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Climatic Variability and Tree Response within the Forest-Alpine Tundra Ecotone

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Abstract. Relationships between climatic variables and tree-ring widths (1954–79) were determined for three sites in the forest-alpine tundra ecotone on Niwot Ridge of the Colorado Front Range. Correlations were tested using regression techniques and results are displayed by response surfaces. Climatic data from within the ecotone (1978–84) indicate the occurrence of large temperature gradients over short distances and frequent inversions. This finding demonstrates that frost-free seasons are shorter in the lower ecotone, although critical winter minima may be experienced in the upper ecotone. Regression techniques indicate that tree-ring widths are significantly and negatively correlated with autumn precipitation of the previous calendar year and significantly and positively correlated with the previous calendar year's autumn temperature and the actual year's late spring/early summer temperature. High winter temperatures as well as large amounts of snow in the early spring show negative correlations with tree-ring width. The temperature correlations were used to reconstruct past climate variability (mean previous-year autumn and actual-year late spring/early summer air temperatures) to the mid-1500s (the limit of the tree-ring chronology). From this reconstruction we conclude that the relevant air temperatures were lower than average in the mid-to-late 1500s, higher during the seventeenth century, variable around the average from 1690–1830, lower from 1830–95, higher from 1925–65, and lower from 1965–79. These results, indicating a close relationship between climatic change and tree-growth response, demand that upper timberline management strategies be developed to take into account natural fluctuations as well as possible human impacts on the forest-alpine tundra ecotone.

Key Words: mountain timberline, temperature gradient, climatic change, tree-rings, growth response.

HIGH-ELEVATION mountain ecosystems in western North America are increasingly subjected to disturbance from human activities. The ability of these ecosystems to withstand such disturbance will influence both the degree of degradation they incur and the extent and rate of their recovery. Recovery is dependent upon many variables, not the least of which are vegetative stability and response both to disturbance and to natural climatic variability. An increase in the quantity and quality of data on the present climate and past climatic variability, together with a better understanding of the resultant vegetative responses, is urgently needed both in terms of adding to our knowledge of these fascinating landscapes and facilitating development of specific management strategies for their protection. Where climate has varied in the past, and where it can be shown that vegetation has responded to these changes, it is reasonable to assume that such relationships will continue into the future. Management strategies, therefore, must incorporate such knowledge as well as respond to the increasing human use of these ecosystems.

Specific responses of high-elevation trees to present-day growing season soil and air temperatures are discussed by Hansen-Bristow (1986). A forest-alpine tundra ecotone stability analysis, based on seedling establishment, macro-fossils and tree-form changes, is elaborated by Ives (1978), Ives and Hansen-Bristow (1983), and Hansen-Bristow and Ives (1984, 1985). Studies concerned with climatic variability during the present (Barry 1973, 1985, 1986; LaMarche

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et al. 1984) and past (LaMarche 1973; LaMarche and Stockton 1974; Douglas and Stockton 1975; Bradley 1980; Short 1985; Jacoby et al. 1985; Luckman et al. 1985; Graumlich and Brubaker 1986) have identified fluctuations and trends from a variety of sites in western North America. This study, concerned with high-elevation tree response to both recent and past climatic variability, corresponds most closely with that by Graumlich and Brubaker (1986) in the Pacific Northwest. Its objectives are as follows: (1) to determine the present short-term variability in air temperatures in a high elevation mountain ecosystem, (2) to understand the response of trees to monthly and seasonal climatic variables, and (3) to reconstruct the climatic history and variability of the ecosystem. Present temperature variability and tree response were determined for the forest-alpine tundra ecotone on Niwot Ridge in the Colorado Front Range. The structure of this ecotone, a transitional belt between two contrasting vegetative communities (upper montane forest and alpine tundra), displays evidence of variations in its controlling, or limiting, climatic factors. Present air temperature data were obtained from climatic stations along an altitudinal transect through the ecotone. Tree response to temperature and precipitation variability was determined by regression analyses of tree-ring growth and climate values, as tree-ring widths from certain sites reflect climatic variation (Fritts et al. 1971). A ring-width chronology was tested against the recent climatic variation and then used to reconstruct long-term climatic variability (mid-1500s onward).

Study site characteristics, methods, analyses, present climatic conditions, present and past tree-ring growth response, and a climatic reconstruction follow. Management implications, stressing the sensitivity of high mountain ecosystems, add significance to the results of this study.

Study Site

Niwot Ridge (40°3'N, 105°35'W) was selected for study because it has been the focus of many long-term research projects during the past 35 years (International Biological Programme, National Science Foundation's Long-Term Ecological Alpine Study). This focus has produced a large body of scientific results, particularly climatic data (from 1954 onward) essential to the present study. In addition the Mountain Research Station of the University of Colorado provided year-round access. The climatic transect, used as a basis for this study, spans the width of the forest-alpine tundra ecotone from 3300–3465 m. Hansen-Bristow and Ives (1985) define the forest-alpine tundra ecotone as a mosaic of forest and alpine tundra species extending between the upper timberline (upper limit of tall, symmetrical, closely-spaced trees of the montane forest) and the upper limit of tree species. Three climate stations were established in 1978 within the ecotone (Fig. 1); they were located on a south- to southeast-facing slope and chosen to represent the differing tree-form sub-belts of the ecotone.

The "Burn" station, at 3300 m, is located within a forest clearing near timberline. The clearing is the result of several forest fires in the late 1800s and early 1900s (Grulke 1978). The clearing is wet to mesic and experiences occasional flooding due to snowmelt during early summer. The "Ecotone" climate station, at 3400 m, is located in a small clearing within the ecotone. Here deep winter snow (up to 7 m) necessitates the gradual raising of the climatic instruments to keep them above the snow surface. "T-Van" at 3465 m, near the tree species limit, is a mesic to dry site. Ground temperature data indicate that the lowest patches of sporadic permafrost occur within the upper part of the ecotone (Ives 1973). The staff at the Mountain Research Station, University of Colorado, has collected longer-term climate data since 1953 at two additional sites ("Niwot Ridge," 3743 m on the ridge crest to the west and "Como" at 3018 m to the southeast). Those data have been processed and analyzed in a variety of publications (Marr 1967; Barry 1972, 1973, 1985, 1986; Losleben 1983, 1984, 1985).

Methods

Present-Day Air Temperatures

Air temperature data were collected using U.S. Weather Bureau Hygrothermographs housed in standard meteorological (Stevenson) screens which provide instrument exposure at 1.2 m above the ground surface. Maximum, minimum, and mean values were obtained using standard techniques of analysis such as de-

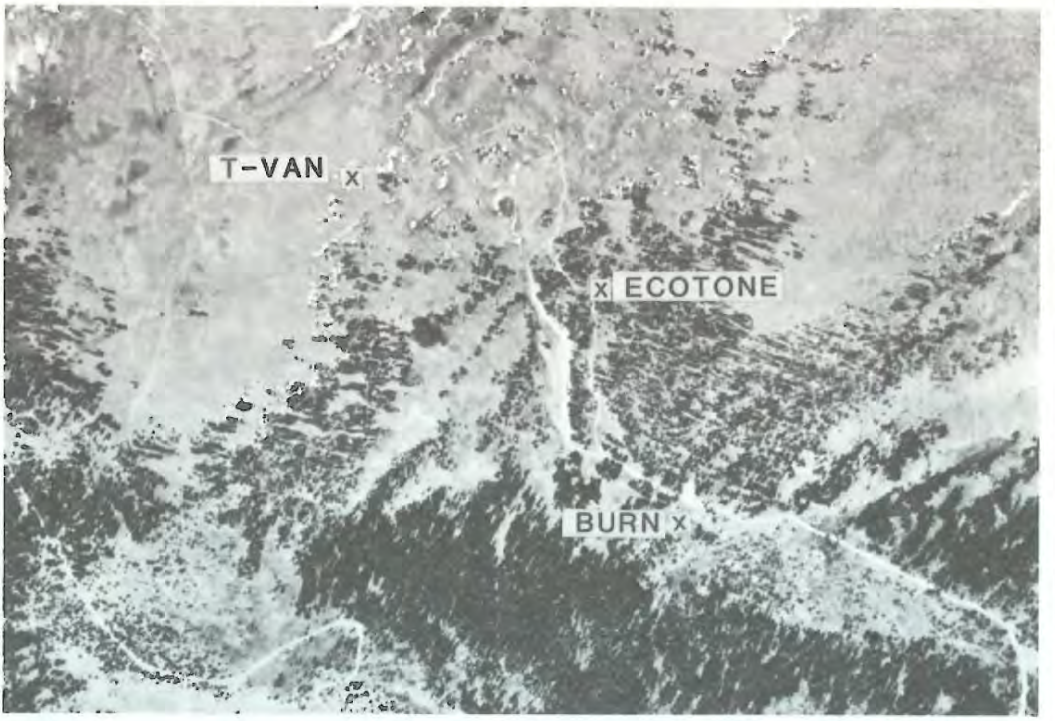

Figure 1. An aerial view, scale 1:24,000, of Niwot Ridge shows the altitudinal transect through the forest-alpine tundra ecotone where climatic data are collected. The "Burn" site is near timberline, the "Ecotone" site is within the ecotonal transition, and the "T-Van" site is near the tree species limit.

scribed by Barry (1973). Lengths of frost-free season values were calculated based on the sum of the number of days for which the daily minimum air temperature remained above 0°C. Changes in air temperature with increase in elevation were adjusted to changes per 100 m. Additional climatic variables (solar radiation, soil temperature, and snow depth and distribution) were measured within this transect and are reported in Hansen-Bristow (1981, 1986).

Tree Growth

A Swedish increment borer was used to extract tree cores for ring width observation from trees within the study site. Cores were collected along two elevational transects on the south- to southeast-facing slope of Niwot Ridge through the ecotone. The collection of cores was restricted to Engelmann spruce (*Picea engelmannii* (Parry) Engelm.), the dominant species (Wardle 1968). All four tree life forms (symmetrical, flag, flag mat, and mat), as described by Hansen-Bristow and Ives (1985), were sampled; this sample included two cores per tree from ten trees per life form.

The Laboratory of Tree-Ring Research at the University of Arizona undertook analysis of the cores. Cross-dating was possible only on those cores collected within the lower sub-belts of the ecotone, near timberline. The cores from the mat conifers at the tree species limit could not be cross-dated with confidence because of the high dissimilarity in ring widths within single trees and between neighbor trees. This dissimilarity reflected excessive sensitivity to a large number of factors (snow, radiation, shading, bi-

ological competition, wind abrasion, and temperature). Composite tree-ring plots were developed and yearly dates were assigned to individual rings. A mean-growth curve, or "trend line," for each plot was constructed using 10-year periods. A standardized ring-width index was then developed for each year by fitting a negative exponential curve to the data in order to remove growth trends associated with age (Fritts 1976). A tree-ring chronology was then developed based on yearly ring width indices.

Tree Growth Response to Climate

To distinguish which seasonal climatic parameters were most related to tree-ring growth, a regression analysis was performed on the data. The climatic data used for this analysis included monthly mean precipitation and air temperature from the U.S. Weather Bureau station at Idaho Springs, CO (a valley site at 2303 m, south of the study site) and 1954–1974 data from two climatic stations on Niwot Ridge ("Como" at 3018 m and "Niwot Ridge" at 3743 m). While the later two stations provided much shorter records, they are located close to the study site. Specific monthly climatic data chosen for the regression analysis provided results that were similar to those from previous tree growth-climate studies at upper timberline (LaMarche and Stockton 1974, Colorado Front Range; LaMarche 1974, White Mountains of eastern California; Tranquillini 1979, European Alps; Hansen-Bristow 1986, Colorado Front Range; Graumlich and Brubaker 1986, Cascade Mountains of Washington). Hence, weighted monthly mean temperature and precipitation data were regressed with the actual year's tree-ring growth in the following groups: (1) individual months from April of the previous calendar year through September of the actual calendar year, (2) weighted means for April through September of the actual calendar year, (3) weighted means for September of the previous calendar year through August of the actual calendar year, (4) weighted means for May through July of the actual calendar year, (5) weighted means for September and October of the previous calendar year, and (6) weighted means for September and October of the previous calendar year combined with weighted means for May through July of the actual year.

Response Surfaces

Based on the significance of responses of tree-ring growth to climate variables (determined by the regression analysis), response surfaces were developed using the SAS-GRAPH G3-GRID program. Response surfaces, representing non-linear relationships between tree growth and climate (Bartlein et al. 1986; Graumlich and Brubaker 1986), display tree growth in the form of a three-dimensional graph, indicating the tree response to a combination of two climatic variables. The X- and Y-axes were constructed using specified combinations of precipitation and temperature values, while the Z-axis was constructed from yearly tree-ring indices. The response surfaces facilitated a visual assessment of the seasonal responses of trees to combinations of climatic values and aided in determination of the regression model for predicting climate from tree-ring widths.

Climatic Reconstruction for Periods Prior to Instrumental Record

Based on the results of the regression analysis and the response surfaces, climatic variation was reconstructed using the tree-ring chronology as the predictor (independent) variable and the climatic data as the predicted (dependent) variable. Several of the procedures reported by Graumlich (1985) and Graumlich and Brubaker (1986) were used to evaluate the statistical reliability of the climatic reconstruction. A univariate Box-Jenkins analysis revealed that the tree-ring chronologies exhibited statistically significant auto-correlations (using analysis of variance at a .05 level of significance). No attempts were made to develop an ARIMA model nor to transform the chronologies to white noise due to the small number of years for which climatic data are available (24 years between 1954 and 1979). Bivariate scatter plots (see Results) of the predicted climate variable and tree-rings did show a strong linear relationship and an absence of outliers that could bias the regression estimates and result in a regressiosn model of reduced precision. Graumlich and Brubaker (1986) state that outliers may arise from short-term, non-climatic influences on growth (i.e., fires, insect infestations) or from the influence of a climatic event not explicitly modeled (i.e., severe growing-season frost, damage due

Table 1. Present Day Mean Maximum and Mean Minimum Air Temperatures, °C

	1978		1979		1980		1981		1982		1983		1984	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
(a) T-Van (3465 m)														
Jan	*	*	*	*	*	*	−5	−12	−6	−12	−6	−13	−11	−17
Feb	−6	−12	−9	−14	*	*	−6	−13	−6	−13	−6	−14	−9	−17
Mar	−2	−8	−5	−12	*	*	−4	−11	−3	−10	−7	−15	−10	−17
Apr	1	−8	−1	−8	*	*	1	−6	−2	−11	−10	−17	−4	−12
May	3	−5	5	−3	*	*	1	−5	4	−3	−2	−10	5	−2
June	11	2	11	2	*	*	11	2	7	−1	9	1	9	0
July	17	7	16	7	*	*	13	4	13	4	11	2	*	*
Aug	14	4	15	6	*	*	10	2	12	4	12	4	*	*
Sept	12	3	12	3	*	*	7	0	6	0	*	*	*	*
Oct	6	−3	5	−5	*	*	−1	−8	0	−7	*	*	*	*
Nov	0	−8	−5	−12	*	*	−4	−12	−5	−12	−5	−13	*	*
Dec	*	*	−3	−10	*	*	−8	−14	−6	−13	*	*	*	*
(b) Ecotone (3400 m)														
Jan	*	*	*	*	*	*	−7	−16	−9	−15	−4	−12	−4	−12
Feb	*	*	−5	−12	*	*	−2	−11	0	−8	−3	−12	−5	−13
Mar	*	*	−3	−11	*	*	1	−9	−4	−11	−3	−11	−3	−10
Apr	*	*	0	−8	*	*	3	−6	0	−10	−2	−11	6	−1
May	*	*	4	−4	*	*	4	−5	3	−4	2	−5	10	1
June	13	2	12	2	*	*	17	5	11	0	8	0	*	*
July	18	4	18	5	17	5	13	1	10	1	16	5	*	*
Aug	15	2	15	4	*	*	11	0	13	3	16	6	*	*
Sept	13	0	14	2	*	*	10	−1	8	0	14	2	*	*
Oct	8	−5	6	−4	*	*	2	−6	1	−8	6	−2	*	*
Nov	0	−9	−6	−14	*	*	1	−11	−2	−12	−1	−9	*	*
Dec	−7	−15	*	*	0	−8	−6	−12	−5	−14	−7	−14	*	*
(c) Burn (3300 m)														
Jan	*	*	−10	−14	*	*	−4	−12	−6	−11	−4	−10	−4	−10
Feb	*	*	−10	−14	*	*	−7	−13	−4	−11	−1	−8	−2	−9
Mar	2	−8	−5	−12	*	*	−4	−12	−4	−10	−1	−8	−3	−9
Apr	*	*	2	−6	*	*	3	−5	−2	−11	0	−8	1	−6
May	8	−1	8	−2	*	*	3	−5	3	−5	0	−8	6	−2
June	16	3	13	2	*	*	13	1	8	−2	8	−1	10	−1
July	18	4	17	4	*	*	14	2	12	1	14	3	*	*
Aug	*	*	12	3	*	*	11	2	12	2	15	4	*	*
Sept	12	−1	13	1	*	*	10	0	6	−2	11	1	*	*
Oct	8	−3	6	−4	*	*	1	−6	0	−8	6	−3	*	*
Nov	0	−9	−6	−14	*	*	0	−8	−5	−13	−2	−10	*	*
Dec	−6	−14	−4	−11	*	*	−8	−13	−6	−14	−9	−14	*	*

* Denotes missing data.

to high winds). Both a strong linear relationship and an absence of outliers are required for utilization of the tree-ring chronology for predicting climatic variables.

The model-building process was partitioned into two steps. First, one-third of the observations were randomly deleted to test or "cross-validate" the model's predictions. The observations withheld from the analysis were compared to the model's predictions using the product-moment correlation coefficient (r). This model-building procedure was then repeated on five different, randomly chosen subsets of data to ensure that the results were representative. Second, the coefficients for the final model were re-estimated using the entire 1954–79 temperature series to ensure that the coefficient estimates were as precise as possible.

Results and Discussion

Climatography of Present Temperatures

Analysis of the data (Table 1) provides documentation of the current air temperature characteristics of the ecotone. This documentation allows for further correlation of temperature variability and vegetation characteristics within the ecotone. The mean annual air temperature for the "T-Van" station (3465 m) is −2.2°C, for the "Ecotone" station (3400 m) −1.2°C, and for the "Burn" station (3300 m) −1.3°C. The lower annual mean temperature at the Burn site, compared to the Ecotone site, is due to the Burn's open location and downslope dense forest margin which induce temperature inversions.

The mean frost-free season across the ecotone is:

T-Van (3465 m) = 68 days (maximum 91, minimum 52, in 5 years)
Ecotone (3400 m) = 57 days (maximum 89, minimum 18, in 5 years)
Burn (3300 m) = 51 days (maximum 68, minimum 34, in 5 years)

These frost-free season lengths can be compared to that at the Como station (3018 m) (59 days; maximum 98, minimum 28, in 18 years) and to that at the Niwot Ridge station (3743 m) (47 days; maximum 74, minimum 26, in 18 years) (Barry 1973). The increased length of the frost-free season with increasing elevation across the forest-alpine tundra ecotone reflects both the frequency of temperature inversions and the longer snow duration (in sites with higher tree densities) at lower ecotonal elevations (Hansen-Bristow 1986). The latter is strongly displayed by the occurrence of the minimum 18-day frost-free season in 1982 at the Ecotone site (3400 m). This finding has many implications for tree viability. Tree establishment, survival, and reproduction could be severely hindered within this belt of the ecotone. The regeneration and growth rate at the "Burn" site also may be influenced by these shorter frost-free seasons and frequent temperature inversions.

Air temperature gradients (Table 2) indicate a high frequency of temperature inversions and variable gradients throughout the ecotone. Mean annual air temperature gradients show that a temperature increase with increasing elevation (inversion) of 0.3°C (100 m)$^{-1}$ exists between 3300 m and 3400 m while a temperature decrease of −1.85°C (100 m)$^{-1}$ with increasing elevation occurs between 3400 m and 3465 m. This large gradient, contrasted with the dry adiabatic lapse rate of 0.98°C (100 m)$^{-1}$, documents a large change in air temperature over a relatively short (65 m) distance.

Table 2. Air Temperature Gradients (°C), Per 100-m Increase in Elevation[a]

	Burn to ecotone	Burn to T-Van	Ecotone to T-Van
(a) Daily mean maximum temperatures			
Jan	−.6	−.8	−1.2
Feb	+2.0	−1.3	−6.4
Mar	+.6	−1.1	−3.7
Apr	−1.2	−2.0	−3.2
May	+.8	−.2	−1.7
June	+.5	−1.0	−3.2
July	+.3	−.6	−2.0
Aug	+1.5	+.06	−2.2
Sept	+1.4	−.7	−4.0
Oct	+.4	−1.3	−3.2
Nov	+1.0	−.7	−3.4
Dec	+1.6	+.5	−1.1
(b) Daily mean minimum temperatures			
Jan	−2.6	−1.3	+.8
Feb	0	−1.7	−4.3
Mar	−1.2	−1.4	−1.8
Apr	−1.8	−1.9	−2.0
May	0	−.5	−1.4
June	+1.4	+.4	−1.1
July	+.7	+1.2	+2.0
Aug	+2.2	+.7	−1.5
Sept	+.8	+1.0	+1.4
Oct	−.2	−.6	−1.2
Nov	−.2	−.4	−.6
Dec	+.6	+.5	+.5

[a] − = temperature decline with elevation increase.
+ = temperature increase with elevation increase (inversion).

Night-time air temperature gradients (reflected by minimum temperatures) show that temperature inversions occur between all sites during the months of July, September, and December. Temperature inversions also occur during the months of June and August between the 3300 m and 3465 m stations. Periods of calm air during these months promote downslope drainage and cold air ponding (Barry 1973).

Daytime gradients, reflected by the maximum temperatures, signify the occurrence of

Table 3. Temperature Extremes (°C), Recorded from 1978 to 1984

	Burn (3300 m)		Ecotone (3400 m)		T-Van (3465 m)	
	Max	Min	Max	Min	Max	Min
January	4	−23	7	−30	6	−34
February	6	−21	7	−27	3	−30
March	9	−16	12	−26	6	−27
April	11	−18	11	−25	9	−29
May	16	−16	15	−16	13	−15
June	20	−11	24	−9	19	−7
July	22	−8	23	−5	21	−2
August	19	−3	23	−6	26	−4
September	20	−12	22	−11	20	−12
October	14	−20	14	−22	12	−20
November	12	−22	13	−23	11	−21
December	8	−28	8	−26	3	−23

a temperature inversion between the 3300 m and 3400 m stations in all months except January and April. Cold air draining from upper slopes to the relatively flat opening at 3300 m evidently becomes "ponded" against the downslope forest border at the "Burn" site. Inversions as large as 1.6°C $(100\ m)^{-1}$ were recorded. Daytime gradients indicate that a temperature decrease with elevation occurs every month between 3400–3465 m. The exceptionally high gradients recorded (yearly mean of −2.9°C $(100\ m)^{-1}$) may be due to strong mixing of the surface and free air at the 3465 m site. The lower site at 3400 m, sheltered by a higher density of flag mat trees, apparently has much less daytime mixing.

Extreme temperature values (Table 3) suggest possible critical limits for tree growth. A minimum of −34°C, recorded at 3465 m, is dangerously near the cold hardiness limitation of −40°C found by Becwar et al. (1981) in Engelmann spruce and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Freezing temperatures were recorded during every month of the year for the period 1978–84. Barry (1984) found at the Niwot Ridge climate site (3743 m) that even in July, night temperatures below 0°C occur on almost every day about once in ten to twenty years. He also found sharp seasonal transitions to occur about June 20th and September 10th; these he defined by the date when the frequency of minima below 0°C crossed the 50 percent level. The unpredictable nature of the growing seasons in alpine environments, as described by Billings (1974a, b), is confirmed for Niwot Ridge by Barry (1985, 1986).

Tree Growth Response to Climate

Correlations of tree-ring width with climate data were found to be highest and most significant using data from the Como station (3018 m) (Table 4), although the direction of the correlation (negative or positive) was generally similar for all climate data sets. The tree-ring width data, collected a short distance above timberline, might be expected to correlate best with climatic data from within a forested site, such as that of the Como station. In contrast, the Niwot Ridge site is characteristic of a harsh, alpine tundra environment, and the Idaho Springs site typifies a low-elevation mountain valley bottom subjected to cold air accumulation, temperature inversions, and a climate quite different from that of the upper mountain ecotone.

The highest correlation ($r = .74$) was found to occur betwen tree-ring width and October temperature of the previous calendar year. High correlations were also obtained using the previous calendar year's September and October ($r = .61$) and September through November ($r = .59$) weighted mean temperatures. The highest correlations between precipitation and tree-ring width were also found for the previous calendar year's autumn months with total October precipitation producing an $r = -.49$ and that of September through November precipitation producing an $r = -.52$.

Response-surface equations for the previous autumn's (September and October) temperature and precipitation explain 35 percent of the

variance in tree growth and reveal nonlinear relationships between tree growth and climatic variables (Table 5, Figure 2a). The method of including the squares and cross-products of the climatic variables in order to represent nonlinear relationships (those that include interactions between the climatic variables), as advocated by Graumlich and Brubaker (1986), was adopted in this study. The results in Figure 2a indicate that the response surface is highest, indicating greatest tree growth, when autumns are warm. The role played by autumn precipitation is not as clear in Figure 2a, perhaps due to the small number of observations (n = 24).

The correlations between maximum tree-ring width and high temperatures and low-precipitation autumn seasons for the previous calendar year indicate a relationship with the tree's physiological acclimation process. Becwar et al. (1981) found that Engelmann spruce on Niwot Ridge underwent deep undercooling and that this enabled the trees to withstand the low temperatures of winter. The process of deep undercooling was initiated with gradual acclimation (a seasonal transition from the tender, frost susceptible, to the hardy, non-susceptible condition) to changing temperature and moisture conditions. The key appears to be gradual environmental change. Higher temperatures, or at least no extremely low temperatures, during the autumn season, appear to allow for this necessary gradual acclimation. During the process of acclimation, partial water is withdrawn from the interior of the plant cell (Levitt 1978) and eventually freezes extracellularly. Tolerance to environmentally-induced dehydration during the autumn season therefore may aid in the acclimation process. Foliage that is not acclimated sufficiently to environmental conditions may be critically stressed later in the winter. In the laboratory (Becwar et al. 1981), freezing was intracellular and lethal when temperatures dropped below the freezing limits of acclimated tolerance (−40°C). When a tree is subjected to inadequate autumn season conditions and the process of acclimation is hindered, stressful winter conditions apparently reduce the growing capacity of the trees during the following growing season.

A positive correlation (r = .55) was obtained between tree-ring width and the temperature of the actual calendar year's late spring/early summer (May through July) growing season. These results support two important and previously developed hypotheses: (1) adequate early growing-season temperatures, assuming sufficient soil moisture supplies, contribute significantly towards lengthening the season and hence promote more growth (r = .62 for May); and (2) the temperatures of the warmest month of the year are significant in maximizing tree growth (r = .51 for July). The first hypothesis has gained additional support from a variety of data sources and geographic areas (LaMarche 1973; LaMarche and Stockton 1974; Tranquillini 1979; Müller 1982; Hansen-Bristow 1986; Graumlich and Brubaker 1986). Müller (1982) found a minimum temperature value of +5°C

Table 4. Correlations (R-values) for Tree-Ring Indices and Climatic Data From the Como Climate Station (3018 m), Niwot Ridge

Monthly correlations	Temperature	Precipitation
Previous year's		
April	.21	−.11
May	.12	−.13
June	.03	.06
July	.18	.36
August	−.01	.28
September	.19	−.12
October	.74	−.49
November	.37	−.31
December	.17	−.02
Actual year's		
January	−.28	−.14
February	−.18	−.07
March	−.22	−.21
April	.14	−.33
May	.62	−.18
June	.06	.20
July	.51	.23
August	−.02	.21
September	.22	.03
Seasonal correlations		
Previous April through actual September	.36	−.11
Previous September through actual August	.35	−.25
Actual May through July	.55	−.09
Previous September and October	.61	−.39
Previous September and October, plus actual May through July	.71	−.09
Previous September through November	.59	−.52
Actual January and February	−.28	−.14

Table 5. Response Surface Regression Results Showing Previous Autumn (P. Aut.) and Actual Late Spring/Early Summer (Act. LS/ES) Climatic Variables Regressed with Actual Tree-Ring Indices

Climatic variables		Variables in the equation						Regression coefficients	
X	Y	a	b_1	b_2	b_3	b_4	b_5	R^{2a}	R_a^{2b}
P. Aut. temp.	P. Aut. precip.	1.0074	.1237	−.0602	−.0075[c]	−.0681	.0138	38.0	35.2
Act. LS/ES temp.	P. Aut. precip.	.8181	−.5903	−.2958	.0060[c]	−.2957	−.2836	30.3	27.1
Act. LS/ES temp.	P. Aut. precip.	.8583	.1830	−.3523	.1885	−.3669	.0086[c]	48.2	45.8

Note: The equation used to predict tree growth as a function of seasonal temperature and precipitation:

$$Z = a + b_1X + b_2Y + b_3X^2 + b_4Y^2 + b_5XY$$

where Z = tree growth indices averaged across sites
X, Y = climatic variables indicated
R^{2a} = squared multiple correlation coefficient of the regression equation
R_a^{2b} = R^2 adjusted for loss of degrees of freedom based on the number of predictors in the equation
b_1[c] = variables had to pass both tolerance and minimum tolerance tests to enter and remain in the regression equations. The SPSSX stepwise multiple regression procedure used here specified PIN (probability of *F*-to-enter) and POUT (probability of *F*-to-remove) values of 0.05 and 0.10, respectively. Variables included in the regression equations have the superscript c accompanying them.

to be of special significance for growth during the main phase of growth (May to mid-June). This +5°C minimum value isotherm for the growth period is found below the ecotone within the closed forest on Niwot Ridge. The second hypothesis supports Köppen's (1900) forest line designation of 10°C mean temperature for the warmest month (often July) of the year. The present-day temperature values recorded within the forest-alpine tundra ecotone (Table 1) place the 10°C July isotherm slightly above timberline.

Response surface equations for late spring/early summer (May through July) air temperatures and the previous autumn (September and October) total precipitation explained only 30 percent of the variance in tree growth (Table 5). In addition, the response surface (Figure 2b) fails to reveal any consistent trends linking tree growth and these climatic variables. The combination of previous autumn (September and October) temperatures and late spring/early early summer temperatures, and their squares and cross product, on the other hand, explains 48 percent of the variance in tree growth (Table 5). This response surface (Fig. 2c) shows that tree growth is greatest when autumn and late spring/early summer temperatures are highest. The response surface low indicates poor tree growth when autumns and late spring/early summers are cool. Again the small number of observations may explain the peaks and troughs to these trends.

Several other monthly and seasonal climate and tree-ring correlations (Table 4) are consistent with the physiological responses noted in this and in other studies. Positive correlations between precipitation and growth during the months of June, July, and August reflect adequate moisture supplies necessary during the growing season. Although the tree-ring width indices show fairly high autocorrelations (expected at this climatically stressed, high-elevation site), correlations with yearly lagged climate data are low.

Negative but low correlations are found between tree-ring width and winter temperatures (Table 4). High air temperatures induce cuticular transpiration and, although this process may contribute to only 3 percent of the total transpiration, during winter (when the stomates are closed) this situation becomes critical (Larcher 1975). On Niwot Ridge cuticular thickness values (a measure of resistance to water loss) decrease significantly with elevation from lower forest to ecotonal sites (Han-

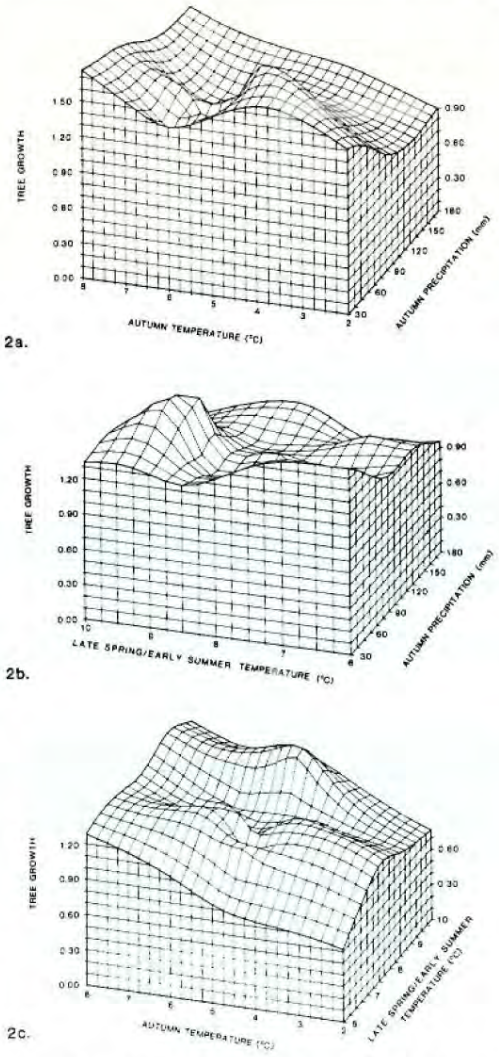

Figure 2. Response surfaces showing the influence of seasonal precipitation and air temperature on tree-ring growth. The visual assessment of these responses aids in determining the regression model for predicting climate from tree-rings. Figure 2a displays tree growth in response to the previous year's September and October temperature and precipitation; Figure 2b illustrates the response of tree growth to the actual year's May through July temperatures and the previous year's September and October precipitation; Figure 2c shows the tree growth response of the previous year's September and October temperatures and the actual year's May through July temperatures.

sen-Bristow 1986). Tranquillini (1979) stated that tree growth at timberline may be significantly limited by winter desiccation. Stressful climate conditions incurred during the winter appear to affect the amount of tree-ring growth during the subsequent growing season. Wardle (1968, 1974) has related winter desiccation to incompletion of hardiness due to preceding short, cool growing seasons.

A negative but low correlation was also obtained between tree growth and spring (March through May) precipitation (snow). Large amounts of snow during this period promote an insulating effect on soil temperatures. Greater snow depth and hence delay in soil warming inhibit the initiation of the growing season, shortening its overall length (Hansen-Bristow 1986). Similar results, in terms of the direction of this correlation, were obtained by Graumlich and Brubaker (1986) at timberline in Washington State. Okitsu and Ito (1984), on the other hand, found that moderate snow depths promoted the best performance of *Pinus pumila* Regel. (a snow-adapted dwarf species) on convex slopes in the high mountains of the Taisetsu Range, Japan. LaMarche and Stockton (1974) found precipitation at the Mount Evans site (Colorado Front Range) to be negatively correlated with tree-ring width in most months, although they caution that this result is quite different from those found for the Almagre Mountain (Colorado Front Range) and other western sites.

Climatic Reconstruction

Despite the existence of significant correlations between the previous autumn (September and October) and actual late spring/early summer (May through July) temperatures and tree-ring growth, reconstructions derived from regression models that express these climatic variables as a function of tree growth would have been unreliable because they cannot account for the effects of other variable(s) on tree growth. In addition, mean annual temperature could not be used for reconstructions in this study as it explained only a small amount of the variation in tree-ring widths ($r^2 = .12$) and, therefore, very little of the combined effects of the previous autumn and actual late spring/early summer temperatures. An additional climatic variable, the mean air temperature for

Table 6. Regression Results for Temperature Reconstruction

	Preliminary models					
	1	2	3	4	5	Final model
Coefficient (b)	4.214	5.134	4.193	4.495	3.996	3.830
Intercept (a)	1.713	.779	1.881	1.561	2.155	2.242
Summary statistics						
R^{2a}	50.0	74.1	49.6	45.7	57.7	50.1
R^{2b}	46.4	72.2	46.0	41.8	54.7	47.8
r^c	.68	.20	.64	.79	.45	—

[a] R^2 = squared multiple correlation coefficient of the regression equation.
[b] R^2 = adjusted for loss of degrees of freedom based on the number of predictors in the equation.
[c] r = correlation between independent observations and predictors made by the model.

the five months included in the previous autumn and actual late spring/early summer periods, provided the best predictor and was therefore used in this study.

The regression results (Table 6) indicate that the preliminary models used in the first part of the model-building process, estimated with the different subsets of observations, vary only slightly in their ability to predict independent temperatures. To ensure that the coefficient estimates for the final model (Table 6) were as precise as possible, they were re-estimated using the entire 1954–79 temperature series (with data for 1956 and 1957 missing).

Reconstructed temperatures for the previous autumn and actual late spring/early summer periods are generally lower than average (6.1°C) from 1545–95, although there is a large range in these values. This variation may reflect the small size of the sample of trees with tree-rings dating back this far. Values tend to be slightly higher from 1600–20, and then fluctuate around the average from 1620–45. Reconstructed temperatures are generally higher than average from 1645–90. Graumlich and Brubaker (1986) reconstructed mean annual temperatures and found a cool episode from 1600–50 followed by a short period of warmth from 1650–90 in the Cascade Range of Washington. The similarity of these reconstructions is striking. Values fluctuate around the mean from 1690–1830, with the high annual variability approximating that of 1965–79.

Lower-than-average temperature values are reconstructed for the period between 1835–1900. Graumlich and Brubaker (1986) found a similar cool episode from 1860–1900 and Douglas and Stockton (1975) indicate a cool autumn and winter but a warm spring in the late-1880s to mid-1890s. Temperatures from 1900–25 increased, although they were slightly lower than average. A late nineteenth and early twentieth century warming has also been documented by previous studies (LaMarche and Stockton 1974; Douglas and Stockton 1975; Jacoby et al. 1985; Graumlich and Brubaker 1986). From 1925–65 the temperature values increased. Again, this increase corresponds with a 1°C higher mean annual temperature from 1914–79 (compared to that from 1590–1913) found by Graumlich and Brubaker (1986).

Climatic records for the Rocky Mountain area (Bradley 1980; Barry et al. 1981) show warmer springs and summers and drier winters in the 1920s and 1940s than around the turn of the century. Global annual mean temperature values, based on land and marine data (Jones et al. 1986) also reflect this increase compared to climatic values dating back to 1861. From 1965–79, temperatures, as reflected by tree growth, decreased slightly initially and then increased. Again the variability of this period is similar to that for 1690–1830. The increase in global mean annual temperatures corresponds to that found by Jones et al. (1986). Spring and autumn seasons on Niwot Ridge for the 1960s and 1970s were found to be cool, although no change from the average was noted for summer values (Barry 1986). Graumlich and Brubaker (1986) found that a decline in tree growth and regional temperatures began in the 1940s within the Cascade Mountains of Washington. In contrast,

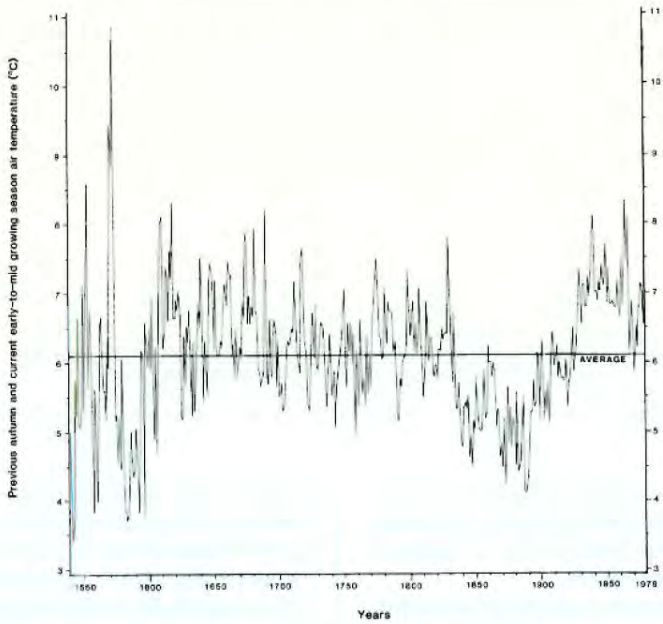

Figure 3. A reconstruction of autumn (previous year) and late spring/early summer (actual year) air temperatures.

LaMarche et al. (1984) noted that tree growth in the White Mountains of eastern California has increased since 1950, due perhaps to a fertilization by carbon dioxide even though there was an observed temperature decrease.

Short (1985), using pollen analyses coupled with fossil insect studies by Elias (1985), provides a long-term record of paleoenvironments for the Colorado Front Range. Her record differs from that proposed by Maher (1972) and covers a larger time span than that provided by this study. She did, however, find evidence for increasingly severe conditions during the last 1000 years. Climatic reconstructions within western North America, derived from a variety of techniques, are summarized in Hansen-Bristow and Ives (1984). In particular, it is noted that the advance of a local cirque glacier (Arapaho Peak) at about 300–100 BP (Benedict 1973) can be correlated with the reconstructed temperatures provided here. Short- to medium-term climatic fluctuations are modeled for the Canadian Rockies by Luckman et al. (1985) and Luckman (1986).

The reconstruction presented here indicates climatic variability and hence a relatively high sensitivity of tree growth to air temperature change within the upper forest-alpine tundra ecotone in the Colorado Front Range. Overall, reconstructed average previous year's autumn and actual year's late spring/early summer air temperatures indicate low values in the mid-to-late 1500s, higher values during the 1600s, fluctuating values from 1690–1830, low values from 1830–95, high values from 1925–65, and low values from 1965–79.

Management Implications

Niwot Ridge was designated a Biosphere Reserve in 1979 (part of the UNESCO Man and the Biosphere (MAB) Programme's international network) and the much larger area of the Front Range, south of Rocky Mountain National Park, became the Indian Peaks Wilderness under President Carter's signature the preceding year. These measures were taken to protect research activities and to provide im-

proved wilderness management, respectively, under the rapidly growing number of summer and winter recreational visitors from both the large east-slope urban corridor and out-of-state. Overnight stays in the Indian Peaks Wilderness continued to accelerate after inauguration and exceeded 125,000 by 1983. While accurate data are not available, day visits probably greatly exceed the number of overnight stays. Continued increase in human impact must be anticipated—trampling, destruction of vegetation around camp sites, fire pits, felling and topping of trees for camp fires, and air and water pollution.

One of the favored scenic areas is the forest-alpine tundra ecotone (Dow et al. 1981; Baumgartner 1983), and it has been argued that this area is one of the most highly sensitive to unthinking human impact. Of particular concern are the intriguing life forms of the prostrate, elfin-wood adaptations of the Engelmann spruce and subalpine fir (Ives and Hansen-Bristow 1983). These vegetatively reproducing, tree species-limit individuals, many of them at least 1000 years old, are often the target of urban garden ornamentation collectors. While in the long-term, *biological* time frame the trees of this ecotone are probably remarkably stable, within the shorter, *human* time frame they are highly susceptible to disturbance. Given the growth in knowledge of micro-climatic conditions and tree response relationships, particularly the augmentation of temperature inversions through the fencing of forest clearings (by fire or human intervention), it is reasonable to conclude that our already naturally stressed ecotones can incur irreparable damage if not managed with great care.

These general points are applicable not only to the Colorado Front Range but to all high elevation areas of the North American West. In addition to the immediate impacts of large numbers of recreationalists, possible impacts of atmospheric acidification (acid rain) and additional climatic variability, due to increasing carbon dioxide and other chemicals and to ozone depletion, cannot be ignored. Even if these larger scale global and regional effects are improved or may have been exaggerated, a combination of good management and better understanding of the dynamics and functioning of mountain ecosystems is an eminently responsible insurance against potential environmental degradation.

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