QUATERNARY RESEARCH 26, 232–243 (1986)

Red Spruce Tree-Ring Widths and Densities in Eastern North America as Indicators of Past Climate

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Received March 5, 1985

Dendroclimatological studies in eastern North America are enhanced by the use of long-time series of maximum latewood densities determined by x-ray densitometry. The densities show higher correlation from tree to tree and site to site than do ring-width measurements from the same trees. Based on the macroclimatic link thus implied, maximum density and width series of *Picea rubens* Sarg. from high elevations in Maine are used to reconstruct up to 310 yr of past spring temperatures at nearby climate stations. The regression equations explain from 33 to 47% of calibrated variance, and verification testing of the reconstructions produces highly significant correlations and high, positive reduction of error statistics. The climate–wood density relationships are considered in light of tree physiological factors that may explain them. Results from this study are applicable to (1) an increased understanding of the relationship of climate to the formation of wood density and (2) further development of paleoclimatological and paleoenvironmental studies via tree rings in mesic regions such as northeastern North America. © 1986 University of Washington.

INTRODUCTION

Tree rings have been useful as proxy sources of climatic reconstructions in studies from many parts of the world (Fritts, 1976; Hughes *et al.*, 1982). Such work has been highly successful in regions where year to year climatic variation appears to be a strongly influential factor in the determination of tree growth patterns, such as in the semiarid southwestern United States or in high-latitude or high-altitude forests near tree line. In parts of the world where the influence of such variation is not as pronounced, such as in the temperate mesic forests of the northeastern United States, ring-width/climate comparisons have in the past produced less spectacular results. Advances in computer facilities and statistical techniques, searches for climatically responsive tree-ring sites, and use of climatic data with closer significance for tree growth have helped to produce stronger dendroclimatic results in such regions (Phipps, 1972; Cook and Jacoby, 1977). More recently, the use of wood density measurement techniques has increased the past climatic information from tree-ring patterns over that available from ring widths alone, especially in such regions where strong dendroclimatic reconstructions were less easily obtainable (Conkey, 1979, 1982b; Hughes *et al.*, 1984).

Wood density studies are especially successful with the anatomically simple conifers, with primarily one cell type, called tracheids, which vary in density within and between annual rings according to changes in cell size and cell wall thickness. Various parameters of wood density (e.g., minimum or maximum values, or averaged over all or part of a ring) can be used, like yearly ring widths, to produce time series of wood density variations. The x-ray densitometric method, in which an x-ray film of the wood is analyzed on an optical densitometer, was first developed in France by Polge (1970), and has since been used and adapted by other laboratories (Lenz *et al.*, 1976; Parker, 1976; Jacoby, 1980; McCord, 1984). Many applications have been in the field of forestry, especially in the assessment of wood quality. However, the apparent strong association between climatic

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and density variations has now also been used to derive climatic histories and to determine the effects of climate on tree growth (Conkey, 1979; Roethlisberger, 1980; Cleaveland, 1983). Strong relationships are documented between the maximum value of latewood density in conifers and late summer precipitation in France (Polge, 1965); late summer temperature in northern Canada (Parker, 1976), in the Alps of Switzerland (Schweingruber *et al.*, 1978), and in Edinburgh, Scotland (Hughes *et al.*, 1984); late summer glacial runoff and temperature in western Canada (Parker and Henoch, 1971); and growing season warm/dry versus cool/wet conditions, also in western Canada (Heger *et al.*, 1974). The purpose of this paper is to present the results of the first such study in eastern North America, documenting a relationship between red spruce wood density in Maine and spring temperatures, thereby indicating the feasibility and important potential of this method for other paleoenvironmental and paleoclimatological studies.

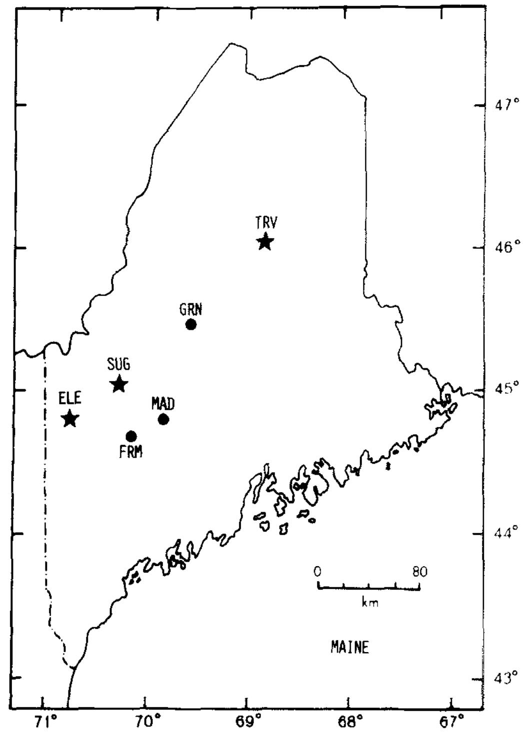

FIG. 1. Location of tree-ring chronologies (stars) and climatic data stations (filled circles). Tree-ring sites: TRV = Traveler Mt., SUG = Sugarloaf Mt., ELE = Elephant Mt. Climatic stations: GRN = Greenville, MAD = Madison, FRM = Farmington.

RESEARCH METHODS

Tree-Ring and Climatic Data

Tree cores were extracted from 15 to 19 red spruce trees (*Picea rubens* Sarg.) from each of three sites located along the mountains of Maine (Fig. 1, Table 1): Traveler Mt. in Baxter State Park, Sugarloaf Mt. near Kingfield, and Elephant Mt. in western Maine. All three sites are above 900 m elevation and are representative of the highest elevation stands of red spruce in this region. The cores were prepared and analyzed densitometrically at the Swiss Federal Institute of Forestry Research, Birmensdorf, Switzerland; the methodology is described in detail elsewhere (Lenz *et al.*, 1976; Schweingruber *et al.*, 1978; Conkey 1984b). Five density and width variables per ring are measured: minimum (earlywood) and maximum (latewood) density, and earlywood, latewood, and total ring width.

Following techniques widely used in dendrochronological research (Fritts, 1976), each width and density series is crossdated among all core series to assure exact dating. In this and other dendroclimatic studies using x-ray densitometric data, maximum density has been found to be the variable most closely related to external environmental changes and its use greatly facilitates crossdating (Polge, 1970; Conkey, 1979), an especially important attribute in areas where crossdating the less variable ring widths makes exact dating of the rings difficult. This is not universally true, however; Bowers (1981) finds that maximum density measurements do not improve the datability of Louisiana baldcypress, a species that is difficult to date with ring widths as well, and Cleaveland (1983) indicates that conifers of the Colorado Pla-

TABLE 1. COLLECTION SITE DESCRIPTIONS AND LOCATIONS

Site name, chronology size	Elevation, map reference	Geologic characteristics	Site description
Elephant Mt. 1667–1976 17 trees sampled, 32 cores used in final chronologies	Elev: 915–945 m ENE slope, 5°–10° Oquossoc quadrangle	Granitic base, little soil development, largely humus. Within drainage of Androscoggin River.	Flat, hummocky area; tall spruce dominant, foliage only in high branches. With balsam fir, birch, wood sorrel, ferns, and mosses.
Sugarloaf Mt. 1776–1976 19 trees sampled, 34 cores used in final chronologies	Elev: 1097 m NE slope, 35° Stratton quadrangle	Igneous base, gabbro/diorite, with sandy solifluction deposits and thick humus. Within Kennebec River drainage.	Steep, exposed slope, densely wooded patches with much fallen dead wood. With balsam fir, paper birch, sorrel, mosses.
Traveler Mt. 1728–1976 15 trees sampled, 26 cores used in final chronologies	Elev: 930–975 m NNW slope, 10°–20° Traveler Mt. quadrangle	Traveler rhyolite base, hummocky humus cover, close to bedrock. Within Penobscot River drainage.	Close to summit of burned-over peak. Few very old fir and birch with the spruce. Many dead snags and logs.

teau also show stronger agreement among the ring widths than among the maximum densities.

Chronologies are constructed by fitting each core series of widths or densities with a best-fit straight line, negative exponential curve, or low-order polynomial curve that best matches the long-term trend in growth that is presumed to be nonclimatic. Indices are derived and averaged year by year (Fritts, 1976) for each parameter at each site, producing five chronologies at each of the three locations. The chronologies from Elephant Mt. are shown as an example [Fig. 2; see Conkey (1982a) for the other site chronologies].

One advantage of the densitometric technique is demonstrated by this standardization procedure. Mesic-region trees are subject to periods of suppressed and released growth due to nonclimatic stand or site effects. It has become standard procedure to use complex mathematical functions such as polynomials, cubic splines, or autoregressive modeling to aid in the standardization of such ring-width series, often leaving uncertainty as to how much climatic information may be removed along with the fitting of such curves. The density series, however, show very little tendency for prolonged periods of high or low values compared to the ring-width series. Thus the densities can be standardized using straight lines, decreasing the potential for inadvertent removal of climatic information through standardization.

Climatic data were obtained (Baron *et al.*, 1980) for three meteorological stations, at Greenville, Madison, and Farmington (Table 2). These are generally in lower elevation areas than the tree-ring sites, and all are within 88 km from the tree-ring site used in comparative analysis with them (Fig. 1). The monthly averages of mean daily temperatures at these stations were available for 67 to 78 yr of record. Scatter plots and correlations between maximum density and monthly combinations of growing season temperatures show that (1) a spring seasonal average of April plus May is most closely related to maximum density values, and (2) the relationship is strongly linear, obviating the need for nonlinear data transformations prior to use in linear regressions. The three April–May temperature series show a high degree of station to

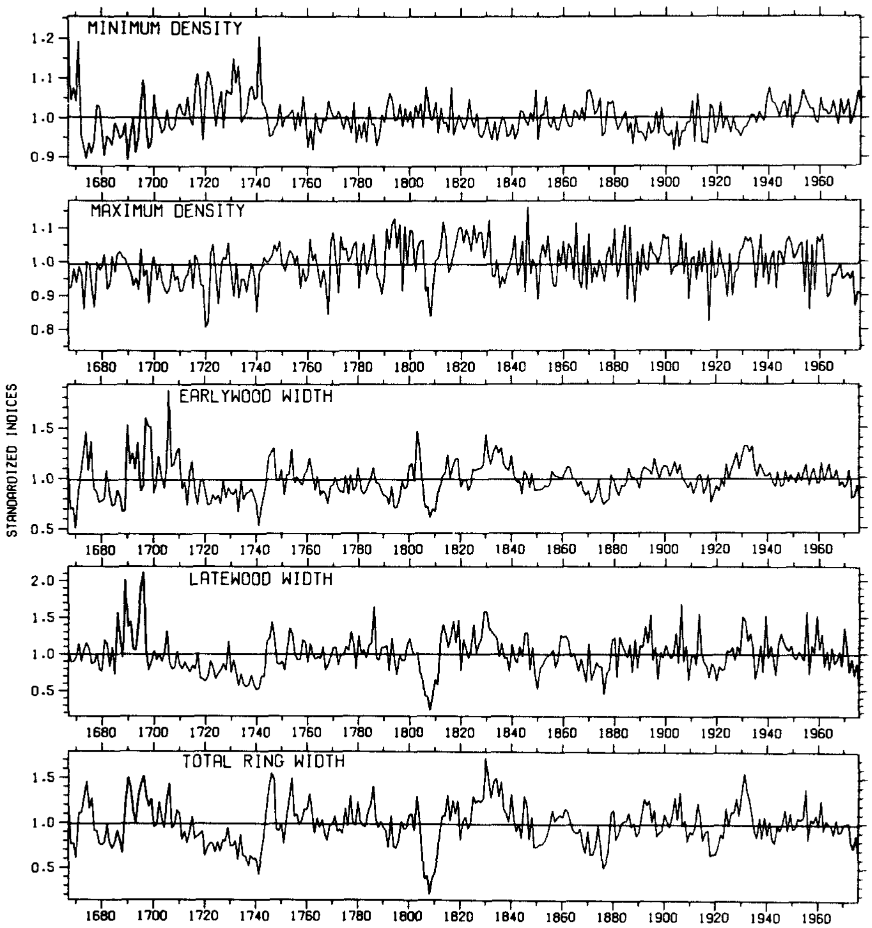

FIG. 2. Five standardized tree-ring chronologies from Elephant Mt., Maine, red spruce. Index values are plotted with the mean calculated for each entire series for minimum density (top), maximum density (second), earlywood width (third), latewood width (fourth), and total ring width (bottom).

station correlation, with values of 0.82 to 0.85.

Data Analysis

Data from individual tree-ring sites and climatic stations were compared statistically, or calibrated, in order to directly test the relationships proposed from biological considerations. The April–May temperature data were used as the predictand, or dependent variable, in calibration involving stepwise multiple linear regression, with the standardized indices of the tree-ring widths and/or densities as predictors, or independent variables. Climatic stations and the closest tree-ring sites were paired as follows: Farmington with Elephant Mt., Madison with Sugarloaf Mt., and Greenville with each of Sugarloaf and Traveler Mts. The years used for analysis were 1920–1974 for studies with Greenville data, and 1920–1976 for Madison and Farming-

TABLE 2. TEMPERATURE STATION INFORMATION

Station name	Length of record	Location	Elevation (m)
Greenville (Piscataquis Co.)	1908–1974	45° 28′ N 69° 35′ W	323
Madison (Somerset Co.)	1905–1976	44° 48′ N 69° 54′ W	79
Farmington (Franklin Co.)	1899–1976	44° 40′ N 70° 09′ W	128

ton data. Significant regression equations were applied to the entire series of ring widths and/or densities, producing a long-term estimate of the temperature records at the reconstructed climate station (Fritts, 1976).

Climatic data prior to 1920 were withheld from the regression analyses, in order to compare them to the reconstructed values (Fritts, 1976) with three statistical tests of association. Two of the three climate stations have records that are less than optimal length for such verification testing; maximizing the calibration period was deemed important for these first density–climate comparisons. The first statistical test is the Pearson product–moment correlation coefficient, which indicates the degree of coherence integrated over all frequencies; a second Pearson product–moment correlation is calculated after taking the first differences of both series, emphasizing in this way the high-frequency degree of correspondence between the two series (Fritts, 1976). The third test is the reduction of error statistic (RE), a rigorous test of reliability of a climatic reconstruction (Gordon and LeDuc, 1981). It cannot be tested for significance but has helpful diagnostic capabilities. Each year by year comparison is squared, so that one very bad yearly estimate may affect the mean RE enough to offset several good estimates, and high, positive values of RE are difficult to obtain. The RE statistic is partitioned into three components, representing the *risk* the regression model takes in making independent estimates seen in the match of reconstructed and actual variances, the *drift* in the mean of the actual observations away from the calibration mean, and the *covariation factor* between the observed and estimated values. These three components can be examined for their relative contribution to a low RE statistic, thus giving information on how to improve the regression model to obtain more reliable climatic estimates.

The regression analyses and verification tests provide the means by which statistical relationships between climate and tree-ring variables can be assessed. This is clearly necessary in order to establish the most accurate estimates of past climate. However, it is also desirable to develop biologically reasonable climate–growth hypotheses based on the physiological relationship of climate to tree growth. This is particularly important for densitometric studies, an area in which little is known about how wood density should correlate with climatic factors.

BIOLOGICAL BASIS OF WOOD DENSITY–CLIMATE STUDIES

Conifer tracheids produced in early spring and summer (earlywood) have large diameters and thin walls, apparently in response to high levels of the phytohormone, auxin, present in the cambium (Egierszdorff, 1981; Savidge and Wareing 1982, 1984) as well as translocated from the shoots, cell turgidity from high moisture content, and low availability of carbohydrates at the cambium (Kramer, 1964; Zahner, 1968). As the growing season progresses, latewood tracheids show much less lumen expansion and a much greater degree of secondary cell wall thickening. The reasons behind these two conditions are complex, as they are apparently only fortuitously synchronous and have their origin in differing physiological conditions (Wodzicki, 1971). The decrease in lumen diameter may be due to environmentally induced water stress in the warmer summer months, affecting both cell turgor and auxin availability (Zahner, 1968; Little and Wareing, 1981). Increased cell wall thickening seems more closely related to long-term supply of photosynthates (Gordon and Larson, 1968) and to concomitant growth regulator supply (Denne, 1979), and thus implicates the importance of bud set conditions in the previous year and of vigor and timing of shoot growth in the spring. Certainly, production and transport of photosynthates in late summer are also dependent on water supply, decreasing when stomata must remain closed and when translocation of food and hormones slows with decreasing turgor. But cell wall thickening appears to be greatest under conditions of mild water stress, when auxin levels are lowered and cambial cell division is restricted but photosynthesis is not seriously reduced (Kramer, 1964; Little and Wareing, 1981). Larson (1969) notes that thickening of the secondary cell wall begins once the new shoot and needle growth is completed to a point where needles begin to export photosynthates instead of importing them from other sources, thus decreasing competition for assimilates. In contrast, Denne (1974; 1976; Skene, 1969) finds that the thicker walls are due to an increase in the duration of the wall thickening phase, and occur in spite of a declining rate of accumulation of wall material. It thus appears that conditions which serve to increase the duration of cambial activity and/or to increase photosynthate supply will produce thicker latewood walls and higher wood density.

Using these considerations of tree physiology, a conceptual model of relationships between climate and wood density is proposed (Fig. 3). The end point of the flow chart indicates that the maximum point of latewood density displays highest values when cell lumen size is small and cell wall thickening is extensive. The literature suggests that prior growth conditions and spring activity levels play the stronger role in determining cell wall thickening (left side of Fig. 3), whereas more immediate conditions of summer water supply more strongly affect cell diameter (right side of Fig. 3). Cell number (center of Fig. 3) is also important to overall wood density of the ring, although its effect on maximum density in very narrow rings may be in part mechanical, due to the densitometer which scans several rows of cells at once, poten-

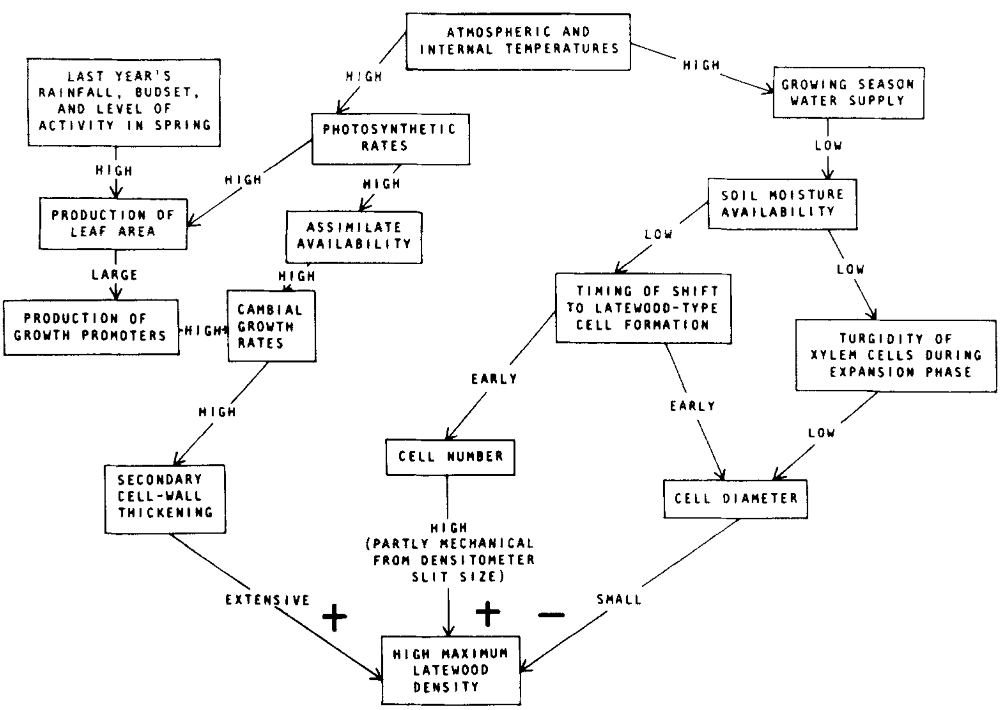

FIG. 3. Maximum density physiological model: Hypothesized influence of atmospheric variables and internal tree conditions on the production of high maximum latewood density. The "sign" of the condition in one box as it leads to the next is depicted by arrows and words (e.g., high, low, early).

tially incorporating both latewood and earlywood cells in the peak density reading. With these three pathways leading to highest maximum latewood density, Figure 3 thus provides information for the consideration of hypotheses of climate–wood density relationships.

HYPOTHESIS OF THE WOOD DENSITY–CLIMATE RELATIONSHIP

Earlier work documented significant correlations among all three sites (Conkey, 1984a), which suggests that maximum ring density and ring width are strongly related to widespread environmental factors which are most likely climate. Preliminary statistical comparisons (Conkey, 1979) likewise indicate strong relationships between these ring characteristics and climate. For density, such relationships are hypothesized to be most important in the current growth year, partly because of the observation of low autocorrelation or persistence from one year to the next in the density series (Conkey, 1979). The physiological model of maximum density (Fig. 3) suggests one possible pathway of climatic influence on this tree-ring characteristic: maximum density may be positively related to temperature in the spring months prior to latewood formation, when dormancy is broken and physiological activity, including cambial activity, is renewed. Earlier than normal warming in spring permits earlier physiological activity, including photosynthesis in previous years' foliage, the bursting of new foliage buds, and basipetal transport of auxin to the cambium, stimulating activity leading to radial growth at the cambium (Gregory and Wilson, 1968; Savidge and Wareing, 1981; Savidge, 1983). The new foliage also may contribute sooner to the phtotsynthetic area for substrate export to the cambium, providing increased photosynthates for a longer period of time during the growing season. Thus, warm or early springs lead to high maximum density values.

Several other workers find that early growing season conditions set the stage for the entire growing season. Brix and Mitchell (1980) suggest that seasonal tracheid production rates in Douglas-fir are closely related to temperature during periods of low water stress, particularly in spring and early summer. Wilson (1964) shows that the size of the active cambial area is established in spring and is maintained throughout the grand period of cell division. He finds that the rate as well as the amount of cell production and differentiation is influenced by the number of cells in the cambial area and by the length of time of cambial activity. Thus, a longer season, one with a favorable warm spring, may lead to increased cell number and rate of differentiation of the cells of the entire ring, including the latewood in which the maximum value of density is found (Fig. 3). Such physiological considerations strongly imply that maximum latewood density may be more dependent on early spring growing conditions than previously thought, indicating an important tree growth–climate relationship to be tested by dendrochronological means.

CLIMATIC RECONSTRUCTIONS

Despite strong correlations between spring temperature and each of maximum density, latewood width, and total ring width (Conkey, 1979; 1982a), intercorrelations among the tree-ring variables themselves keep any more than one of them from entering significantly into the multiple regression. In all cases, maximum density correlates most strongly to spring temperature; thus, that variable always enters into regression first. Earlywood width, which shows weaker correlation with maximum density but apparently has some independent information on temperature, occasionally enters as a second significant independent variable in regression equations.

The calibration results of four growth–climate regression combinations are presented in Table 3. Each regression equation

TABLE 3. CALIBRATION RESULTS OF SELECTED APRIL-MAY TEMPERATURE MODELS[a]

A	B	C	D	E
Tree-ring site	Climatic station	Regression equation	Adjusted r^2 (%)	F level
Sugarloaf	Madison	$Y = 26.51 + 20.22X_1$	33	28.9
Sugarloaf	Greenville	$Y = 19.61 + 20.86X_1 + 2.72X_2$	47	25.0
Traveler	Greenville	$Y = 23.48 + 19.88X_1$	34	28.8
Elephant	Farmington	$Y = 22.94 + 24.70X_1$	37	33.9

[a] Column B: 1920–1974 for Greenville, 1920–1976 for Madison and Farmington. Column C: X_1 = maximum density, X_2 = earlywood width. Significant at the 0.95 level. Column D: Percentage of variance calibrated, adjusted for loss of degrees of freedom. Column E: F level of regression equation with significantly entered variable(s).

is given, along with its diagnostic F level and the percent of variance calibrated.

The Sugarloaf/Greenville regression incorporates both maximum density and earlywood width chronologies, and has the highest percentage of calibrated variance. That variance is much greater than the highest percentages attained in a previous ring-width-based dendroclimatic analysis in New England, in which 15.5% was the highest calibrated variance of a spring temperature comparison, and 38.5% the highest variance overall, for a winter temperature analysis (Conkey, 1982b). Maximum density enters as the only significant predictor of spring temperature in the other three regressions, with percent variance figures that likewise compare well to previous studies.

The regression equations in Table 3 were used to estimate past spring temperatures at Madison, Greenville, or Farmington. The four estimates are strongly statistically verified in their ability to reconstruct past climate, as all four show significant correlations with pre-1920 climatic data, at all frequencies and at the high frequency alone (Table 4). The slightly lower high-frequency correlation for the Sugarloaf/Greenville verification may be due to the inclusion in the regression equation of earlywood indices, which show less high-frequency variation than the maximum densities (Conkey, 1982a). Notably, the reduction of error statistic results are all positive, and are equal to or greater than the proposed lower limit of acceptable RE values (Gordon and LeDuc, 1981); thus, they are a strong indication that the reconstructions add substantially more information on past climate than merely using the mean of the climate data.

The reconstructions are plotted with the actual meteorological observations in

TABLE 4. VERIFICATION RESULTS OF SELECTED APRIL–MAY TEMPERATURE MODELS[a]

A	B	C	D	E	F	G	H	I	J
			Verification period test results:						
Tree-ring site	Climatic station	Adjusted r^2 (%)	r	r_{-1}	RE	risk	drift	covariation	n
Sugarloaf	Madison	33	0.75	0.90	0.481	−0.271	−0.004	0.756	15
Sugarloaf	Greenville	47	0.50	0.69	0.244	−0.273	0.006	0.512	12
Traveler	Greenville	34	0.75	0.84	0.516	−0.297	0.002	0.811	12
Elephant	Farmington	37	0.50	0.83	0.175	−0.641	0.059	0.757	21

[a] Columns A–C: As in Table 3. Columns D, E: r = correlation; r_{-1} = correlation of the first differenced series. All values are significant at the 0.95 level or greater. Columns F–I: RE = reduction of error statistic; risk, drift, and covariation terms are components of RE. No significance level can be determined (Gordon and LeDuc, 1981). Column J: n = verification period (pre-1920) sample size.

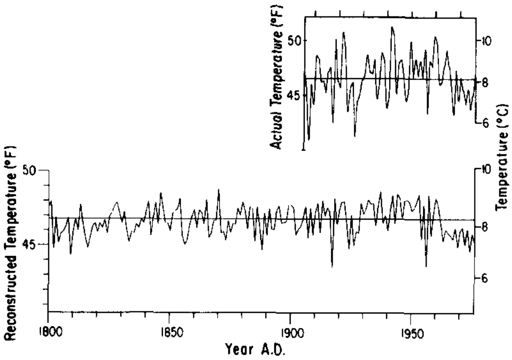

FIG. 4. Madison (ME) April–May temperatures, reconstructed (lower plot) from Sugarloaf Mt. maximum density. The meteorological observations from Madison are in the upper plot.

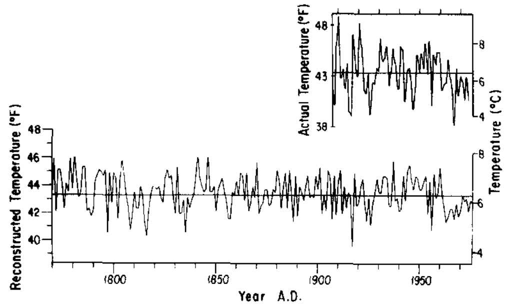

FIG. 6. Greenville (ME) April–May temperatures, reconstructed from Traveler Mt. maximum density (as in Fig. 4).

Figures 4–7. Figures 5 and 6 are both reconstructions of Greenville, one from maximum density and earlywood width from Sugarloaf (Fig. 5) and the other from maximum density from Traveler (Fig. 6). Although the former shows a higher percentage of calibrated variance, the latter's verification statistics are higher. The two estimates are very similar most of the time and correlate significantly at 0.67; differences are notable in the magnitude of peaks and troughs in the 1820s, 1840s, 1865–1885, 1940s, and 1970s, when Traveler predicted higher temperatures than Sugarloaf, and in the 1810s and 1830s when Traveler predicted slightly cooler temperatures.

Because the climatic record for verification testing is short, especially at Madison and Greenville, a comparison with other data that are independent of the calibration records is desirable. Historical climatic data from the New England region, especially in the Massachusetts Bay area, are available both as carefully recorded measurements ("records") and as estimates quantified from qualitative diary descriptions ("diaries"; Baron, 1980). Two such series are compared to the four temperature reconstructions; the strongest comparisons are shown in Table 5. The Salem record of Edward Holyoke (Baron, 1980) correlates significantly with both the Elephant/Farmington and the Traveler/Greenville reconstructions; all of the comparisons with Salem and the Medway diary are significantly related at the high frequencies. Thus the historical data help to verify the tree-ring reconstructions during time periods that are not possible to test with modern instrumental records, and substantiate their climatic reliability.

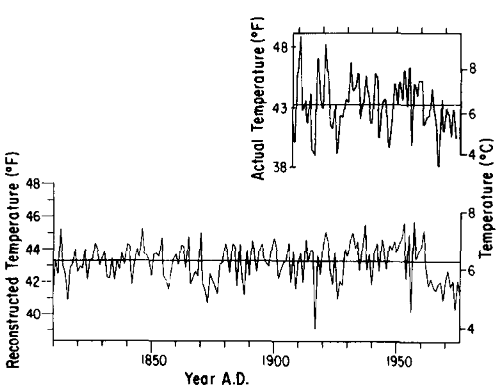

FIG. 5. Greenville (ME) April–May temperatures, reconstructed from Sugarloaf Mt. maximum density and earlywood widths (as in Fig. 4).

Three of the four reconstructions are created from simple, or one-factor, regressions; thus, they are susceptible to all variation that is found in those original maximum density series (Figs. 4, 6, and 7). Much of the maximum density pattern is replicated and widespread enough to suggest that it is due to climate, and the reconstructions themselves correlate well (0.68 to 0.77), but some variation may be caused by nonclimatic perturbations. For instance, the low-density period centered on 1808 at

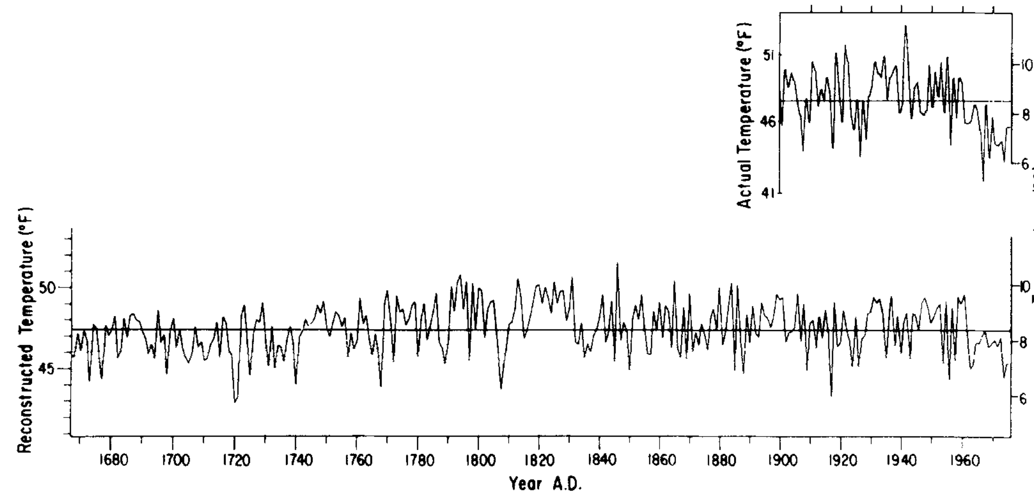

FIG. 7. Farmington (ME) April–May temperatures, reconstructed from Elephant Mt. maximum density (as in Fig. 4).

Elephant Mt. (Fig. 2) is not as low at the other sites, nor do the historical data from Salem and Medway show temperatures at that time to be as low as those reconstructed at Farmington (Conkey, 1982a). This low maximum density at Elephant may thus not be due to macroclimate (Conkey, 1984a). Historical records indicate that 1816 was a year of very low spring temperatures throughout New England (Ludlum, 1976); the Traveler reconstruction of Greenville (Fig. 6) estimates 1816 to be one of the coldest springs, but in the Elephant reconstruction of Farmington (Fig. 7), the dip is barely noticeable in comparison to 1808, a year not mentioned in connection with cool springs (Ludlum, 1976; Baron, 1980). Greater confidence is engendered by troughs and peaks that are synchronously reconstructed by all regression models, such as in the 1830s, the 1860s, 1870s, and late 1880s. On the other hand, it may be that the apparent nonclimatic information in the chronologies can be exploited further to understand a wider range of stand dynamics and forest history in addition to the climatic information already reconstructed (Conkey, 1984a).

CONCLUSIONS

Dendroclimatic analyses with density data have not been widely reported thus far; the study described here is the first to be carried out in eastern North America and thus adds significantly to our experience with them. These results indicate that in Maine, red spruce maximum density is strongly related to spring temperature, par-

TABLE 5. VERIFICATION OF CLIMATIC RECONSTRUCTIONS USING HISTORICAL DATA[a]

A	B	C	D	E	F	G
					Verification results	
Tree-ring site	Climatic station	Historical data site	Years	Distance (km)	r	r_{-1}
Sugarloaf	Madison	Medway diary	1776–1819	328	0.24^N	0.37
Sugarloaf	Greenville	Medway diary	1776–1819	380	0.23^N	0.31
Traveler	Greenville	Salem record	1786–1820	352	0.59	0.55
Elephant	Farmington	Salem record	1786–1820	252	0.44	0.54

[a] Columns A, B, F, and G as in Table 4; N indicates lack of significance at the 0.95 level. Columns C and D from Baron (1980); both sites are in Massachusetts.

ticularly in April and May; comparable analyses with summer moisture and temperature variables were also explored, with less successful results (Conkey, 1982a). Previous research has emphasized correlations of maximum density and conditions in the summer months of its formation (Polge, 1965; Parker and Henoch, 1971; Schweingruber *et al.*, 1978; Conkey, 1982b; Hughes *et al.*, 1984); thus, the strength of the spring temperature results is unexpected. Although its physiological reasons remain unproven, the existence of the relationship for red spruce in Maine is well substantiated.

There are advantages to the incorporation of density determinations in dendroclimatic work. First, the increased ease of crossdating is indicative of the increase in macroclimatic information that can be obtained with the inclusion of density variables. Second, climatic information is maximized by the greatly simplified standardization procedures. A third advantage has been demonstrated here, that wood density measurements increase the ability to derive verifiable dendroclimatic reconstructions in mesic, temperate regions, and thus increase the potential global coverage of climatic proxy information that can yield strong estimates of past climate.

ACKNOWLEDGMENTS

This research was supported by a Fulbright-Hays administered Swiss government grant to the author, by NSF Grant ATM-812171 to H. C. Fritts, by State of Arizona funding to the Laboratory of Tree-Ring Research at the University of Arizona, by the Swiss Federal Institute for Forestry Research and O. Lenz and F. Schweingruber, and by the University of Maine's Institute for Quaternary Studies (with Hal Borns) and the College of Forest Resources (with Fred Knight) for fieldwork logistical support. I thank Hal Fritts and Val LaMarche for guidance and project review, Fritz Schweingruber, Otto Braeker, and Ernst Schaer for densitometry guidance, Brenda Keller for computer help, Marna Ares Thompson for drafting, and Bob Brakenridge for field assistance and support throughout. I am especially appreciative of careful reviews of the manuscript from Bob Brakenridge, Geoff Gordon, Malcolm Hughes, Frank Telewski, and one anonymous reviewer.

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