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MEDITERRANEAN CLIMATE EFFECTS. II. CONIFER GROWTH PHENOLOGY ACROSS A SIERRA NEVADA ECOTONE[1]

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Growth and xylem water potential of the lower elevation conifers *Pinus jeffreyi* and *Abies concolor* and the higher elevation *Pinus monticola* and *Abies magnifica* were monitored in their montane Mediterranean habitat of the southernmost Sierra Nevada mountains of California. Measurements were made across the ecotone between the midmontane and upper montane forests and through light and heavy snowfall years.

Radial stem growth, averaging ~1.5 mm/yr, started 2 wk after snow melt, providing that maximum air temperatures had reached 21°C, and ended when predawn water potentials fell rapidly at the onset of the summer drought. Leader growth started on or after a fixed date, providing that minimum air temperatures were above −4°C for *Pinus* species or +2.5°C for *Abies species*. The cue for leader growth was inferred to be photoperiodic. Leader growth ended when either a determinate internode length of ~1 mm was reached or predawn water potentials fell rapidly. *Abies magnifica* grew more rapidly than the low-elevation species, but had a shorter growth period; its annual leader growth, as a consequence, was only 35 mm/yr vs. 50 mm/yr for the low-elevation species. Needle growth was similarly determinate in the absence of early drought. This growth phenology contributes to determining species distribution across the ecotone.

Key words: *Abies*; conifer; ecotone; growth phenology; Mediterranean climate; *Pinus*; Sierra Nevada; snowpack.

The montane Mediterranean climate of the Sierra Nevada range of California is characterized by heavy winter precipitation—rain and snow in the midmontane forest and snow in the upper montane forest—and an extended period of summer drought (Oosting and Billings, 1943; Axelrod, 1976; Major, 1990). The ecotone between the midmontane forest and upper montane forest is marked by a major discontinuity in the distribution of conifer and other species (Mellmann-Brown and Barbour, 1995; Barbour and Minnich, 2000). In the southernmost Sierra Nevada this ecotone occurs at elevations between ~2400 and 2700 m. The overall objective of the work reported in this and in a companion paper in this issue (Royce and Barbour, 2001) was increased understanding of environmental factors and their interactions affecting conifer species distribution across this ecotone.

The midmontane (mixed conifer) forest of the southernmost Sierra Nevada is dominated by yellow pine (*Pinus ponderosa* Laws or *Pinus jeffreyi* Grev. & Balf.), Sierra white fir (*Abies concolor* Gordon & Glend. var. *lowiana* (Gordon) Murray), sugar pine (*Pinus lambertiana* Douglas), incense cedar (*Calocedrus decurrens* (Torry) Florin), and black oak (*Quercus kelloggii* Newb.). The upper montane (red fir) forest is dominated by Shasta red fir (*Abies magnifica* Murray, var. *shastensis* Lemmon) and western white pine (*Pinus monticola* Douglas). Trees found within the ecotone include *P. jeffreyi, P. monticola, A. concolor,* and *A. magnifica* (Barbour and Minnich, 2000; Royce and Barbour, 2001; nomenclature follows the Jepson Manual [Hickman, 1993]).

The summer drought limits growth, growth ending on or before drought onset (Kozlowski, Kramer, and Pallardy, 1991; Kramer and Boyer, 1995; Pallardy et al., 1995). At the same time, spring growth can begin only when air and soil warming become adequate to support growth (Emmingham, 1977; Lassoie, 1982; Kozlowski, Kramer, and Pallardy, 1991) and to preclude frost damage to tender growing tissue (Tranquillini, 1979; Kozlowski, Kramer, and Pallardy, 1991). Response to this warming may be immediate or may show a species-specific delay (Fowells, 1941; Emmingham, 1977; Pavlik and Barbour, 1991) perhaps through a photoperiod requirement.

Thus, growth can be expected to occur only within a window that begins with the melting of the snowpack and ends with the onset of the summer drought. Species that begin their growth substantially later than the melting of the snowpack (possibly because of a late photoperiod requirement) should have a shorter growth period than those that begin growth at the earliest opportunity. Such growth period shortening may occur at lower elevations (with early snow melt) or where soil moisture is rapidly depleted by competing vegetation or in years of limited snow pack and early snow melt.

Our objectives were to determine the species-specific timing of critical events in the phenology of conifer growth and to quantify how this timing interacts with the progression of weather to affect species distribution in the relatively unstudied southernmost Sierra, where the summer drought is most severe. Competition between conifer trees and between trees and shrubs for soil moisture should also affect conifer growth, and we wanted to identify the contribution of growth phenology to accentuating or mitigating such competitive effects. We expected that species would be more sensitive to environmental effects in or near the ecotone, because they would be at a limit of their range. In addition, the study area was near the southern limit of red fir, so we expected red fir to be particularly sensitive to environmental factors there.

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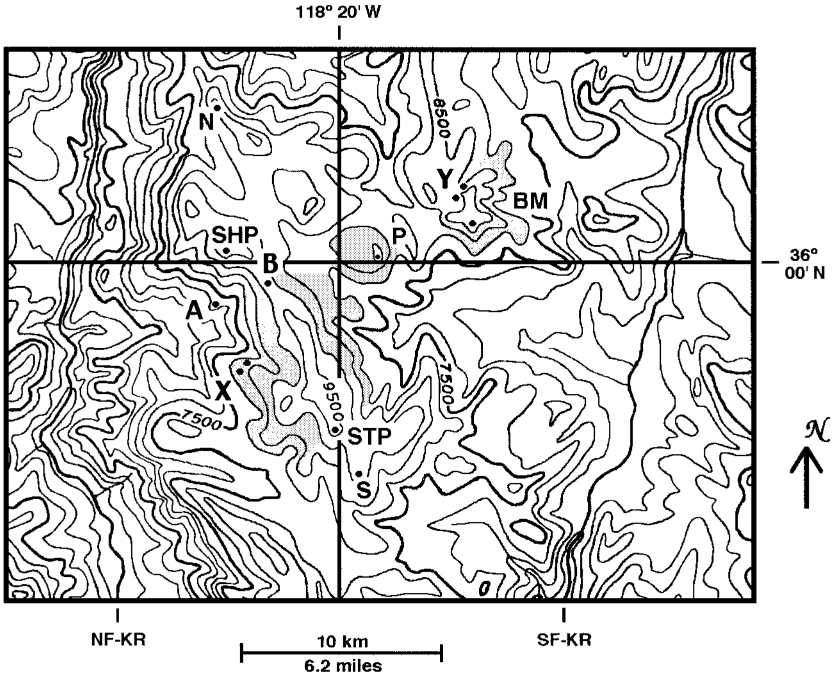

Fig. 1. Southern portion of the Kern Plateau of the Sierra Nevada, bounded on the west by the north fork of the Kern River (''NF-KR'') and on the east and south by the south fork of the Kern River (''SF-KR''). The contour interval is 152 m (500 ft). On the west side of the plateau, the Sirretta–Sherman Peak divide (between ''S'' and ''N''), extending 19 km (12 miles) from south of Sirretta Peak (''STP,'' 3041 m, 9977 ft) north past Sherman Peak (''SHP,'' 3020 m, 9909 ft), is generally between 2700 m (~8900 ft) and 2900 m (~9500 ft) elevation. Other high ground includes peak 2765 m (''P,'' 9070 ft, no name), 5 km (3 miles) east and Bald Mountain (''BM,'' 2860 m, 9382 ft), 11 km (7 miles) east. The locations of the 167 survey sites are indicated by the shaded areas. The permanent study sites are the low- and high-elevation reference sites, designated ''A'' and ''B,'' respectively, the west-side ecotone sites (two sites) designated ''X,'' on the west side of the Sirretta–Sherman Peak divide, and the Bald Mountain ecotone sites (two sites), designated ''Y'' (edited section of a U.S. Geological Survey map).

We report measurements of the progression of conifer growth and parallel measurements of air temperature and of water status that suggest mechanisms by which the montane Mediterranean climate of the Sierra affects the growth and distribution of conifer species.

SITE CHARACTERISTICS AND METHODS

Our 100-km^2 study area was located on the Kern Plateau in the southernmost Sierra Nevada, in Sequoia National Forest ~70 km south of Sequoia National Park, near 36°00′ N and 118°20′ W (Fig. 1). Climate in the 570 km long Sierra Nevada shows a gradient from mesic in the north to xeric in the south (Parker, 1994), and vegetation shows a parallel gradation of species cover (Barbour and Minnich, 2000). By working in the southernmost Sierra, we maximized the opportunity to study the effects of xeric conditions. Our quantitative results, then, constitute a point at the end of a gradient characterizing the entire Sierra, and this should be kept in mind in applying them to other Sierra sites.

Winter storms approach the Sierra Nevada predominantly from the northwest off the north Pacific Ocean with winds from the southwest, resulting in the deposition of most precipitation on the west side of the range, and thus, more xeric conditions on the shadowed east side (Major, 1990; California Department of Water Resources, 1998). In the southernmost Sierra, the broad Kern Plateau offers the highest terrain, and snow deposition is heavy on its west slope. In the study area, the Sirretta–Sherman Peak divide (with elevations generally of 2700–2900 m and peaks at 3041 and 3020 m) constitutes the western portion of the Kern Plateau, and its west slope and crest receive this heavy snow deposition. More xeric conditions prevail downwind, such as on peak 2765 m and Bald Mountain (2860 m), prominent 11 km east of the divide (Fig. 1).

Data were collected over the 1994 and 1995 seasons. The winter of 1994 began a drought year in California, while the winter of 1995 saw extremely heavy winter snowfall (Royce and Barbour, 2001). The large differences between conditions in 1994 and 1995 assisted in the identification of effects of differing winter snow conditions on spring growth.

Research sites—Results of a 1992 preliminary survey of 167 sites within the ecotone allowed us to select six permanent sites for intensive continuous study in 1994–1995. The permanent sites were regularly visited on a 1–3 wk cycle from the spring snowmelt until late fall. Sites were less regularly visited through the remainder of the year and through 1996 to monitor temperatures and precipitation. (1996 was a year of near-normal snowpack.) The permanent sites were selected with vegetation typical for their elevation, aspect, and general location, with as many tree species as possible present, and with minimal human disturbance (Fig. 1, Table 1).

Four of the six permanent sites were within the ecotone, two pairs of sites each consisting of a north- and a south-facing site, in order to test for the effects of insolation differences (sites within each pair ~0.7 km between each other). Regression analysis on the survey-site data was used to identify species relative cover expected for particular environmental conditions, and data for the permanent sites were compared with these model predictions to establish that the ecotone permanent sites were, indeed, ''typical'' (Royce, 1997).

Of the four ecotone sites, one pair, sites XN (north-facing) and XS (south-facing), were located in the deep snow belt on the west side of the Sirretta–Sherman Peak divide at an elevation (2500 m) within the lower portion of the ecotone. Two storm-shadowed permanent sites, YN (north-facing) and YS (south-facing), were located in the area to the immediate north of Bald Mountain, at an elevation (2660 m) within the upper portion of the ecotone. Like the west side (X site) pair, the Bald Mountain (Y site) pair was located on opposite sides of a minor west-trending spur. Although sites YS and YN were located at higher elevations than sites XS and XN, and although snow pack is generally greater and snow melt later at higher elevations, sites YN and

TABLE 1. Permanent research site characteristics: (A) physical characteristics and (B) tree cover (%).

A) Physical characteristics

Site	Elevation	Slope	Aspect	No-snow date[a]	Last-water date[a]
Sites just below or just above the ecotone					
A	2.23 km (7.33 kft)	Level	—	8 April (98)	4 May (124)
B	2.82 km (9.25 kft)	Level	—	4 June (155)	4 June (155)
Sites within the ecotone					
XN	2.51 km (8.25 kft)	15°	NNW	28 May (148)	28 May (148)
XS	2.49 km (8.17 kft)	13°	S	8 May (128)	8 May (128)
YN	2.66 km (8.72 kft)	24°	NNW	16 May (136)	16 May (136)
YS	2.66 km (8.72 kft)	22°	SSE	24 April (114)	5 May (125)

B) Tree cover (%)

		Relative cover[b]						
Site	Total cover	ABCO	ABMA	PIJE	PILA	PIMO	CADE	QUKE
A	30	17	—	47	11	—	10	15
B	20	—	80	—	—	20	—	—
XN	25	15	58	2	—	25	—	—
XS	20	38	5	54	3	—	—	—
YN	30	38	12	22	—	28	—	—
YS	30	38	—	60	—	—	—	—

[a] No-snow and last-water dates are the dates when the ground was two-thirds bare and when soil was last saturated with water, respectively, and are averages over the 1994, 1995, and 1996 seasons. Dates in parentheses are Julian dates.

[b] Species: ABCO = *Abies concolor*; ABMA = *A. magnifica*; PIJE = *Pinus jeffreyi*; PILA = *P. lambertiana*; PIMO = *P. monticola*; CADE = *Calocedrus decurrens*; QUKE = *Quercus kelloggii*.

YS received less snow and had earlier snowmelt dates because of storm shadowing. Comparison of data from these shadowed and unshadowed sites was used to test for the effects of differing snowpack and snowmelt date separately from other possible effects of elevation.

Finally, two permanent reference sites were located outside the ecotone in the heavy snowfall belt on the Sirretta–Sherman Peak divide. A level midmontane forest site (A, 2230 m) was located on top of a spur on the west side of the divide, and a level upper montane forest site (B, 2820 m) was located on top of the Sirretta–Sherman Peak divide.

All sites were typically 100–200 m across. Sites were of a woodland character, with 20–30% overstory cover and often with extensive shrub and forb cover where trees were absent. Soils were sandy to loamy entisols or inceptisols, 0.5–1.5 m deep, with extensive rock outcrops. All sites were located where the soil parent material was the common southern Sierra granodiorite.

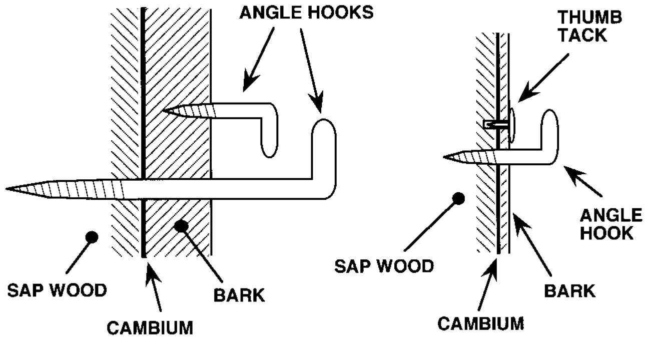

Fig. 2. Schematic cross sections of the two dendrometer designs used to measure cambial growth. The design on the left was used for large trees with thick bark, while the design on the right was used for saplings with thin bark. In each case an angle hook was threaded into the sap wood, where it remained motionless as growth took place. In the mature-tree design, a second, smaller angle hook was threaded into the bark and moved outward as the bark moved outward with cambial growth. In the sapling design, a simple thumb tack was glued to the bark to replace the second hook. The shank of the thumb tack was placed in a predrilled hole, so that it would not bind to the sap wood. The relative positions of the two angle hooks were measured directly with a dial caliper. Relative positions of the angle hook and the thumb tack were measured with the caliper used in its depth gage mode. The design is similar to dendrometers used by Reineke (1932) and Fowells (1941).

For each conifer species found at each of these six permanent sites, three 1–2 m tall saplings were selected for the measurement of leader growth, top branch growth (firs only), needle growth, radial stem growth, and water potential. One or two juvenile or pole-sized trees, ~15 cm in diameter at 1.5 m, and one or two mature trees were selected for the measurement only of stem growth and water potential. A total of 74 saplings, 41 pole-sized trees, and 27 mature trees were monitored.

Temperatures and precipitation—On-site temperatures were monitored using Taylor maximum–minimum thermometers, spot checked against two two-point thermographs. Both thermometers and thermograph sensors were mounted in shelters ~1.5 m above ground level. Individual temperature readings and differences between readings at different sites both had an estimated accuracy of ±1°C. Extreme values of the maximum and minimum temperatures recorded by the maximum–minimum thermometers over 10–20 d periods and thermographs over these periods agreed within 1°C. A plastic U.S. Weather Bureau funnel-type bulk rain gage was mounted in an open location near the thermometer enclosure at each site.

Water status—Xylem water potential was monitored for all trees and shrubs at all sites (Royce and Barbour, 2001).

Growth—Stem (radial) growth consisted of the formation of new sapwood and bark, specifically the increase in the thickness of a layer that included all living stem tissue plus part of the outer sapwood and part of the inner bark. Two dendrometers of the design shown on the left of Fig. 2 were installed ~1.5 m above ground on the trunk of each pole-sized and mature tree. They were installed on the east and west sides of the tree in order to detect any formation of reaction wood, the prevailing wind being from the west. One dendrometer of the design shown on the right of Fig. 2 was installed 3–5 dm above ground on the west side of each sapling. Depth to the cambium at each location on each tree was determined while drilling a hole that was later used as a clearance hole for the large hook. A dial caliper was used to make repeated measurements of the distance between the two hooks or between the hook and thumb tack, until a standard error of 0.02 mm was achieved. Stem growth measurements were made shortly after sunrise and (1994 only) mid-afternoon. All methods are fully detailed elsewhere (Royce, 1997).

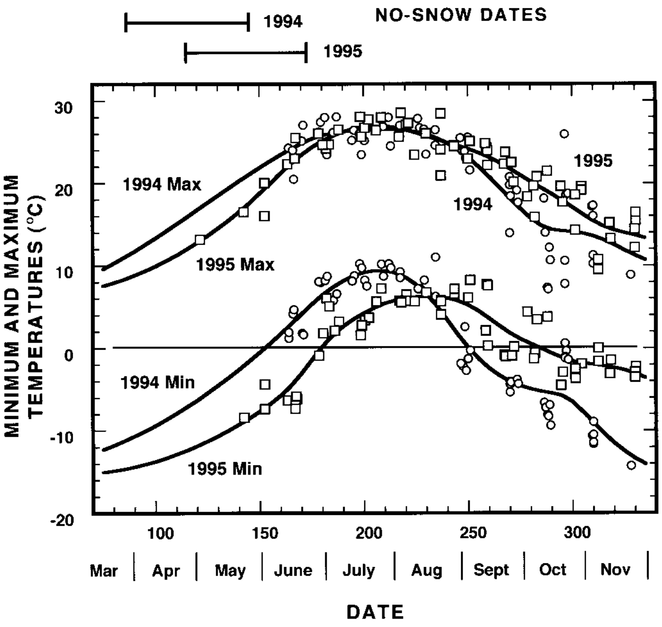

Fig. 3. Spline fits for maximum and minimum temperatures in 1994 and 1995. The fits are applicable to an elevation of 2600 m (8520 ft). The data points shown are temperature readings from the maximum–minimum thermometers at the permanent research sites (circles, 1994 data; squares, 1995 data). Temperatures were adjusted to the 2600 m elevation using the elevation gradient measured between the high- and low-elevation sites, given by the expression,

$$(\partial \text{ temperature}/\partial \text{ elevation})_{\text{latitude, date}} = A \cos [(2\pi/365)(\text{date} - B)] + C,$$

where the variable date is the Julian date. For minimum temperatures, $A = 3.3$°C/km, $C = -5.8$°C/km, and $B = -37$ d, and for maximum temperatures, $A = -3.3$°C/km, $C = -7.7$°C/km, and $B = -8$ d. This gradient was also used to calculate temperatures at particular sites from the spline fits. The ranges of no-snow dates shown are for the permanent sites.

Leader and new needle growth on conifer saplings (except *C. decurrens*) is from buds formed the previous season (Cannell, Thompson, and Lines, 1976; Lanner, 1976; Hallgren and Helms, 1988; Fielder and Owens, 1989; Kozlowski, Kramer, and Pallardy, 1991), and growth of the new leader or "candle" was monitored. On fir saplings with lateral branches in well-defined whorls, the mean growth of the two longest lateral branches from the topmost whorl was also monitored. Needle length was determined by sampling needles on the new leader.

RESULTS

Environmental conditions—Differences in temperature minima between the low- and high-elevation sites A and B, when temperatures were at their highest in midsummer, corresponded to an elevation gradient of −9°C/km, while differences in temperature maxima between the same two sites in midsummer corresponded to an elevation gradient of −3°C/km. (Since both sites were locally level, their insolation should have been similar. Since they were located on ridge tops, they should not have been subject to the accumulation of cold air from drainage winds.) The value of the gradient in the minimum temperature became less negative at earlier and later dates, while the value of the gradient in the maximum temperature became more negative at earlier and later dates. (See the caption to Fig. 3.) These values may be compared to the dry adiabatic lapse rate of −9.8°C/km and midsummer ambient values reported for the Sierra Nevada of −5.8°C/km at nearby Sequoia National Park (Major, 1990) and −4.3°C/km at Yosemite National Park (Parker, 1994).

Temperature differences of up to 10°C between the years 1994 and 1995 in maximum and minimum temperatures persisted for several weeks at times during the ~6 mo long intensive monitoring periods (Fig. 3). These year-to-year differences appeared to be due to unseasonable regional or local warming or cooling, because temperature differences between sites on the same dates showed less year-to-year variation than did the temperatures themselves (Royce, 1997).

We defined a no-snow date as the earliest spring date on which two-thirds of the ground at a site was free of snow, drifts typically remaining in shaded spots. This was the date when appreciable soil warming above 0°C might be expected, warming that might have constituted a stimulus for growth activity. No-snow dates on the permanent sites became later by 95 d/km (SE = 7) of elevation; became earlier by 16 d (SE = 3) if storm shadowed, as on Bald Mountain; and became earlier by 10 d (SE = 2) if south facing or later by 10 d (SE = 2) if north facing (linear model: RMS error = 5 d; $r^2 = 0.96$; P for each of the variables < 0.0001). Differences related to elevation and storm shadowing arose mainly through differences in snow deposition. Differences related to aspect arose from differences in melt rates, both during the spring period of rapid snowmelt and earlier during clear winter days. If late spring snow or rain storms brought substantial additional water to a site, we defined a last-water date as the last date when the soil column was saturated with water. This was the date when uninterrupted soil drying began due to evaporation and transpiration. Uncertainty in the determination of the no-snow and last-water dates was ±3 d.

A less sharply defined low-moisture date, typically 60 d after the last-water date, marked the transition from the spring growth period to the summer drought period. This date was marked by the beginning of a sustained decline of predawn water potentials and the termination of growth (Royce and Barbour, 2001).

Growth—At all sites and for all growth modes—radial expansion of the main stem or elongation of the leader, topbranchs, or needles—growth rates for individual trees appeared to be nearly constant during the period of most rapid growth. (Data for *P. jeffreyi* shown in Fig. 4 are typical.) An abrupt start and end of growth marked well-defined start and end dates. However, among trees of the same species at the same site, there was a substantial variation in these dates (up to 30 d), in the magnitude of growth (often by a factor of two or three), and in response to drought. Needle growth was not monitored until new needle tissue had hardened sufficiently not to be damaged by the manipulation that accompanied the measurements, so for all species, the needle growth start date was actually obtained by a back extrapolation. For some species the period over which growth was measured was too short to allow making this extrapolation reliably, and no analysis was possible.

The average timing of conifer growth outside the ecotone showed similar patterns for all species (Fig. 5). At the low-elevation, midmontane site A, the start of stem growth was delayed over a month from snowmelt, and the start of leader growth by additional weeks. These delays were roughly similar in 1994 and 1995, even though the no-snow dates for these two years differed by 3 wk. At the high-elevation, upper montane site B, snowmelt occurred later, and delays to the start of

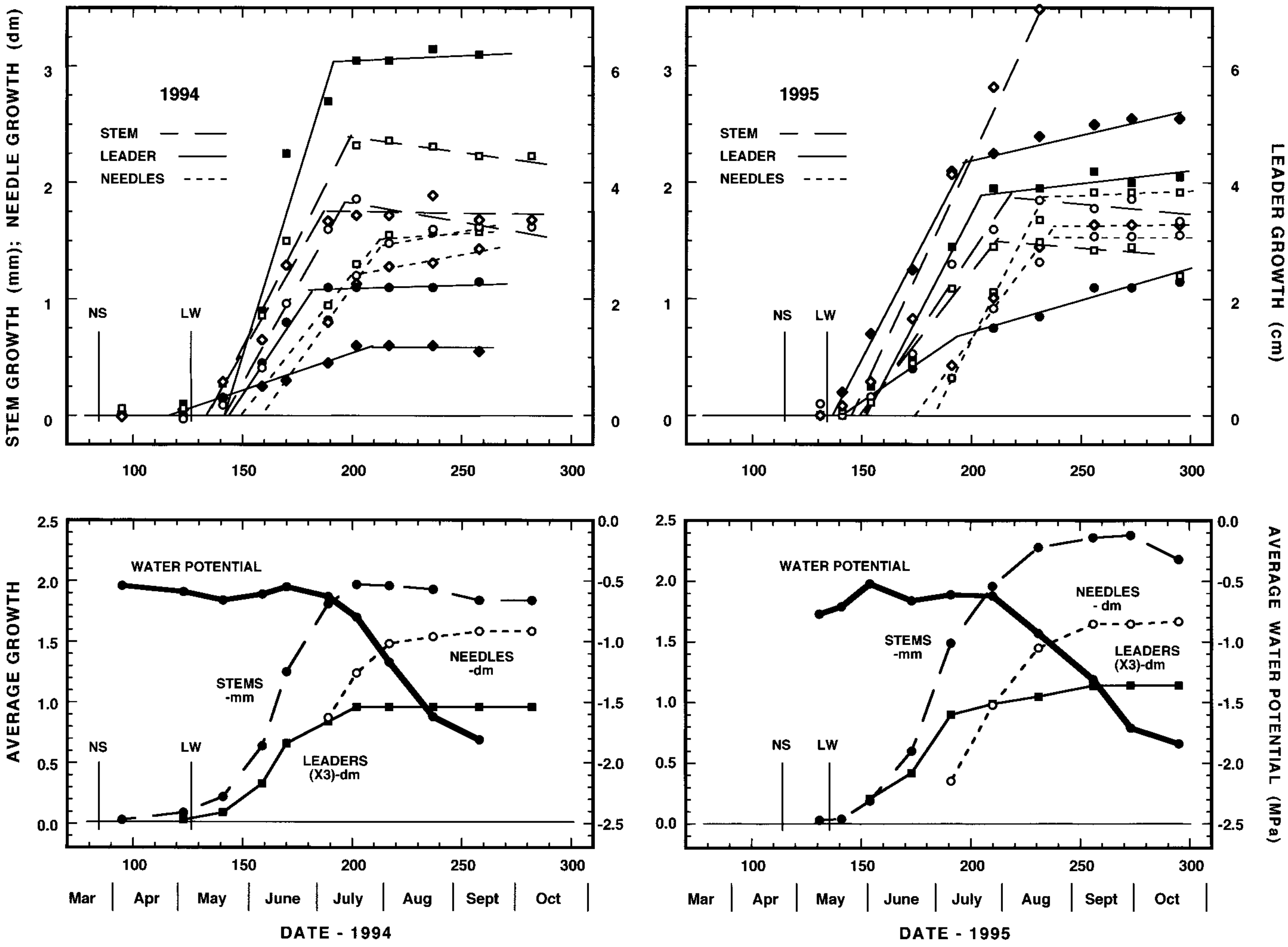

Fig. 4. Growth of the three jeffrey pine (*Pinus jeffreyi*) saplings at the low-elevation site A, as measured over the 1994 and 1995 seasons. Data for the other conifers studied are similar (Royce, 1997). The upper two panels show data for individual trees and the straight-line fits made to those data, while the lower two panels show these data averaged. Also shown is the predawn xylem water potential averaged over these trees. The no-snow (NS) and last-water (LW) dates at this site are marked by vertical lines.

growth were minimal, particularly in 1995 when snowmelt was later than 1994 by 4 wk. Needle growth on the pines *P. jeffreyi* and *P. lambertiana* started ~2 wk after the start of leader growth, but there was no such delay for *A. magnifica.*

ANALYSIS

Temperatures—The influence of temperature on growth rates and growth timing was distinguished from other possible (unidentified) effects of elevation by exploiting differences in the progressions of temperature between 1994 and 1995, particularly the springtime depression of temperatures associated with the late snowmelt in 1995. Recorded maximum and minimum temperatures at all sites were reduced to an elevation of 2600 m with the use of the date-dependent elevation gradients measured between the lowest and highest sites, A and B. The combined data for all sites were then fitted with cubic splines of stiffness $\lambda = 10\,000$, separate fits being made for maximum and minimum temperatures and for each year (Fig. 3). Combining data from all sites in this fashion provided greater statistical power than would have been the case with separate fits for each site.

Growth—While for all modes of growth, individual trees displayed nearly linear growth during their main period of rapid growth, at the end of this period, dendrometers usually showed a reversal, reflecting stem shrinkage, presumably due to the loss of stored water during the summer drought. Leaders sometimes showed continued slow growth at the end of their rapid growth. Growth data for individual conifers were fitted with three straight lines—before growth starts (=0), during growth, and postgrowth (Fig. 4). The complete growth data were then characterized by four parameters. The "growth start" date was taken as the date marking the intersection of the growth line with the horizontal axis. The "growth end" date was taken as the date corresponding to the intersection of the growth and postgrowth lines, and "annual growth" was taken as the growth corresponding to that intersection.

The slope of the postgrowth line, if any, was needed to precisely determine the end date but not further analyzed. Henceforth, "growth" refers only to the period of rapid growth. Rounding of the growth curves at the start and end of rapid growth was sometimes seen, but overall, the fit described above proved a better match to the data than did a logistic function.

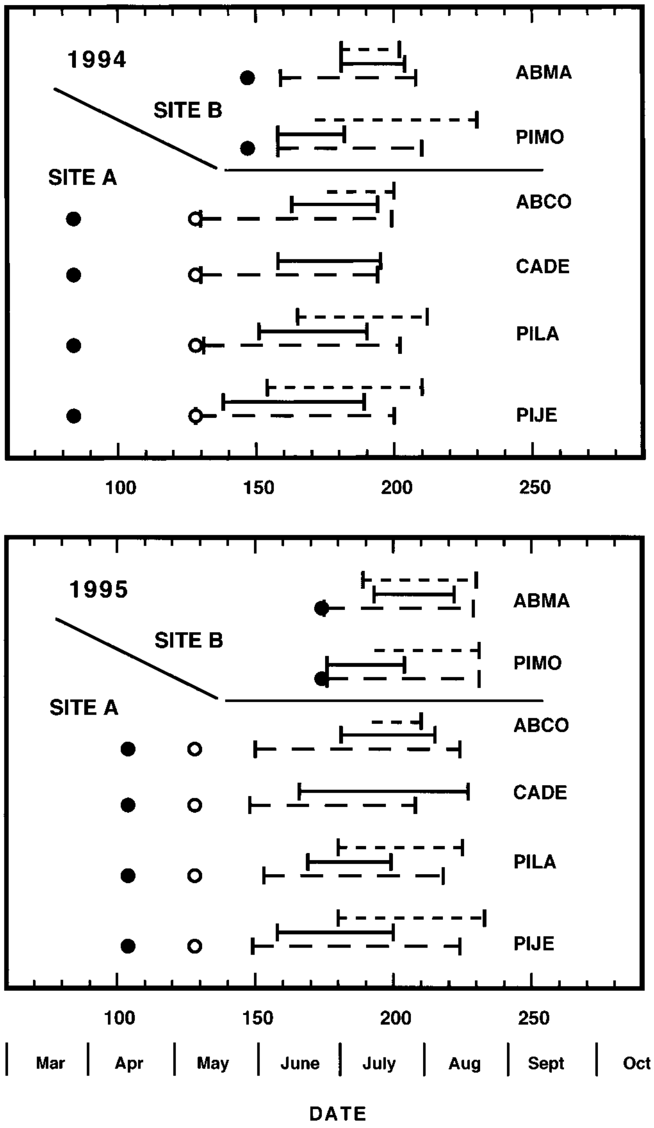

Fig. 5. Growth time lines for the conifer species studied at the lowest (Site A) or highest (Site B) sites, both immediately outside the ecotone. Cambial growth = long dashed line. Leader growth = solid line. Needle growth = short dashed line. Dates shown are averages of measurements on multiple trees. Local no-snow (filled circle) and last-water (open circle) dates are also shown.

The three parameters characterizing the growth period itself—start date, end date, and annual growth—were analyzed in terms of environmental variables using ANOVA and regression analysis (JMP, version 3.2; SAS Institute, 1995). Data were analyzed with trees divided into two groups—saplings and large trees—or with all trees together. The numbers of pole-sized and mature trees were inadequate to permit the separate analysis of each of these groups with confidence.

Growth phenology—The analysis of growth phenology consisted of a search for environmental variables whose values at either the start or the end of growth were the same for all trees of a species at all sites and in both years of observation. Such variables we termed "threshold variables" in the sense that growth started only after a threshold value of the variable was reached or growth ended before or when a threshold value was reached. We identified these variables by the fact that their values at either the growth start or end dates, for each tree of a species in both years, appeared subjectively to be closely clustered. We tested the identification of these variables as threshold variables with ANOVA, where we sought large values of P (usually >0.2) in ANOVA of that variable with site–year, a non-numeric variable combining site and year of observation. Conversely, variables yielding small values of P (<0.05) did not qualify as threshold variables, because their values at the start (or end) of growth were significantly different at different sites and/or in different years.

In these analyses, site variables included elevation, slope, the observed no-snow date, site itself, and year (of observation); aspect was parameterized as the cosine of the aspect angle measured from north. Site, year, and site–year were treated as discrete, with repeated measures at each value. Elevation, slope, cosine(aspect), and the no-snow date were treated as continuous numeric variables. Air temperatures were estimated for specific dates from the spline fits (Fig. 3), corrected to the elevation of the site of interest. Daily maximum, minimum, and daytime average temperatures [$=0.5\ (T_{\max} + T_{\min}) + 0.212\ (T_{\max} - T_{\min})$; Running, Nemani, and Hungerford, 1987] were estimated for the start or end dates for each mode of growth on each tree in each year. Temperatures were treated as continuous variables. Other tree-specific variables treated as continuous included growth rates, total growth, and the growth start and end dates themselves (Julian values).

Start of growth—When data from individual trees at all of the permanent sites were analyzed, the start of radial stem growth and leader elongation each showed two types of behavior (Fig. 6). For cases (site–year) where the no-snow date was early (most sites in the drought year 1994 and some low-elevation or south-facing sites in 1995), the start of stem growth appeared to be associated with a threshold in the daytime maximum temperature of $>\sim 21°C$ for all species. For these early cases, ANOVA showed no significant variation of these temperatures with site–year (*P. jeffreyi*, $P > 0.8$; *P. monticola*, $P > 0.4$; *A. concolor* and *A. magnifica*, $P > 0.2$). The date itself and the minimum temperature were not threshold variables, because ANOVA showed significant variations between cases characterized by site–year (*P. jeffreyi*, $P < 0.004$ and $P < 0.03$, respectively; *A. concolor* and *A. magnifica*, $P < 0.001$ and $P < 0.0001$, respectively, Table 2).

The start of leader growth for these early snowmelt cases occurred on fixed dates for *P. jeffreyi*, *A. concolor*, and *A. magnifica* ($P > 0.3$). On the other hand, neither the minimum nor the maximum temperature were threshold variables, with ANOVA again showing significant differences between cases (*P. jeffreyi*, *A. concolor*, and *A. magnifica*, $P < 0.05$). *Pinus jeffreyi* leader growth started about 2 wk before *A. concolor*, and *A. magnifica* almost 3 wk after *A. concolor* (Table 3).

Start dates for stem growth associated with late no-snow dates were delayed a constant amount of ~2 wk from the no-snow dates. These delays were greater on heavily shrub-covered locations (*P. jeffreyi* and *A. magnifica*, $P > 0.6$; *A. concolor*, $P > 0.3$) than on open sites ($P \sim 0.1$). ANOVA showed significant differences between cases for the date itself and the minimum and maximum temperatures, so these variables were not threshold variables (*P. jeffreyi*, *A. concolor*, and *A. magnifica*, $P < 0.0004$).

Late start dates for leader growth were associated with a

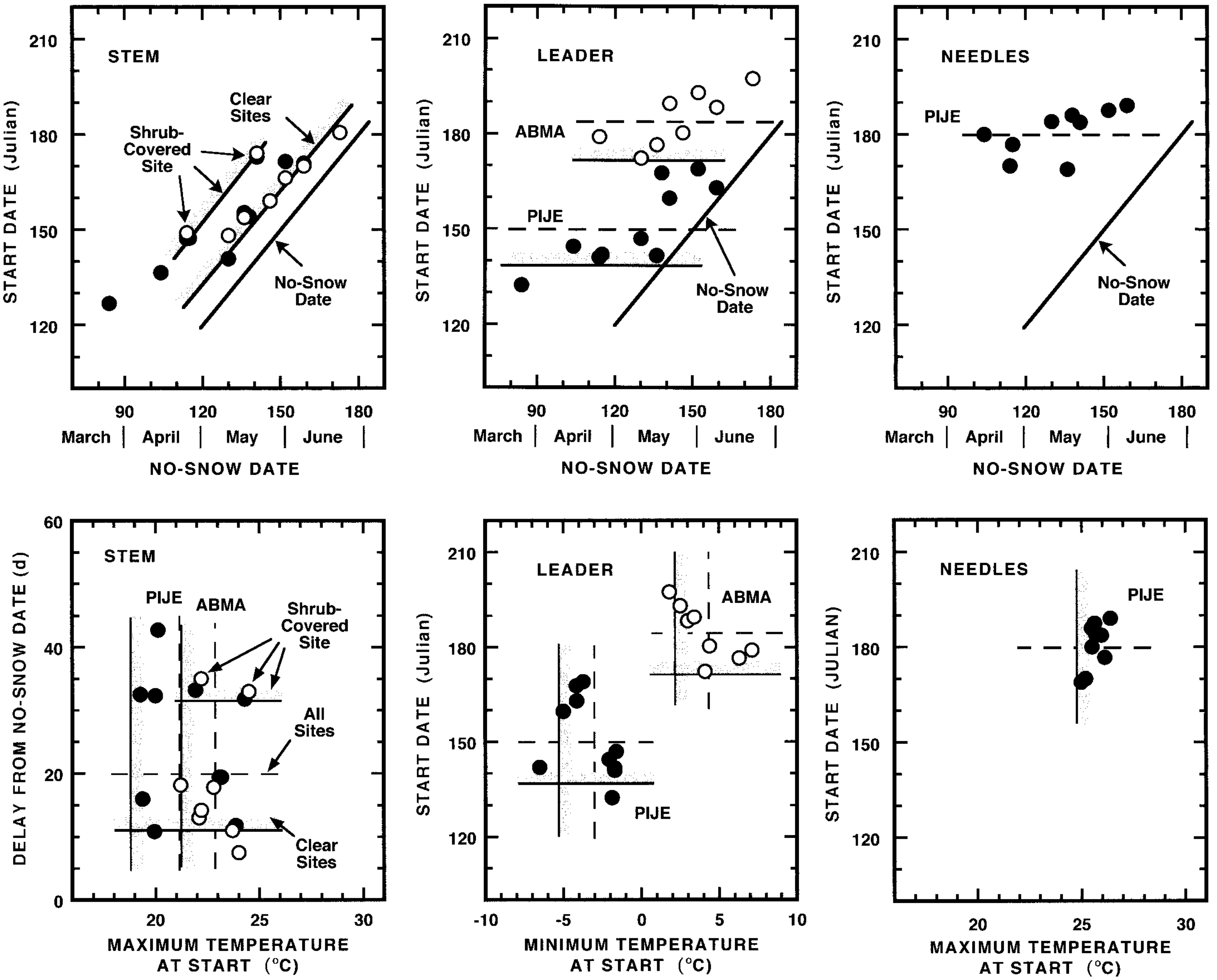

Fig. 6. Contrasting environmental conditions for the start of stem, leader, and needle growth of the dominant midmontane conifer *Pinus jeffreyi* (solid symbols) and the dominant upper montane conifer *Abies magnifica* (open symbols). Each symbol represents an average over all trees of a species for a particular site–year. Standard deviations around these plotted site–year averages are: start date, 5 d; maximum temperature, 0.9°C; minimum temperature, *A. magnifica,* 0.6°C; minimum temperature, *P. jeffreyi,* 1.1°C. Solid shaded lines, interpreted as threshholds, are offset one standard deviation (listed above) from values obtained by averaging the individual plotted site–year averages over groups of site–years that appear to be governed by a single threshhold. Dashed lines are average values for all trees where site–years fall into more than one threshhold group. Maximum and minimum temperatures are at the start date and were calculated from the fit shown in Fig. 3, corrected to the elevation of each site.

threshold in the daily minimum temperature of >-4°C for *P. jeffreyi* ($P > 0.9$) and $>+2$°C for the firs ($P > 0.3$). For both pines leader growth started 3 wk before *A. concolor* leader growth, and *A. magnifica* (found at higher elevations) started leader growth 1 wk after *A. concolor.* The date itself and the maximum temperature were ruled out as threshold variables for the late group, because date values were later than values exhibited by the early group, and maximum temperature values were higher than those characterizing the start of growth in the early group. No differences were observed in the start of stem growth between saplings and large trees.

For *P. jeffreyi,* start dates for needle growth on the leader were all characterized by a similar maximum temperature ($P > 0.1$), ~5°C higher than for the start of growth of the leader itself. Sufficient data for analysis were not collected on the start of needle growth on the other species (Table 4).

Each element of a multiple threshold for the start of growth appeared to be necessary but not sufficient (Fig. 6). Where an early-group threshold appeared to be controlling, the late-group threshold had already been met, and vice versa. Depending on the no-snow date in a particular year, trees at a particular site could fall into either the early or late groups. While the three principal ecotone conifers, *P. jeffreyi, A. concolor,* and *A. magnifica,* showed the same general threshold behavior, threshold values were different for each species (Tables 2–4). Data for *P. monticola,* found on only three of the six permanent sites, were inadequate to provide clear results in many cases.

TABLE 2. Environmental factors affecting stem growth (radial trunk growth). Data are averages over all size classes and all cases (site–years) or cases in groups. An asterisk indicates a probable controlling or limiting threshold. Standard errors for means are about one-third the standard deviation; standard deviations are shown in parentheses. No entry is made for correlations or regressions if ANOVA indicates $P > 0.05$. "Correlation" is the relevant coefficient; "slope" refers to the relevant regression. PIJE = *Pinus jeffreyi*; PIMO = *P. monticola*; ABCO = *Abies concolor*; ABMA = *A. magnifica*.

Environmental factor	PIJE		PIMO		ABCO		ABMA	
Average start date (Julian)	153	(17)	163	(11)	154	(14)	164	(13)
Early group								
Date (Julian)	138	(11)	161	(11)	142	(9)	150*	(8)
Min. T_{max} (°C)	20*	(1)	22*	(1)	21*	(1)	22*	(1)
Min. T_{day} (°C)	13*	(1)	15*	(1)	14*	(1)	15*	(1)
Late group								
Date (Julian)	163	(10)	165	(10)	168	(3)	173	(7)
Min. delay from no-snow date (d)								
Open sites	16*	(7)	12	(7)	14*	(4)	9*	(5)
Brushy sites	32*	(5)			31*	(5)	34*	(9)
Average end date (Julian)	221	(22)	215	(19)	217	(15)	220	(15)
Min. predawn water potential (MPa)								
Average	−0.7*	(0.1)	−0.4	(0.1)	−0.6	(0.2)	−0.6*	(0.1)
Early group	−0.7*	(0.1)	−0.5	(0.1)	−0.7*	(0.2)	−0.6*	(0.1)
Duration (d)	68	(14)	53	(14)	64	(10)	56	(12)
Growth rate (μm/d)	20	(12)	22	(8)	25	(9)	24	(9)
Dependence on maximum temperature over the growth period								
Correlation	0.4						0.6	
Slope (μm·d^{-1}·degree^{-1})	4						7	
Total annual growth (mm/yr)	1.4*	(0.8)	1.2*	(0.5)	1.6	(0.6)	1.4	(0.6)
Dependence on maximum temperature over the growth period								
Correlation	0.40		0.42		0.29		0.64	
Slope (mm·yr^{-1}·degree^{-1})	0.3		0.2		0.2		0.5	
Temperature averages during growth								
T_{max} (°C)	25	(1)	25	(1)	26	(1)	26	(1)
T_{min} (°C)	4	(2)	4	(2)	4	(2)	4	(2)

End of growth—As the season progressed, water potentials measured on each tree became more negative, and growth stopped as potentials began to fall rapidly (Fig. 4). Stem growth on *P. jeffreyi* and *A. magnifica* stopped when their predawn water potentials fell below threshold values. Predawn xylem water potentials for each tree were converted to soil moisture fraction (SMF) values using curves determined by measurements on large trees (Royce and Barbour, 2001). Threshold values for *P. jeffreyi* were −0.68 MPa and SMF = 0.55 ($P > 0.7$), and for *A. magnifica* −0.56 MPa and SMF = 0.58 ($P > 0.2$), though large *A. magnifica* sometimes exceeded the threshold ($P < 0.02$) (Fig. 7). Similar water potential thresholds were observed for *A. concolor* and *P. monticola* (*A. concolor* large trees, $P > 0.5$), but unidentified factors produced significant differences among some trees.

Leader growth on *P. jeffreyi*, *P. monticola*, and *A. magnifica* stopped at a similar internode length for members of the same species (*P. jeffreyi*, $P > 0.6$; *P. monticola*, $P > 0.1$; *A. magnifica*, $P > 0.4$). *Abies magnifica* data fell into two groups (Fig. 7), one group responding more specifically to a water potential minimum (−0.59 MPa and SMF = 0.51, $P > 0.6$) and one to maximum internode length ($P > 0.5$) if the water threshold was not reached. Water potential decline was particularly important in terminating growth in the drought year 1994 or at site B, with the shallowest soil. Similar final internode length and water potential thresholds appeared to be important for *A. concolor*, but some trees exhibited anomalous earlier termination of growth ($P < 0.01$). The phenology of top lateral branch growth generally paralleled that of leader growth for both firs.

The end of needle growth on the leader for *A. magnifica* and *P. monticola* occurred when a fixed needle length was reached ($P > 0.4$). Additionally, for *P. jeffreyi*, low-elevation and storm-shadowed cases showing early termination of growth were characterized by a water potential threshold of −1.12 MPa (SMF = 0.50) ($P > 0.6$).

Duration of growth—The duration of stem growth for *P. jeffreyi* and *A. concolor* averaged 66 d, somewhat longer than for *P. monticola* and *A. magnifica*. The duration of *P. jeffreyi* and *A. concolor* stem growth increased on south-facing sites (*P. jeffreyi*, $P < 0.001$; *A. concolor*, $P < 0.02$), and the duration of *A. magnifica* stem growth decreased with elevation ($P < 0.0001$). The aspect effect may have resulted from two factors. First, on south-facing sites, the no-snow date was sufficiently early that in two cases (site–years XS–94 and YS–95) growth-period soil moisture was augmented substantially by late-spring rainstorms. Second, soils on the two south-facing sites appeared subjectively to be less rocky at the surface and may have been deeper and have held more moisture than on other sites. The elevation correlation may have been associated with an unusually shallow soil layer at the highest elevation site B and the high-elevation ecotone site YN.

The duration of leader growth appeared to be fixed at 51 d

Table 3. Environmental factors affecting leader elongation in saplings. Data are averages over all saplings and all cases or cases in groups. Notation is as in Table 2.

Environmental factor	PIJE	PIMO	ABCO	ABMA
Average start date (Julian)	150 (13)	161 (11)	172 (15)	184 (9)
Early group				
Date (Julian)	141* (7)	154 (6)	158* (5)	177* (6)
Min. T_{max} (°C)	21* (1)	21* (1)	23 (1)	25 (1)
Min. T_{day} (°C)	14* (1)	15 (1)	17 (1)	20 (1)
Late group				
Date (Julian)	164 (7)	166 (11)	185 (4)	192 (5)
T_{min} (°C)	−4* (2)	−4 (2)	+2* (1)	+3* (1)
Average end date (Julian)	202 (13)	198 (20)	207 (10)	211 (11)
Min. predawn water potential (MPa)				
Average			−0.5 (0.1)	−0.5 (0.1)
Early group	−0.6 (0.1)	−0.4 (0.1)	−0.7* (0.1)	−0.6* (0.1)
Internode length (mm)				
Average	1.1* (0.4)	1.1* (0.4)	1.1 (0.5)	0.6 (0.2)
Late group	1.1* (0.4)	1.1* (0.4)	1.4* (0.4)	0.8* (0.2)
Duration (d)	51* (15)	36 (17)	35 (7)	27* (7)
Internode growth rate (μm/d)	23 (9)	34 (21)	33 (19)	25 (11)
Dependence on maximum temperature over the growth period				
Correlation			0.3	
Slope (μm·d^{-1}·degree^{-1})			0.4	
Internode/needle number, see Table 4.				
Total leader annual growth (mm/yr)				
Average	50 (31)	21 (6)	49 (37)	35 (16)
Late group	71* (30)	21* (6)	71* (46)	45* (14)
Dependence on maximum temperature over the growth period				
Correlation				0.6
Slope (mm·yr^{-1}·degree^{-1})				12
Temperature averages during growth				
T_{max} (°C)	25 (1)	25 (21)	26 (1)	26 (1)
T_{min} (°C)	3 (2)	2 (2)	6 (2)	6 (2)

for *P. jeffreyi* and 27 d for *A. magnifica* (*P. jeffreyi*, $P > 0.4$; *A. magnifica*, $P > 0.2$). The duration of *P. monticola* and *A. concolor* leader growth fell between these two values. With the exception of one case (site–year YS–94, where the water potential threshold was reached early), the duration of *P. jeffreyi* needle growth was also a fixed value, 55 d ($P > 0.4$).

Growth rates—Daily rates of radial stem growth were ~23 μm/d for all species. For *P. jeffreyi* saplings, *A. concolor* large trees, and all *A. magnifica*, the daily stem growth rate was proportional to the daily maximum and average daytime temperatures, either temperature averaged over the growth period of each tree (Fig. 8, *P. jeffreyi* and *A. magnifica*, $P < 0.0005$;

Table 4. Environmental factors affecting needle elongation. Data are averages over all saplings and all cases or cases in groups. Notation is as in Table 2.

Environmental factor	PIJE	PIMO	ABCO	ABMA
Start date (Julian)	180 (8)			
Min. T_{max} (°C)	26* (1)			
Min. T_{day} (°C)	19* (1)			
End date	231 (13)			219 (12)
Predawn water potential (MPa)				
Averages	−0.8 (0.3)			
Early group	−1.1* (0.2)			−0.7 (0.2)
Needle length (mm)				
Averages	133 (69)	35* (5)	10* (3)	10* (2)
Late group	152* (16)	35* (5)	10* (3)	10* (2)
Duration (d)	55 (9)			
Needle growth rate (mm/d)	2.5 (0.6)			
Needle number[a]	136 (59)	104 (21)	45 (21)	55 (13)
Total needle length on leader (m)	18 (9)	3.7 (1.0)	0.5 (0.3)	0.5 (0.2)

[a] Internode numbers are equal to these values for ABCO and ABMA, one-third these values for PIJE, and one-fifth these values for PIMO.

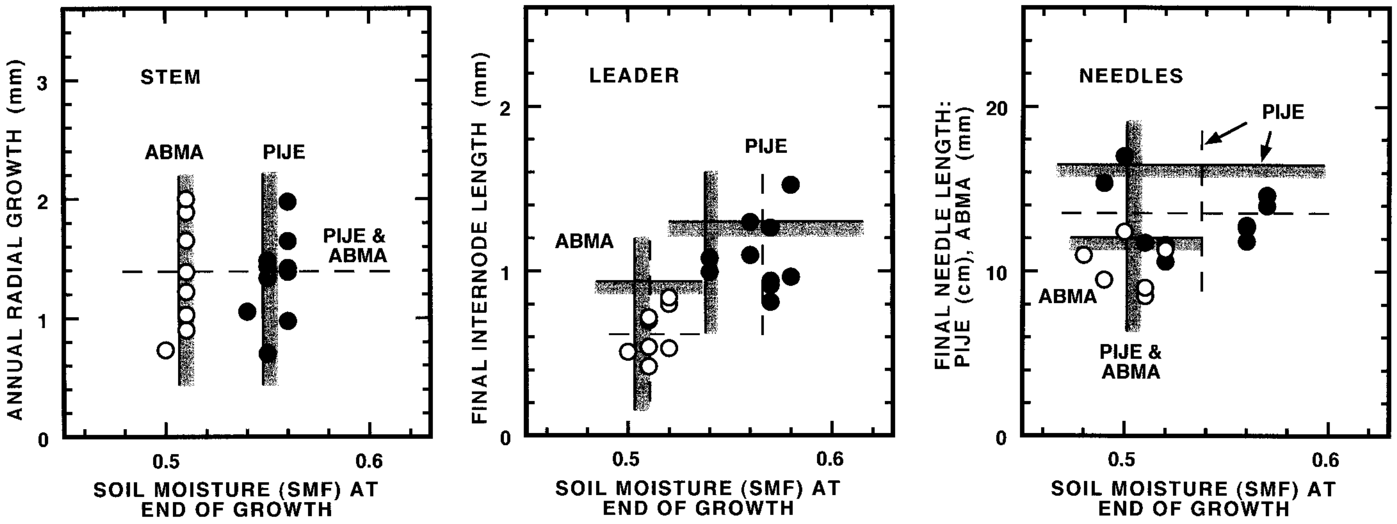

Fig. 7. Contrasting environmental conditions for the end of stem, leader, and needle growth of the dominant midmontane conifer *Pinus jeffreyi* (solid symbols) and the dominant upper montane conifer *Abies magnifica* (open symbols). Notation is as in Fig. 6. Standard deviations around plotted average values are: stem growth, 0.5 mm; internode length, 0.2 mm; needle length, *A. magnifica,* 1.5 mm; needle length, *P. jeffreyi,* 1.5 cm; Soil moisture fraction (SMF), stem, 0.004; SMF, leader, 0.003, SMF, *A. magnifica* needles, 0.003; SMF, *P. jeffreyi* needles, 0.007. Water potential values in the analysis were converted to soil moisture values using curves reported elsewhere (Royce and Barbour, 2001).

A. concolor, $P < 0.01$). However, large *P. jeffreyi* trees showed no dependence on environmental variables ($P > 0.97$).

Annual stem growth averaged 1.4 mm/yr for all species. Its dependence on the environmental variables generally paralleled that of the daily growth rate. Annual growth was just the product of daily growth and duration of growth, since growth was linear, and variations in the former were much larger than in the latter. Sapling annual growth for *P. jeffreyi* and *A. magnifica* depended on the maximum growth-period temperature ($P < 0.0005$). Large trees showed no dependence on any environmental variable (*P. jeffreyi,* $P > 0.8$; *A. magnifica,* $P > 0.2$), with the exception of *A. concolor*, where annual stem growth showed the same dependence on maximum growth-period temperature as saplings of *P. jeffreyi* and *A. magnifica* ($P < 0.002$). *Abies concolor* saplings showed little variation with site–year, except for an anomalously high growth for site–year YS–95.

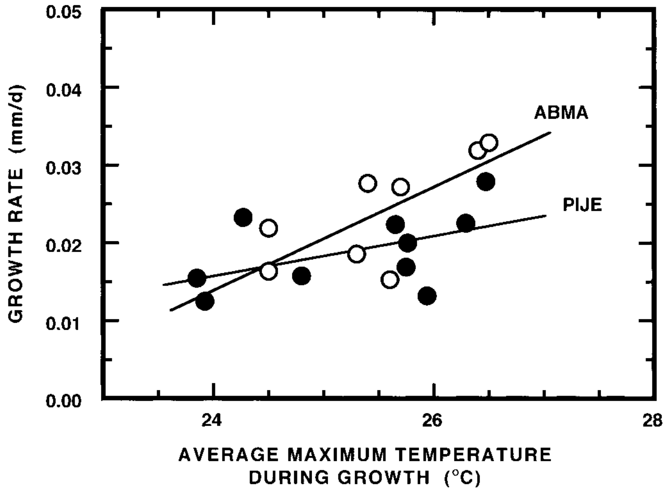

Fig. 8. Rates of stem growth of the dominant midmontane conifer *Pinus jeffreyi* and the dominant upper montane conifer *Abies magnifica.* The average maximum temperature during growth is the maximum temperature calculated from the fit shown in Fig. 3, corrected to the elevation of each site, and averaged over the duration of growth of each tree. Standard deviations around plotted values are: growth rate, 0.007; *P. jeffreyi* temperature, 0.3; *A. magnifica* temperature, 0.8.

Internode growth on the leader for *P. jeffreyi* and *A. magnifica* averaged 24 μm/d and showed no dependence on environmental variables ($P > 0.6$). The *P. monticola* and *A. concolor* growth rate was higher. *Abies concolor* growth had a positive dependence on the maximum temperature averaged over the growth-period ($P < 0.0005$). The *P. jeffreyi* needle growth rate showed only a weak dependence on aspect (south-facing sites favored) and maximum growth-period temperature ($P \sim 0.1$).

Internode numbers on the leader (equal to fir needle primordium or pine fascicle primordium numbers) averaged ~45 for *P. jeffreyi* and *A. concolor,* 21 for *P. monticola,* and 55 for *A. magnifica.* As a result, the total leader daily growth rate was fastest for *A. magnifica.* Total leader annual growth for *P. jeffreyi* and *A. concolor* averaged 50 mm, but only 35 mm for *A. magnifica* because of its short duration of growth, and only 21 mm for *P. monticola* because of its smaller number of internodes. For *P. jeffreyi* and *A. concolor* the number of primordia was greater on the south-facing sites ($P < 0.002$), perhaps because of better soils, as discussed earlier. Annual total leader growth showed the same variation with aspect as internode number (*P. jeffreyi,* $P < 0.001$; *A. concolor,* $P < 0.02$), and as did total annual needle growth on the leader (*P. jeffreyi,* $P < 0.04$; *A. concolor,* $P < 0.006$). For *P. monticola* and *A. magnifica,* needle number was insensitive to the environmental variables, as was total needle growth on the leader ($P > 0.4$). However, *A. magnifica* annual total leader growth responded to maximum growth-period temperature ($P < 0.006$).

DISCUSSION

Environmental factors affecting growth—Temperature appears to be the principal environmental factor controlling the start of conifer growth. Soil temperature thresholds between 4°C and 7°C and air temperature heat sum requirements for both stem activity and bud swell have been widely reported for several conifers (e.g., Cleary and Waring, 1969; Waring, Emmingham, and Running, 1975; Cannell, Thompson, and Lines, 1976; Lopushinsky and Kaufmann, 1984; cf. Kozlowski, Kramer, and Pallardy, 1991). In our study, the start of stem growth was found to be delayed at least 2 wk past local snowmelt, perhaps reflecting a need for soil (and root) warming. In the central Sierra, Kunz (1988) found *A. concolor* and *A. magnifica* started stem growth each year on a date closely associated with snowmelt. In the present study, the start of growth was further delayed if the immediate area where the trees were growing was heavily shrub covered, probably because shade cast by the shrubs delayed soil warming. If snow melt was exceptionally early, the start of stem growth was further delayed, until a daily maximum air temperature was reached. The start of *P. jeffreyi* needle growth appeared to be similarly associated with a threshold in the daily maximum air temperature.

Damage thresholds for growing shoots of cold-adapted pines, such as those in the Sierra, have been reported between −4° and −18°C, with a threshold around −12°C for *P. ponderosa* (closely related to *P. jeffreyi* but growing at lower elevations). Thresholds for other conifers were near −4°C (Parker, 1955; Glerum, 1973; Christersson, 1985; Berrang and Steiner, 1986; Burr et al., 1989, 1990). In our study, leader growth was found to start only after daily minimum air temperatures were above threshold values, around −4° for the pines with their large, heavily insulated terminal buds, and between +2° and +3° for the firs, with their smaller terminal buds. This delay, in response to minimum air temperature, presumably protected the growing shoot from nighttime frost damage.

The start of leader growth was found to require that a specific date also be reached, if minimum air temperatures had warmed to above threshold values early, as in the drought year 1994 or at the lower elevation sites. This requirement for the start of growth was found not to be associated with any temperature threshold, so we infer that it was a photoperiod requirement. The total requirement for the start of leader growth, then, was that both minimum temperature and photoperiod thresholds be exceeded. (Cf. Tranquillini, 1979; Kozlowski, Kramer, and Pallardy, 1991.) The delays that we observed between start dates for *A. concolor* and *A. magnifica* leader growth of 1 wk for minimum-temperature control or of 3 wk for photoperiod control are consistent with a 2-wk delay observed between *A. concolor* and *A. magnifica* in the central Sierra (Pavlik and Barbour, 1991; see also Kunz, 1988).

The termination of the growth of conifers in the Sierra has been associated with the decline of water potentials (Hallgren and Helms, 1988; Pavlik and Barbour, 1991), as is the case more generally (reviews by Bradford and Hsiao, 1982; Kozlowski, 1982; or Pallardy et al., 1995). Increased total conifer stem growth (Zahner and Donnelly, 1967; Howe, 1968; Lassoie and Salo, 1981; Robertson, Jozsa, and Spittlehouse, 1990) and canopy growth (Myers, 1988) are associated with continuing water availability. In our study, stem growth was found to end when predawn xylem water potentials became more negative than threshold values, and *P. jeffreyi* needle growth was found to behave similarly.

Conifer internode length has been reported to be determinate, so that total, final conifer leader length is controlled only by internode number (fir needle or pine fascicle number). In general this final leader length has been reported to depend on conditions the previous year, when needle (or fascicle) primordia were formed. Drought the previous year reduced primordia numbers and leader length, and high temperatures increased primordia numbers and leader length (e.g., Lassoie, 1982; Junttila, 1986; Fielder and Owens, 1989; cf. Kozlowski, Kramer, and Pallardy, 1991). However, conifer leader growth is also reported to be terminated early due to a falling predawn xylem water potential associated with soil drying (e.g., Clements, 1970; Garrett and Zahner, 1973; Cannell, Thompson, and Lines, 1976; Hallgren and Helms, 1988; cf. Pallardy et al., 1995).

In our study we found that final internode and/or final total leader length appeared to be ''conditionally determinate,'' i.e., that growth ended when a maximum length was reached, but only when a drought condition did not develop and terminate growth prematurely. Both the completion of determinate growth and a premature drought termination of growth appear to occur commonly in the study area.

Determinate conifer needle growth has been reported, but needle growth of pines has also been reported to continue as long as water was available (e.g., Garrett and Zahner, 1973; Cannell, Thompson, and Lines, 1976; Linder et al., 1987; Myers, 1988). In our study, final needle length appeared to be conditionally determinate, as in the case of leader length, except that for some *P. jeffreyi* cases, the maximum needle length was not reached if water potentials became too negative early.

As reported for other conifers (Kramer and Kozlowski, 1979), stem growth rates were found generally to increase as the maximum temperature over the growth period increased. The average rates observed in our study were similar to those measured on saplings of *A. concolor* and *A. magnifica* in the central Sierra (Pavlik and Barbour, 1991).

Conifer leader growth rates have been observed to increase with temperature (Junttila, 1986; cf. Kramer and Kozlowski, 1979), as has been seedling annual growth (Hellmers, 1966; Cleary and Waring, 1969; Lavender and Overton, 1972; Heninger and White, 1974). In our study, daily internode growth rates for *P. jeffreyi* and *A. magnifica* were found to show no particular temperature dependence, while the rate for *A. concolor* increased with temperature. Internode numbers (and fir needle or pine fascicle primordium numbers) on the leader were larger for *A. magnifica* than *P. jeffreyi* and *A. concolor*. With an only slightly reduced internode growth rate, the total leader growth rate was faster for *A. magnifica.* This faster growth rate increased with temperature and was supported by an apparently higher rate of soil moisture uptake (Royce and Barbour, 2001). However, annual leader growth in *A. magnifica* was reduced over that of *A. concolor* and *P. jeffreyi* because of its shorter duration of growth.

Pavlik and Barbour (1991) found both a peak daily leader growth rate and a total, annual leader growth for *A. concolor* to be some three times the values we report here. For *A. magnifica* they found daily rates to be almost two times the rate we report here and annual growth to be some three times the value reported here. However, their measurements were made in the central Sierra Nevada, where the environment was more mesic, soils may have been deeper, and where trees were probably from different genetic populations (Mitton, 1995). The latter is certainly true of *A. magnifica*, since our Kern Plateau measurements reported here were on the variety *shastensis*, whereas the central Sierra measurements were on the more widespread variety *magnifica.*

In previous Sierran studies, Hallgren and Helms (1988) reported increased needle primordium formation in fir seedlings with watering, but total leader growth in the next year was insensitive to the resulting increase in the number of nodes, consistent with a drought cut-off of leader growth rather than any control by a determinate internode length. Kunz (1988) found annual leader growth to increase with the previous winter's precipitation.

At high elevations in mountains of the north or of continental interiors, low winter temperatures may produce frost damage or frost–drought damage (Hinckley, Lassoie, and Running, 1978; Kozlowski, 1982; Kozlowski, Kramer, and Pallardy, 1991; Havranek and Tranquillini, 1995). However, the relatively mild minimum temperatures of the Sierra are not likely to cause such damage. Normal winter nighttime minimum temperatures at the elevation of the ecotone are around −8°C, with daytime maxima above freezing (Baker, 1944; NOAA, 1992). In our study, the lowest temperature recorded was −17°C, though rare extremes down to −25°C have been reported for the southern Sierra (Baker, 1944). Damage thresholds for winter-hardened tissues of temperate-zone conifers, however, are generally below −30°C (e.g., Glerum, 1973; Sakai and Weiser, 1973; Timmis, 1976; Sakai, 1978, 1979, 1982; Sakai and Eiga, 1985; Öquist and Martin, 1986; Sakai and Larcher, 1987; Burr et al., 1989, 1990; Thomas and Lester, 1992; reviewed in Havranek and Tranquillini, 1995).

Growth phenology and ecotone position, a critical timing model—The no-snow and last-water dates appear to be key parameters in determining progression of the environmental conditions important to conifer growth. The local no-snow date influences the temperature regime at the site. Because the start of growth often appears to be controlled by temperature thresholds, growth is keyed to this date. The last-water date sets the timetable for eventual soil moisture depletion by evapotranspiration and, hence, the end of growth. This means that a last-water date falling later than the no-snow date will extend the time available for growth. Any additional delay in the start of leader growth imposed by a photoperiod requirement will shorten the time available for growth.

The following model for growth in the presence of interspecies competition for soil moisture appears to account for the distribution of conifer species in our area. The model assumes that species will be at a competitive advantage if leader growth starts sufficiently early to allow the completion of determinate growth before soil moisture depletion terminates growth. In the presence of shrub competition or competition from other conifers for water, this timing becomes particularly important to success, because such competition advances the onset of drought conditions.

The model suggests that species successful in the upper montane forest, where the no-snow and last-water dates generally coincide, would be at an advantage if they grew more rapidly than species found only in the midmontane forest, where there is an earlier no-snow date but a last-water date the same as that at higher elevations. This prediction was born out in the faster total leader growth rate of the upper-montane dominant *A. magnifica* as compared to midmontane *P. jeffreyi* or *A. concolor.* The competitive ability of *A. magnifica* was enhanced by its ability to deplete soil moisture rapidly early in the growth period, and the importance of this ability was accentuated by the limited moisture available in the shallow soils at the high-elevation sites where *A. magnifica* was found (only ~50 cm to parent material at the highest elevation site B). Similarly, shallow soils, when present in the midmontane forest, should enhance the vulnerability of conifers to early growth termination due to competition for moisture, such as from shrubs (Royce and Barbour, 2001).

At lower elevations or in drought years, the start of leader growth will be controlled by the photoperiod requirement, independent of external environmental conditions, but an early termination of growth due to early drought onset will shorten the duration of growth. The absence of *A. magnifica,* with an exceptionally late photoperiod requirement, from the midmontane forest may be associated with such a reduction of the duration of leader growth. Kunz' (1988) observation from the central Sierra that the annual leader growth of fir increases in years of heavy winter precipitation is consistent with this model, because such years should also have delayed snowmelt and summer drought. His observation that this effect is more pronounced in *A. magnifica* than *A. concolor* can be explained by the later start of growth for *A. magnifica* and its resulting growth period being relatively more sensitive to end-date variations.

Under appropriate circumstances competition for moisture may not be critical in limiting leader growth, though it will still limit stem growth. This is apparently the case where determinate growth of *A. magnifica* leader internodes was seen in nondrought years on sites with deeper soils and where such determinate growth for all *A. concolor* and *P. jeffreyi* cases was seen on lower elevation sites mostly with deeper soils (80–160 cm at the lowest elevation site A).

We conclude that the interaction of species-specific controls on growth phenology (particularly an inferred photoperiod threshold for the start of leader growth) and the site-specific microenvironment (characterized by the no-snow and last-water dates) appears to have a critical influence on total growth, and hence, on the competitive ability of conifer species at higher elevations. The distribution of conifer species across the midmontane–upper montane forest ecotone appears to be a result of this competition.

These results may be useful in predicting the success of reforestation following logging. They may also be useful in understanding post-fire succession or effects of fire suppression on forest composition. Further, they suggest a rather complex potential response to climate change, depending on the time of year when such changes occur. Reduced winter snowfall (accompanied by an earlier no-snow date) should favor low- vs. high-elevation conifer species, thereby shifting the midmontane–upper montane forest ecotone to higher elevations. Such a winter effect by itself should not have a major effect on conifer growth away from the shifting ecotone. On the other hand, reduced late-spring rainfall should adversely affect growth more widely, primarily throughout the midmontane forest. Both of these climate changes and responses would be expected from a long-term persistence of la niña conditions (like the year 2000); a similar persistence of el niño conditions (like 1995 or 1998) would have the opposite responses.

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