nicolussi et al. 1995; Hättenschwiler et al. 1996), but to date there is no conclusive evidence of a primary mechanism (Graumlich 1991; Innes 1991). In addition, some high-latitude and high-elevation sites have not experienced growth increases (Briffa et al. 1998*a*, 1998*b*), suggesting that the bi-

ological response to changing environmental conditions may vary among species and across spatial scales (Peterson and Peterson 1994; Ettl and Peterson 1995).

The case for increases in growing season temperature as the dominant factor limiting tree growth is based on annual-scale positive correlations between growing season temperature or length of growing season and annual ring widths of some high-elevation tree species. However, over the long term, other factors could become more limiting (Vaganov et al. 1999), or the effects of temperature could become negative when there are sustained temperature increases, particularly in moisture-limited systems. The case for N fertilization is inferred from models that predict increased productivity in N-limited systems (e.g., Aber et al. 1991), but N fertilization has also been implicated in forest decline (Schulze 1989) and reduced growth among conifers (Vitousek et al. 1997; Fenn et al. 1998); thus, predicting a long-term positive response to N fertilization is problematic. The effect of elevated atmospheric CO_2 on tree growth has been the subject of extensive experimental study (Norby et al. 1992; Idso and Kimball 1994; Olszyk et al. 1998a, 1998b; DeLucia et al. 1999; Ward and Strain 1999). There is experimental evidence of short-term increases in photosynthesis and increased growth rates among seedlings exposed to elevated CO_2 (Ward and Strain 1999; but see Olszyk et al. 1998a, 1998b) and enhanced carbon storage in complete forest systems under free-air CO_2 enrichment (FACE) experiments (DeLucia et al. 1999). Elevated CO_2 may increase water-use efficiency in some species, thereby alleviating the stress associated with drought periods (Ward and Strain 1999). This suggests that the greatest response to increasing atmospheric CO_2 might be observed in arid sites.

Although experimental studies inform us about some responses to CO_2, results should not necessarily be extrapolated to the growth response of mature trees, because results to date are based on experimental data from seedlings measured over short periods (Jasienski and Bazzaz 1997; Tissue et al. 1997; Jach and Ceulemans 1999). Similarly, experimental studies do not account for in situ growing conditions of trees, where soil nutrient limitations, competition, and variable climate may interact with or ameliorate the CO_2 effect (Hättenschwiler et al. 1996; but see DeLucia et al. 1999). Finally, experimental studies have examined single-species responses in unique locations (Norby et al. 1992), making it difficult to extrapolate the results to broader geographic areas or multiple species (Eamus and Jarvis 1989; Körner 1996).

Given the variety of environmental factors that affect annual variations in tree growth (e.g., precipitation, snow depth, temperature), CO_2 fertilization, nitrogen deposition, and temperature increases may all play some role in long-term trends. Species may respond differently in different parts of their ranges; thus, broad-scale studies involving multiple species are needed to suggest the geographic breadth of environmental influences. A dominant environmental driver, either of long-term growth increases or multidecadal variation, should be manifest in coherent broad-scale spatial patterns (Innes 1998). For example, if temperature increases are mainly responsible for long-term trends, then these trends should be clearest at those high-elevation and high-latitude sites at which temperature clearly limits growth. If CO_2 fertilization is mainly responsible, then trends should be clear at all sites, at high-elevation sites where partial pressure of CO_2 is reduced (LaMarche et al. 1984) or at sites with significant moisture stress where CO_2 fertilization may increase water-use efficiency (Tolley and Strain 1985; Ward and Strain 1999). More complex patterns would suggest interactions among environmental drivers, species-specific responses, or the predominance of local versus regional effects.

Although some studies have established regional-scale associations between climate and tree growth, these have addressed patterns occurring at decadal or shorter time scales and primarily focus on climatic reconstruction (e.g., Brubaker 1980; Briffa et al. 1988; Cook and Cole 1990; Meko et al. 1993; Woodhouse 1996; Hughes and Graumlich 1996). In this paper, we investigate low-frequency growth trends among western North American conifer species between 1850 and 1980 A.D., focusing on the trends and variation in tree growth over multidecadal to century-long time scales. Our objectives were to quantify the spatial patterns of low-frequency variability in radial growth and to identify species-level differences and geospatial variables (e.g., elevation, longitude, latitude) that explain the variability in these patterns. If coherent, regional patterns of increased tree growth exist among multiple species, further research could uncover mechanisms responsible for these observed increases in growth by linking tree-ring records to coarse-scale models of CO_2 fertilization or increases in temperature or N deposition.

Methods

Data compilation

We selected site chronologies for conifer species from the International Tree Ring Data Bank (ITRDB) (ITRDB 1999) that met the following criteria: (i) sites are located in western North America (United States and Canada); (ii) individual tree-ring series are at least twice as long as the period (130 years) analyzed (Cook et al. 1995), and (iii) individual series extend to at least 1980 A.D. (only a small subsample of the series extends past 1980). Some chronologies (19) included in this study were originally collected in conjunction with studies of disturbance caused by insects. However, these chronologies were all taken from stands of nonhost trees (e.g., *Pinus* species) located near, but not inside, stands affected by insect-caused disturbance (Lynch and Swetnam 1992; Swetnam and Lynch 1993; Wickman and Quigley 1992) and were probably not influenced by the disturbance events. There were 185 sites in western North America that met the selection criteria.[2] The chronologies for these sites contained single-species tree-ring measurements for between 10 and 60 individual cores. The most common species included in the analysis was ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.; 46 sites), followed by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; 24 sites) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.; 20 sites) (Table 1). Eleven of 24 species were represented by fewer than 5 sites. Al-

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[2]Detailed information about the sites is available from the authors or may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

Table 1. Summary of species and sites represented by tree-ring records extracted from the International Tree Ring Data Bank.

Species code	Species	No. of sites	Elevation (m)		Latitude (N)		Longitude (W)	
			Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
ABAM	*Abies amabilis* Dougl. ex Forbes	4	840	1560	46°09′	57°42′	122°09′	130°00′
ABLA	*Abies lasiocarpa* (Hook.) Nutt.	2	1825	2000	48°44′	48°45′	120°38′	120°39′
JUOC	*Juniperus occidentalis* Hook.	10	800	2731	37°17′	44°54′	116°48′	121°48′
LALY	*Larix lyalli* Parl.	3	1925	2050	48°42′	48°44′	120°39′	120°39′
LAOC	*Larix occidentalis* Nutt.	1	1800	1800	48°42′	48°42′	118°20′	118°20′
PCEN	*Picea engelmannii* Parry ex. Engelm.	20	1530	3700	35°26′	53°20′	105°02′	120°40′
PCGL	*Picea glauca* (Moench) Voss	7	600	1400	54°54′	63°40′	110°58′	149°35′
PCSI	*Picea sitchensis* (Bong.) Carrière	6	5	459	55°01′	60°31′	130°05′	149°30′
PIAL	*Pinus albicaulis* Engelm.	1	2050	2050	48°41′	48°41′	120°38′	120°38′
PIAR	*Pinus aristata* Engelm. in Parry & Engelm.	5	3535	3660	35°35′	39°38′	104°59′	111°40′
PIBA	*Pinus balfouriana* Grev. & Balf.	6	2460	3505	36°27′	40°02′	118°13′	122°52′
PICO	*Pinus contorta* Dougl. ex Loud.	2	2850	3000	37°10′	37°48′	118°28′	119°15′
PIED	*Pinus edulis* Engelm. in Wisliz.	7	1377	2225	32°56′	35°05′	105°39′	111°49′
PIFL	*Pinus flexilis* James	6	1200	3400	38°46′	51°10′	104°58′	114°40′
PIJE	*Pinus jeffreyi* Grev. & Balf. in A. Murr.	4	1975	2280	35°26′	36°43′	118°11′	118°53′
PILO	*Pinus longaeva* D.K. Bailey (= *Pinus aristata* var. *longaeva*)	9	2590	3475	36°16′	40°33′	111°04′	118°13′
PIMO	*Pinus monophylla* Torr. & Frem. in Frem.	8	1996	2347	37°46′	41°03′	114°11′	119°40′
PIPO	*Pinus ponderosa* Dougl. ex. Laws.	46	738	2896	32°12′	45°58′	104°52′	117°58′
PIST	*Pinus strobiformis* Engelm. in Wisliz.	1	2441	2441	32°13′	32°13′	110°33′	110°33′
PSMA	*Pseudotsuga macrocarpa* (Vasey) Mayr.	6	1400	1600	33°59′	34°16′	116°45′	117°17′
PSME	*Pseudotsuga menziesii* (Mirb.) Franco	24	267	2950	31°27′	48°20′	105°16′	124°00′
THPL	*Thuja plicata* Donn ex D. Don	2	560	700	49°32′	49°32′	123°02′	123°02′
TSHE	*Tsuga heterophylla* (Raf.) Sarg.	1	980	980	46°21′	46°21′	122°05′	122°05′
TSME	*Tsuga mertensiana* (Bong.) Carrière	4	1020	2550	40°27′	49°25′	121°31′	125°14′
	All species	185	5	3700	31°27′	63°40′	104°52′	149°35′

though the pattern of increased growth in the 20th century has been described for some of these sites, many sites were originally used for reconstructing interannual climatic variability or for other dendroecological purposes. As a result, the original standardization procedures (sensu Fritts 1976) did not necessarily maintain low-frequency trends in many of the original chronologies, and long-term trends in growth were not reported.

Standardization

A principal use of tree-ring data is to model growth responses to short-term (annual to decadal) climatic variation. Thus, low-frequency variation (at multidecadal and longer scales) is typically removed from tree-ring time series by any of a number of detrending procedures, and the residual series are examined for correlations to climatic variables (Cook et al. 1990). Detrending procedures are designed to remove both the biological growth signal of the tree and confounding responses to disturbance. Although these procedures are a fundamental part of tree-ring analysis, they may remove other low-frequency signals of interest (Briffa et al. 1996). The more flexible detrending methods, such as locally weighted regression (LOESS) or nonparametric splines (Cleveland et al. 1988; Cook et al. 1990), are particularly efficient at removing long-term trends. We used two conservative techniques, traditional detrending (TD) and no detrending (ND) to identify low-frequency variation since 1850. These techniques preserve the low-frequency variability expected to be associated with recent environmental change while removing the biological growth trend. Detrending was performed on each individual core from each site. The first technique (TD) uses widely accepted dendrochronological procedures for standardizing time series (Cook and Kairiukstis 1990). In the second technique (ND), the growth trend is removed only where its effects are extreme. Although each detrending approach

has shortcomings, we expected that the two methods would over- and under-estimate recent growth increases, respectively, thereby providing a range within which actual growth increases should fall.

Traditional detrending (TD)

Individual tree ring series from each core were detrended using either a modified negative exponential curve or a linear regression with negative slope or slope equal to 0, using the ARSTAN module from the ITRDB program library (Grissino-Mayer et al. 1996). This approach removes a long-term "biological" growth trend (Briffa 1990) but may exaggerate positive trends for recent decades because of the shape of the imposed model. Thus, we expected that this method would overestimate the number of sites with growth increases. Individual series were standardized to unit variance and divided by their means, then averaged to form site chronologies. The 185 site chronologies for the years of interest were combined into a model data base.

No detrending (ND)

For the ND analysis, we did not attempt to remove the biological growth trend through curve fitting, to avoid exaggerating recent positive trends. Instead, we used a species-specific approach to identify the portion of each tree ring series (core) that is not significantly influenced by the biological growth trend. For each species, we selected one to four sites in a quasi-random fashion (some species are represented by only one site). For each core, we extracted a time series of the first 200–400 years of growth (depending on species longevity), regardless of start date. These series were temporally aligned (assumed to start and end at the same time), and the means for each "year" combined into an average series representative of the site and species. The resulting series were examined graphically for a "flattening" of the biological growth trend,

using a stiff LOESS curve (Cleveland et al. 1988). LOESS fits a series of regressions along subsets of a scatterplot. The regressions are weighted based on distance from the center of the subset. A qualitative estimate (rounded to 50 years) of the threshold age after which the biological growth trend was no longer significant was then made for each species.

At each site, trees younger than the threshold age in 1850 were not included in building ND site chronologies. The number of trees per site was thus reduced from 0 to 20%, depending on species longevity; however, a minimum of five trees was included for all sites. This approach does not necessarily remove the entire biological growth trend, thereby muting rather than amplifying recent positive trends. Thus, we expected this method to underestimate the number of sites with growth increases.

Data analysis

The output from both the TD and ND analyses was used to identify broad-scale spatial patterns in the low-frequency response to environmental conditions. Identical analyses were performed on the TD and ND data, with the objective of creating a range of estimates of growth increases.

We used factor analysis (Rencher 1995) to establish similarities among site chronologies and to identify underlying growth patterns common to multiple sites. Factor analysis, sometimes referred to as "rotated principal components" (Richman 1986), may reveal "factors," or underlying patterns (often assumed by authors to be surrogates for mechanisms) that may contribute to the variation in a multivariate data set and has been used to uncover correlations between tree growth and biophysical variables (e.g., Peterson and Peterson 2001). Factor scores can also reveal low-frequency variation. Only consistent, interpretable factor analysis results are reported here.

We used classification and regression trees (CART; Breiman et al. 1984) to model the magnitude of growth trends at each site as a function of geospatial variables (latitude, longitude, elevation) and species. CART is a nonparametric alternative to linear models when relationships among variables are complex and nonadditive, and where factors (e.g., species) have many levels (Clark and Pregibon 1992). CART, or "tree-based," modeling uses binary recursive partitioning based on reduction in deviance to split the data into increasingly homogeneous subsets. We used an adaptive estimation method (Breiman et al. 1984) to minimize the complexity of each model (number of branches and nodes) without sacrificing goodness of fit. This method first fits an overly large tree, then uses a cost-complexity criterion to "prune" branches that do not contribute significantly to the reduction in deviance (Breiman et al. 1984).

Factor analysis

In factor analysis, the number of factors must be chosen in advance (Rencher 1995), so we ran preliminary trials on subsets of the data, which suggested that two interpretable factors were appearing consistently. Therefore, the number of factors extracted from all subsequent runs was restricted to two. Because estimation in factor analysis is based on the covariance matrix of the data, the number of observations must be greater than the number of variables to maintain nonsingularity (Rencher 1995). We had fewer observations (131 years) than variables (185 sites), so we used a resampling approach in which factor analysis with an orthogonal (varimax) rotation was performed 20 times, each time on a random selection of 100 sites from the original 185. Factor scores were compared among the 20 runs to determine whether the factor estimates were consistent and, therefore, robust.

Factor loadings were used to evaluate the strength of the association between each variable and the factors. However, the total number of appearances of each site varied (binomial expected value ≈ 11, variance ≈ 5) because of the resampling approach.

Therefore, we identified thresholds based on the total appearances for each site to determine whether sites "loaded high" on each factor. For a site to load high on factor 1, it had to load higher than 0.6 in 90% of its appearances in factor analyses. For a site to load high on factor 2, it had to load higher than 0.5 in 90% of its appearances, because the proportion of variance explained by factor 2 was expected to be lower. These thresholds are conservative compared with factor loadings that have been interpreted as significant in a number of published analyses.

We identified common characteristics of all sites loading high on each factor, and the mean factor scores for all 20 analyses were plotted over time to identify low-frequency patterns in regional tree growth. Sites that consistently loaded high on each factor were also used to identify the spatial extent represented by each factor.

CART models

We used the slope of the growth trend for the period 1850–1980 as a response variable. This slope was estimated by a linear regression of the annual growth index on the year. (Years were normalized to [0,1] to adjust slope coefficients into a range in which they could be compared easily.) We did not compute significance levels of slope parameters in these linear regressions, because we only needed the unbiased estimates of slope to use as our response variable in the CART models. However, because observations of the response variable (a time series) were correlated, we also fit autoregressive models of order 2 (AR(2)) to each annual growth index. This type of model assumes that responses from year to year are correlated and uses the two previous years' responses as predictors for the current year (Brockwell and Davis 1996). Correlations between fitted values from the regression and AR(2) models were used as qualitative indicators of confidence that the estimates of slope parameters by linear regression were not compromised by autocorrelation in the response variable.

Using these slopes as responses in a CART model, we identified predictor variables that could differentiate among sites with respect to the magnitude and direction of growth trends. The initial set of predictors included latitude, longitude, elevation, and species (an unordered factor with 24 levels). "Marked" growth increases or decreases predicted by the regression tree model were identified by examining histograms of the predicted slopes for sharp discontinuities on either side of zero. Geographic coordinates of the sites were imported into a point coverage in ARCINFO. Maps were generated that highlighted sites with high loadings on any of the important factors identified in the factor analysis.

Results

Standardization

For the TD data, detrending techniques varied among species. For example, most ponderosa pine series were fit by a negative exponential function, but series from high-elevation sites, with a less consistent biological growth trend, could often be fit only by a horizontal line through the mean (Table 2). For the ND data, the cutoff age (by 1850) for inclusion in a site chronology was 100 years for most species but 200 years for some long-lived and slow-growing species such as the bristlecone pine variants (*Pinus aristata* Engelm., *Pinus longaeva* D.K. Bailey), and foxtail pine (*Pinus balfouriana* Grev. & Balf.). These cutoff ages still permitted a minimum of five trees for each site chronology.
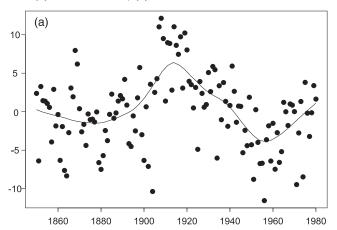
Factor analysis

Comparison of the 20 factor analyses of the TD data indicates that the factor estimates were consistent and robust. All 20 runs produced similar scores for the first two factors;

Table 2. Summary of procedures used for the two detrending methods by species.
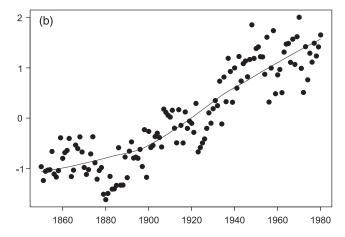
Species	Total no. of cores	TD data			ND data
		Negative exponential	Linear regression (negative slope)	Line through mean	Years of biological growth trend removed
ABAM	94	44.7	31.9	23.4	100
ABLA	76	9.2	44.7	46.1	50
JUOC	559	54.0	25.0	20.9	100
LALY	212	35.4	24.1	40.6	50
LAOC	24	75.0	4.2	20.8	100
PCEN	790	50.5	25.3	24.2	100
PCGL	174	30.5	33.3	36.2	150
PCSI	104	32.7	26.0	41.3	100
PIAL	36	55.6	25.0	19.4	200
PIAR	136	55.1	10.3	34.6	200
PIBA	139	56.8	12.2	30.9	200
PICO	45	68.9	17.8	13.3	100
PIED	363	59.0	31.4	9.6	100
PIFL	347	52.2	29.1	18.7	100
PIJE	153	74.5	22.2	3.3	100
PILO	219	34.2	11.9	53.9	200
PIMO	308	63.3	28.6	8.1	100
PIPO	1322	69.7	23.7	6.6	100
PIST	36	63.9	30.6	5.6	100
PSMA	157	45.2	31.8	22.9	100
PSME	814	64.3	23.8	11.9	100
THPL	18	72.2	0.0	27.8	200
TSHE	15	6.7	13.3	80.0	50
TSME	122	50.0	33.6	16.4	150
Total/mean	6263	51.0	23.3	25.7	

Note: For the TD data, individual cores were detrended by three methods. Column entries are the percentage of total cores for that species detrended by each method. For the ND data, the earliest years of each core were removed, the amount depending on species. See Table 1 for species codes.

Fig. 1. Means of factor scores, with flexible LOESS smoother plotted over time, from the 20 iterations of factor analysis on the TD data: (*a*) factor 1 scores; (*b*) factor 2 scores.
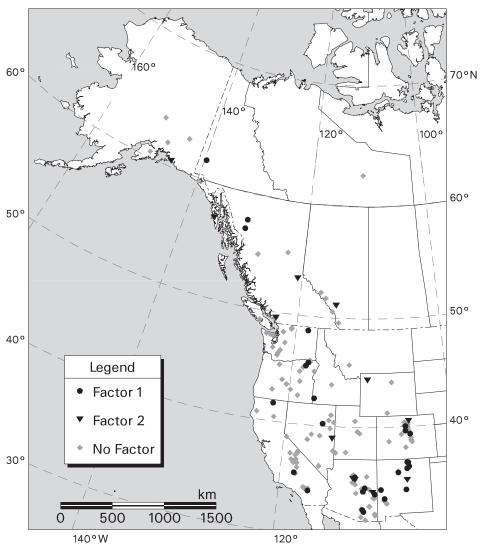

mean factor scores are shown in Fig. 1. In addition, factor loadings of each chronology are consistently either high or low; most chronologies either load highly on a factor more than 90% of the time or less than 10% (see Methods). Of the total 185 chronologies, 27 load high on factor 1. Chronologies that load highly on factor 1 are mostly ponderosa pine and Douglas-fir chronologies collected at moderate elevations from the Southwest. Only 12 of 185 chronologies, taken from high elevation and some maritime high-latitude

sites, load high on factor 2. Thus, 146 sites are not represented by either factor. The cumulative variance explained by the first two factors is similar (26–29%) in all 20 runs. Geographic patterns of high loadings on both factors are clustered, with high loadings on factor 1 in the Southwest, and high loadings on factor 2 in the Great Basin, southern Rocky Mountains, and several locations along the Pacific coast (Fig. 2).

When plotted over time, the TD factor scores reflect two

Fig. 2. Sites with high loadings on factors 1 and 2 (TD data).

low-frequency patterns of variation of tree-ring growth (Fig. 2). Factor 1 exhibits variability at multidecadal time scales, whereas factor 2 represents consistently increasing growth over the length of the period analyzed, with increasing short-term variability between 1950 and 1980.

For the ND data, factor estimates were not consistent over the 20 analyses. For both factor 1 and factor 2, two patterns of factor scores, in addition to the patterns evident from the TD data, emerged from the 20 runs, although the pattern we identified as factor 1 from the TD analysis was recognizable as either factor 1 or factor 2 in all the 20 iterations. We assumed that factor estimates from these data were not robust, and clearly no interpretation was possible from the means of 20 runs. This lack of robustness highlights the sensitivity of tree-ring analyses to detrending methods; the difference between the factor analysis results may be somewhat an artifact of the difference in detrending procedures (see Discussion). We include results from only the TD data in interpreting the factor analysis and linking them to results from the CART models.
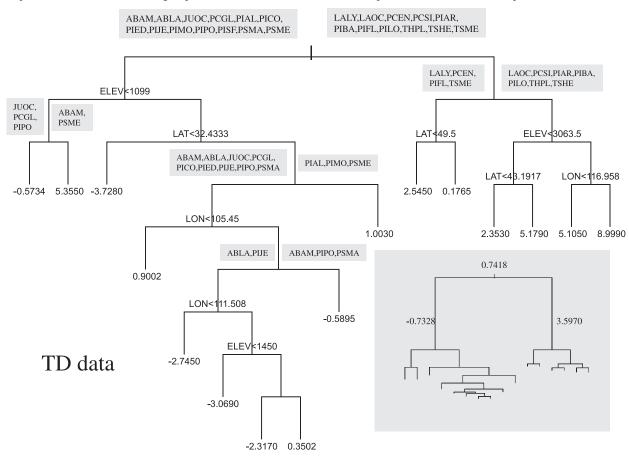
CART models

For both the TD and ND data, species, latitude, longitude,

and elevation are significant predictor variables. Proportional reduction in deviance (PRD, roughly equivalent to R^2) is 0.48 for the ND data and 0.50 for the TD data. For both data sets, the primary partition occurs on species and constitutes almost half the variance explained for both models (Figs. 3 and 4). This partition almost completely separates sites with predicted negative growth from those with predicted positive growth. There are notable exceptions, however, in which species generally associated with negative slopes are positive in a particular range of other predictors, and vice versa. For example, in the TD model low-elevation Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and Douglas-fir sites are predicted to have positive slopes (Fig. 3, left branch, left sub-branch), and in the ND model six species within a narrow longitudinal range are predicted to have negative slopes (Fig. 4, right branch, left sub-branch).

Standard diagnostics (quantile-normal plots and skewness and kurtosis statistics) revealed that the distributions of predicted slopes ($n = 185$) from both models were approximately normal, although slightly positively skewed. We therefore identified the sites whose predicted slopes were more than two standard deviations away from the mean pre-

Fig. 3. Regression tree model for the TD data. Predicted values for a site are obtained by moving down the tree and branching left at a split if the plot meets the condition represented by that split, or branching right if it does not. The insert shows the proportional deviance explained at each branch, and group means for all sites and for the first partition. See Table 1 for species abbreviations.

diction (corresponding to sites outside a 95% confidence interval for the mean). These sites were the same as those showing "marked" growth increases or decreases identified by histograms (see Methods).

The TD model predicts that more sites will have positive slopes (increasing growth) than the ND model (Fig. 5). The TD model predicts marked or significant growth increases (positive slopes) for sites at high elevations and for sites with a combination of high latitude and low elevation (Fig. 5). The ND model identifies similar areas in environmental space with growth increases but is more conservative, predicting fewer sites with significant growth increases, although the high-elevation – low-latitude sites predicted to have positive slopes are the same for both models (Fig. 5).

Predicted slopes for the two data sets are strongly positively correlated (Pearson's $R = 0.81$, $p < 0.0001$). Factor 2 loadings for the 185 sites are also strongly correlated with predicted slopes from the CART model for the TD data (Pearson's $R = 0.70$, $p < 0.0001$). Mean loadings on factor 2 for sites with positive predicted slopes from the CART models were 0.45 and 0.48 for the TD and ND data, respectively. In contrast, mean loadings for insignificant slopes were 0.13 and 0.20 and for negative slopes were –0.15 and –0.05. Thus, we conclude that there is broad-scale spatial correspondence between predicted positive slopes and high loadings on factor 2, although individual sites often differ. For
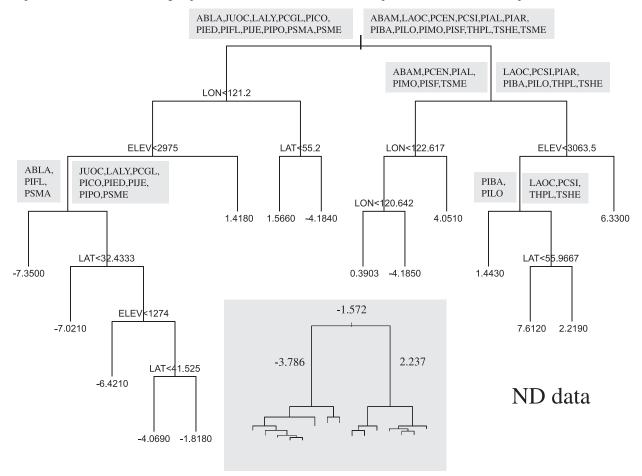
both ND and TD data, all sites above 3000 m elevation have positive predicted slopes (Fig. 5) and for both data sets, the greatest predicted growth increases are from high-elevation, low-latitude sites and low-elevation, high-latitude (maritime) sites.

Mean factor 1 scores, representing mainly sites from the southwestern United States display a quasi-periodic pattern (Fig. 1a). The scores corresponding to the period 1895–1980 are strongly correlated with the Palmer drought severity index (PDSI) (Pearson's $R = 0.59$, $p < 0.0001$) for the Southwest region (33°N, 108°W) over the same period. Cross-spectral analysis (Bloomfield 1976) of the combined time series reveals a strong coherence between factor 1 and PDSI at a period of 8–9 years (Fig. 6). The coherence spectrum of two time series is the analogue in spectral analysis to a correlation coefficient computed at each frequency, except that it explicitly accounts for autocorrelation in the two time series.

Discussion

There are two significant temporal patterns of tree growth in western North America corresponding to factors 1 and 2 (TD data only): a decadal to multidecadal signal associated with Southwestern sites and a much lower frequency signal associated with high-elevation and high-latitude, maritime

Fig. 4. Regression tree model for the ND data. Predicted values for a site are obtained by moving down the tree and branching left at a split if the plot meets the condition represented by that split, or branching right if it does not. The insert shows the proportional deviance explained at each branch, and group means for all sites and for the first partition. See Table 1 for species abbreviations.

sites (Fig. 2). The two temporal frequencies represented in factors 1 and 2, along with previous research on short-term variability in tree growth (Fritts 1966; Jacoby and D'Arrigo 1989; Hughes and Graumlich 1996; Cook et al. 1999), suggest that associations between tree growth and environment exist at multiple temporal scales in western North America.
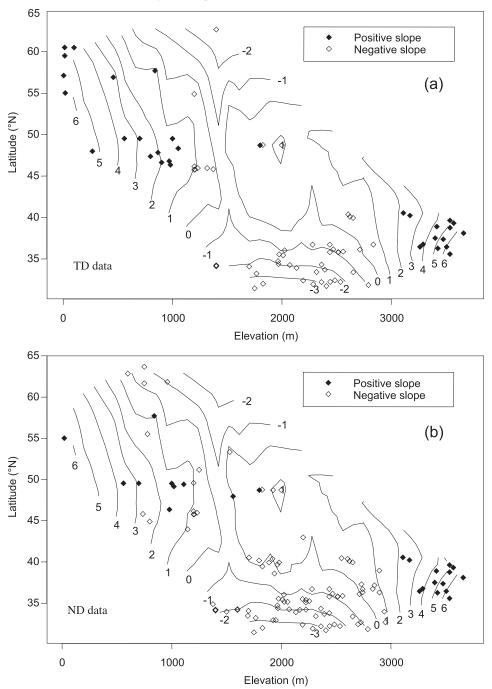
The conservative thresholds we established for factor loadings in our resampling technique meant that a minority of sites in our data base (39 of 185) were identified as associated with the two factors and, therefore, with regional-scale temporal patterns of growth. In our analysis, the benefits of a larger sample were traded for greater confidence that the observed patterns were real. In an exploratory analysis such as this one, the primary objective is the identification of clear patterns in the data, rather than increased power of statistical inference.

High loadings on factor 1 for Southwestern U.S. tree-ring sites (TD data set), and the strong association of factor 1 mean scores with PDSI, suggest that this factor represents growth-limiting environmental conditions (drought) in the Southwest. Other southwestern chronologies that do not load high on factor 1 are probably less influenced by this low-frequency, broad-scale pattern and may respond more to local climatic conditions. For species sensitive to cool-season precipitation in the Southwest, Swetnam and Betancourt

(1999) observed a period of slow growth between 1942 and 1957 and an unprecedented increase in tree growth following the mid-1970s. They attribute the period of slow growth to a drought in the Southwest during the 1950s and the recent period of increased growth to an unusual string of El Niños and associated high precipitation that occurred between 1976 and 1998. The pattern of slow growth during the 1950s, followed by large increases in growth during the 1970s, is reflected in the temporal pattern of our factor 1 scores.

The regional coherence of growth with drought in the Southwest is not surprising given previous studies and exemplifies decadal to multidecadal temporal variability in the association between tree growth and environment. In contrast, the pattern of increasing growth during 1850–1980 for other chronologies suggests long-term, unidirectional changes in environmental conditions that are favorable for tree growth. Both the factor analysis (TD data) and the CART models (both TD and ND data) identify consistently increasing growth at high-elevation, mostly arid sites, and at mid- and high-latitude maritime sites. By using two techniques for removing the biological growth trend in the tree-ring series, we demonstrated consistent patterns of increasing tree growth at multiple locations that are independent of the standardization procedure. The best estimate of a linear approximation
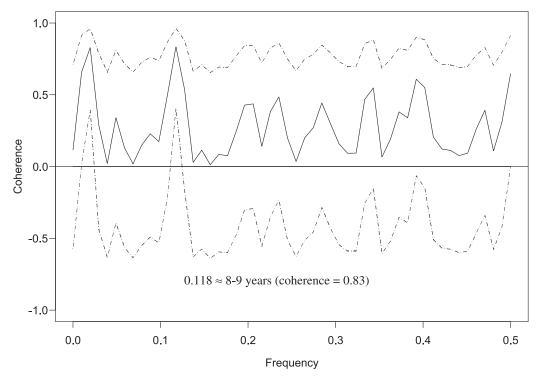
Fig. 5. Smoothed contours of predicted slopes from the CART models, and locations of sites with significant (more than two standard deviations from the mean) positive and negative slopes, in the two-dimensional space of elevation and latitude: (*a*) TD data; (*b*) ND data. Species with positive slopes were *Pinus aristata, Pinus longaeva,* and *Pinus balfouriana* (both data sets, high elevation and low latitude), and *Picea sitchensis*, *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, and *Abies amabilis* (both data sets, low elevation and middle to high latitudes). Species with negative slopes from TD data were *Pinus ponderosa*, *Pinus jeffreyi*, and *Pseudotsuga menziesii* (low latitude) and *Picea glauca* (high latitude). For the ND data, these species plus *Pinus flexilis*, *Juniperus occidentalis*, and *Picea engelmannii* (low to middle latitude) had negative slopes.

of the growth increase (slope) and number of chronologies demonstrating a growth increase likely lies somewhere between the estimates generated from the ND and the TD models. The spatial pattern of increasing growth is similar in both the ND and TD models, with the same high-elevation, low-latitude sites identified and, to a lesser extent, the same low-elevation, high-latitude sites (Fig. 5). Species differences are clearly important in determining the nature of growth responses (primary partitions in Figs. 3 and 4), although some species evidently respond differently in different regions. For example, Douglas-fir at middle elevations in the Southwest show a negative response, whereas even after

Fig. 6. Coherence spectrum, with 95% confidence bands, of factor 1 (mean scores) and PDSI for the American Southwest (1895–1980). The coherence spectrum of two time series is computed from the smoothed periodograms of the individual series and is the analogue in the frequency domain to the cross covariance in the time domain. Thus, it functions like a correlation coefficient that takes autocorrelation into account.

$0.118 \approx 8\text{-}9 \text{ years (coherence} = 0.83)$

liberal detrending (TD data, Fig. 6), they show a neutral-to-positive response at low elevations in the Pacific Northwest. Site-level variability may be responsible for different responses within a single species. For example, variable growth responses for Douglas-fir have been found in British Columbia where trees on a moist site experienced increased growth in the 20th century, while trees on drier sites did not demonstrate any increases (Parker 1987).

Although the trend observed in factor 2 scores and the results of the CART models strongly suggest that tree growth at high-elevation and some high-latitude sites increased during 1850–1980, the mechanisms responsible for this increase cannot be inferred directly from the spatial and temporal patterns observed here. In many of these locations, climate-related variables (e.g., mean annual or seasonal temperatures, mean annual or seasonal precipitation or snowpack, growing-season length) are correlated with short-term variability in tree growth (e.g., Jacoby and D'Arrigo 1989; Peterson and Peterson 2001; Luckman et al. 1997). However, extrapolation to long-term climatic forcing would be unwise, even though mean global temperatures increased during the period we studied, because climate influences growth over multiple temporal scales and may have delayed influences (Fritts 1976). Similarly, although mean temperatures have increased globally, local and regional temperatures have not always followed this pattern (Houghton et al. 1995). Furthermore, for particular species and sites, temperature-related growth increases may be sustainable only for short periods before other factors become limiting (Briffa et al. 1998*b*; Vaganov et al. 1999).

Previous studies have postulated that trees growing on

high-elevation, arid sites may respond positively to the effects of elevated CO_2 (LaMarche et al. 1984; D'Arrigo and Jacoby 1993), although this may be confined to individuals with distinct morphological traits (e.g., strip-bark bristlecone pine; Graybill and Idso 1993). The paucity of sites with high loadings on factor 2 indicates that on most sites in western North America CO_2 fertilization is not a reasonable explanation for increased growth. Low-elevation, maritime (moist) sites also appear to be responding to changing environmental conditions with increased growth, indicating that more than one mechanism may be responsible for similar patterns in growth.

In this study, we identify regional-scale patterns in tree growth based on a variety of coniferous tree species and a variety of sites. The data included in this analysis were collected chiefly for dendroclimatic reconstructions of annual climate, but the criteria for site and tree selection varied among studies. Consequently, our results should not be considered representative of all tree growth across geographic regions but should be considered the response of sensitive trees often growing at their environmental limits. By standardizing and detrending the data sets in a consistent manner, we hoped to eliminate some of the unique growth responses associated only with individual sites. However, some sites that demonstrate a growth increase since 1850 may still be responding to site-specific factors; therefore, the results should be interpreted at a broad spatial scale and not used to make site-specific predictions.

The explanatory power of our models is typical of coarse-scale investigations that include many species and cover a broad geographic range (e.g., Ohmann and Spies 1998;

McKenzie et al. 2000); however, it may indicate that environmental change produces a strong signal in only some populations. The unexplained variation and chronologies without high loadings on either factor suggest that site-specific factors are responsible for much of the variability in mid- and long-term growth. The increased variance in factor 2 in recent years (Fig. 2) also suggests multiple influences on growth.

We were unable to compare factor analyses from the ND data to those from the TD data, because the analyses from the former were inconsistent and, therefore, nonrobust and certainly unsuitable for comparisons of mean factor scores. The ND data included all 185 sites, but cores from younger trees were excluded from many sites. We suspect that the ND method may not have completely adjusted for a biological growth trend even in older trees, that the effectiveness of the method was substantially different for different cores, or both. As a result, the long-term growth signal (factor 2, TD data) may have been muted sufficiently so as not to appear consistently as one of the two factors in the ND analysis. This suggests that, although results from the TD factor analysis correspond well to those from the CART models, any analysis of low-frequency variation in tree-ring time series will be sensitive to the detrending methods used. Further research into the sensitivity of analytical methods (e.g., factor analysis, or response function analysis for reconstructions) is needed.

Some regions of western North America are well represented in the ITRDB (e.g., Southwest), whereas others are poorly represented (e.g., high-latitude, non-maritime sites); inclusion of more sites from the latter category might produce other significant patterns or otherwise influence the models. However, even with the uneven representation of regions, our analysis identifies multiple temporal scales of growth–environment interactions. The mechanisms associated with variability in growth may differ with both the spatial and temporal scales of observation (Innes 1998) and with the confounding of climatic signals by the artifacts of tree-ring standardization (Briffa et al. 1996).

Many tree-ring series in the ITRDB end by the 1980s, leaving current growth rates unknown. Briffa et al. (1998a, 1998b) observed a decoupling of tree growth from regional climate between 1970 and 1990, and Vaganov et al. (1999) observed a recently reduced sensitivity to temperature at high latitudes. Clearly, no monotonically increasing climatic variable can continue to positively influence growth indefinitely, because physiological limits will intervene. Empirical models of changing, interacting environmental influences on growth (e.g., Visser and Molenaar 1992), along with more mechanistic approaches, will improve our predictions of broad-scale changes in vegetation patterns. Tree-ring chronologies from high-elevation, high-latitude or arid sites are particularly valuable for understanding the response (in terms of biomass, carbon fixation, etc.) of vegetation to climatic and environmental variability and can serve as an indicator of how vegetation may be responding to directional changes in the atmospheric environment. Now that sites with long-term growth trends have been identified, these sites could be revisited at 5- to 10-year intervals to provide current information on the response of vegetation to climatic and environmental changes. Future research on these "responsive" sites in relation to local climate and CO_2 may provide new insights into the mechanisms responsible for the spatial and temporal patterns of growth described here.

Acknowledgments

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