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CLIMATES OF SUBALPINE PINE WOODLANDS

T. Weaver

ABSTRACT

The climate of whitebark pine (Pinus albicaulis) *woodlands is generally cold (average daily maxima and minima in January are -2 and -11 °C, respectively) and snowy 1 to 3 m maximum pack) in winter and warm (July average temperatures are 21 and 4 °C, respectively) and dry (July to September precipitation averages 102 mm and individual months can be rain free) in summer. The tree's lower altitudinal limit probabily is set by the competition of trees better able to compete for necessary resources such as light, water, and nutrients. In contrast its upward extension may be limited zonally by summer frosts and locally by desiccation. While the presence of one stone pine species is apparently a good indicator of an equivalent climate for other stone pine species, its presence does not indicate an identical climate and may therefore not indicate an equivalent climate for nonpine species with different climatic requirements.*

INTRODUCTION

Climate is a major determinant of plant (or community) presence, and due to this linkage, particular climax communities suggest particular climates and vice-versa. Extant vegetation and climatic data cannot, however, predict each other perfectly because other factors also affect dominance; these include propagule availability, substrate, biotic (for example, grazer or pathogen) or abiotic (for example, fire or windthrow) disturbance, and time. While they are less than universal, good predictions can be had by stratifying out the confounding factors one by one, that is, by focusing on one biotic region, one substrate, only undisturbed stands, and only mature stands.

Plant or community indicators of climate have been useful historically to new settlers of unexplored, undisturbed, and uninstrumented areas. And they are still useful in areas too complex to instrument economically. Climate-vegetation relationships have been studied at the world and continental levels by ecologists including Clements (1916), Holdridge (1947), Schimper (1903), Walter (1973), Walter and others (1975), and Whittaker (1975). The work is naturally extended to mountain regions where managers wrestle with moderately large land units containing "a world of variation." Work relevant to the Northern Rocky Mountains includes that of Baker (1944), Callison and Harper (1982), Daubenmire (1956), Harper and others (1980), Holdridge (1947), Price and Evans (1937), and Weaver (1980).

This paper describes and compares climates of pine woodlands near timberline. Its objectives are: (1) to characterize the climate of whitebark pine (*Pinus albicaulis*) communities with respect to factors important to the tree and its associates, (2) to compare the climate of whitebark pine woodlands with those of communities immediately above and below them with the object of generating hypotheses to explain the distribution of each type, and (3) to compare the whitebark pine climate with the climates of Eurasian stone pines as a test of the hypothesis that stone pine woodlands indicate similar climates worldwide.

METHODS

The climates of whitebark pine woodlands were characterized by summarizing data (CDOT 1961-70; Leeson 1989; Losleben 1983; and USDC 1951-80) collected in stands representative of the community. The temptation to include data from stations not in whitebark pine woodlands, but in some imagined "whitebark zone," was resisted because the heterogeneity of high-altitude microclimate makes it probable that such data would misrepresent the vegetation studied. While use of a longer record would have been desirable, data were summarized for 10 years, because few stations have a longer record and use of the same record length facilitates comparison of extremes. Ecologists consulted on the choice of stands are listed under "Acknowledgments." Data from Kings Hill, MT, Crater Lake, OR, and Old Glory Mountain, BC, were complete. Temperature data were unavailable from Ellery Lake; thus I violated my approach and substituted temperature data from a site (White Mountain I = Crooked Creek [3,123 m]) without whitebark pine, but with similar latitude, longitude, and altitude, and a more continental climate. Data from the Sunshine Station at Banff were gathered for avalanche forecasting, and only those from 1978 were sufficiently complete for my application.

Whitebark pine climates are contrasted with those of adjacent vegetation types. Instrumented subalpine fir environments with occasional or seral whitebark pine appear at Yellowstone Lake, WY, and Cooke City, MT (Despain and Rankin 1989). Alpine stations would ideally be paired with whitebark woodland sites from the same region—as the Lake or Cooke and Kings Hill sites almost are—but no data from alpine stations other than Niwot Ridge, CO, and White Mountain, CA, were available.

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While White Mountain II (Barcroft, 3,837 m) temperature data probably represent conditions above whitebark krumm- holz reasonably, the White Mountains are far drier than mountains usually containing whitebark pine. Data from Niwot Ridge, CO, undoubtedly represent conditions above whitebark krummholz better (Billings 1989).

Climates of environments dominated by closely related stone pines (Lanner, this proceedings; Mirov 1967) were compared with those of whitebark pine by summarizing data from stations in those types. Decade-long data sets from three *Pinus cembra* sites were supplied by Tranquillini (1989). Since *Pinus sibirica* and *Pinus pumila* occupy more homogeneous "plains areas," I felt reasonably confident in summarizing data from stations chosen with the help of Critchfield and Little (1966), Lieth (1988), and Mirov (1967). Stations used to represent *Pinus sibirica* were Serov (24), Surgut (28), Kolpasevo (30), Jenisejsk (32), Irkutsk (34), Tura (41), Kirensk (47), and Krasnojarsk (73). Stations used to represent *Pinus pumila* were Anadyr (13), Apuka (14), Petropavlovsk-Kamcatskij (37), Vitujsk (48), Jakutsk (49), Verchojansk (51), Ochotsk (53), and Zyranka (54). The numbers following each place name indicate the station number in Muller's (1982) compendium of climatic data.

Some climatic parameters were studied as indices of "killing conditions." Absolute maximum and minimum temperatures and absolute maximum and minimum monthly precipitation recorded in a decade suggest long-term values, but these undoubtedly underestimate extremes experienced by long-lived trees (Gumbel 1954).

Other parameters are reported as indices of average conditions likely to have a greater influence on the performance (for example, photosynthesis, respiration growth, and seed yield) of established trees: mean monthly maximum and minimum temperatures, mean annual precipitation, and mean summer (July to September) precipitation. While data from a 10-year record are minimal for estimating extremes, a decade of observations should reasonably represent average conditions.

RESULTS

Data for describing extreme conditions in the climates of three whitebark pine woodlands (Ellery Lake, CA, Crater Lake, OR, and Kings Hill, MT) and two krummholz stands (Old Glory, BC, and Banff, AB) are presented in table 1. The seasonal progression of temperature and precipitation data for one woodland (Kings Hill) and one timberline (Old Glory) site are presented graphically in figures 1 and 2.

Data comparing the climates of sites in which whitebark pine woodlands are climax with forest sites below them and alpine tundra sites above them also appear in table 1. Data from stands representative of subalpine fir forests below the whitebark pine zone (Cooke City, MT, subalpine fir with occasional and seral whitebark pine), whitebark pine woodland (Kings Hill, MT), krummholz (Old Glory Mountain, BC), and alpine tundra (Niwot Ridge, CO) above the range of the tree are compared in figures 1 and 2.

Data comparing the climates of *Pinus albicaulis* (whitebark pine), *Pinus cembra*, *Pinus sibirica*, and *Pinus pumila* appear in table 2.

THE CLIMATE OF WHITEBARK PINE WOODLANDS

The climate of woodlands where whitebark pine dominates (latitude 37° to 47° N.) is interpolated from data gathered in the Sierra (Ellery Lake, CA), the Cascades (Crater Lake, OR), and the Rocky Mountains (Kings Hill, MT). I summarize the data from all three stands with a description (following paragraph) organized around the passage of seasons in a whitebark pine woodland; please refer to table 1 to develop a feeling for regional variation in the woodland climate.

The average January day warms from a nightly low of –11 °C (–14 to –8 °C) to a high of –1 °C (–3 to 1 °C). The snow pack maximizes at 1 to 3 m in February to April and shields roots, decomposers, and small animals from hard frosts. Melt-out proceeds rapidly in May, when swelling buds and newly exposed organisms may experience frosts as cold as –10 to –19 °C. While the average July day warms from a low of 4 °C (3 to 5 °C) to a high of 21 °C (19 to 22 °C), the probability of a frost (0 °C) is still about 7 percent. Because the coarse soils of whitebark pine sites are usually more than saturated by snow melting in May to June, large differences in winter snowpack between sites or seasons are dissipated by runoff and probably go unexpressed in summer production. Production above a minimum set by the site's soil water holding capacity may be supported by July to September rains whose total deposits range from 25 mm to 180 mm (average 92 mm). The rain is deposited in five to 11 monthly showers, of which over half are so small (less than 2.5 mm) that they are probably useful only to insects and nonvascular plants (Weaver 1985). While snow showers occur in September and October, snow does not accumulate permanently until near the first of November.

CHANGES IN CLIMATE ACROSS THE WHITEBARK PINE ZONE

In the Northern Rocky Mountains, USA, whitebark pine is absent from foothill grasslands, Douglas-fir (*Pseudotsuga menziesii*) forests, and the lower part of a subalpine zone largely dominated by fir (*Abies lasiocarpa* at climax) and pine (*P. contorta* at subclimax). The species appears as an occasional and seral tree in the upper half of the subalpine zone, dominates woodlands just below timberline, is often important in krummholz, and is absent again in the alpine tundra. One would ideally describe changes in climate along this altitudinal-vegetational gradient by summarizing data from weather stations arranged along two to three geographically well-separated transects across the gradient (Marr 1961; Price and Evans 1937). In the absence of such data, changes in climate across the gradient are demonstrated on a synthetic gradient, that is, with graphs comparing, one by

Table 1—Climate[1] of high-altitude environmental types of the western United States

	Environmental type and location[2]								
	High-elevation fir		WB woodland			WB timberline		Alpine	
	Lake WY	Cooke MT	Ellery CA	Crater OR	Kings MT	Glory BC	Sunshine AB	Niwot CO	White CA
Temperature (°C)									
Abs. minimum	–44	–39	–32	–29	–38	–38		–38	–37
Abs. May min	–19	–16	–19	–13	–10	–13		–26	–17
Jan. mean min	–18	–16	–13	– 8	–14	–12	–21	–17	–12
Jan. mean max	–5	–6	1	1	–3	–7	–15	–10	– 5
July mean min	4	3	3	4	5	6	1	4	2
July mean max	22	23	19	20	22	14	17	12	12
Abs. max	33	29	26	32	31	27	30	21	20
July frost days	4	3	6	4	2	3		1	6
Precipitation[3] (mm)									
Mean annual	559	672	604	1,611	755	757		1,059	497
July–Sept.	130	159	68	89	120	130		137	86
Driest summer month	7	9	0	0	15	1		1	0
Wettest summer month	127	118	87	136	90	150		95	114
Summer shrs >0.02	11	11	5	6	11	10	10	11	4
Summer shrs >2.54	6	7	2	4	7	5	5	6	2
Snow[4]									
Months >0 cm		7		8	7	7			7
>30 cm		4		6	6	5			5
>50 cm		4		6	4	5			4
Mean max (cm)		102F		290M	135M	173A			81M
Location									
Latitude (°N)	44	45	37	42	46	49	51	40	37
Longitude (°W)	110	109	119	122	110	119	115	105	118
Altitude (ft)	7,700	7,553	9,545	6,475	7,300	7,700	7,042	12,165	12,470
(m)	2,369	2,324	2,937	1,992	2,246	2,369	2,167	3,743	3,837
Decade	61-70	70-79	71-80	61-70	51-60	61-70	1978	71-80	61-70

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[1] Climatic descriptions are based on a decade specified near the bottom of the table; standard error of the means would be smaller and extremes larger if a longer period had been used. Because summer data from Sunshine are available for 1978 only, only 1978 data are reported.

[2] Stations are Yellowstone Lake, WY, Cooke City, MT, Ellery Lake, CA, and White Mountain I, CA, Crater Lake, OR, King's Hill, MT, Old Glory Mountain, BC, Sunshine-Banff, AB, Niwot, CO, and White Mountain II, CA. Because no temperature data were recorded at Ellery Lake, temperature data were taken from a White Mountain Station with a similar latitude (37), longitude (108), and altitude (3,123 m).

[3] Precipitation (mm) is reported for the entire year, the dry season (July to September), the driest summer month in the decade, and the wettest summer month in the decade. The average number of showers (>2.5 mm = 0.1 inch and >0.025 mm = 0.01 inch) is reported for the June to September period.

[4] The duration of snow pack greater than 0 cm, 30 cm, and 50 cm is reported along with the maximum depth reported and its month (February, March, April).

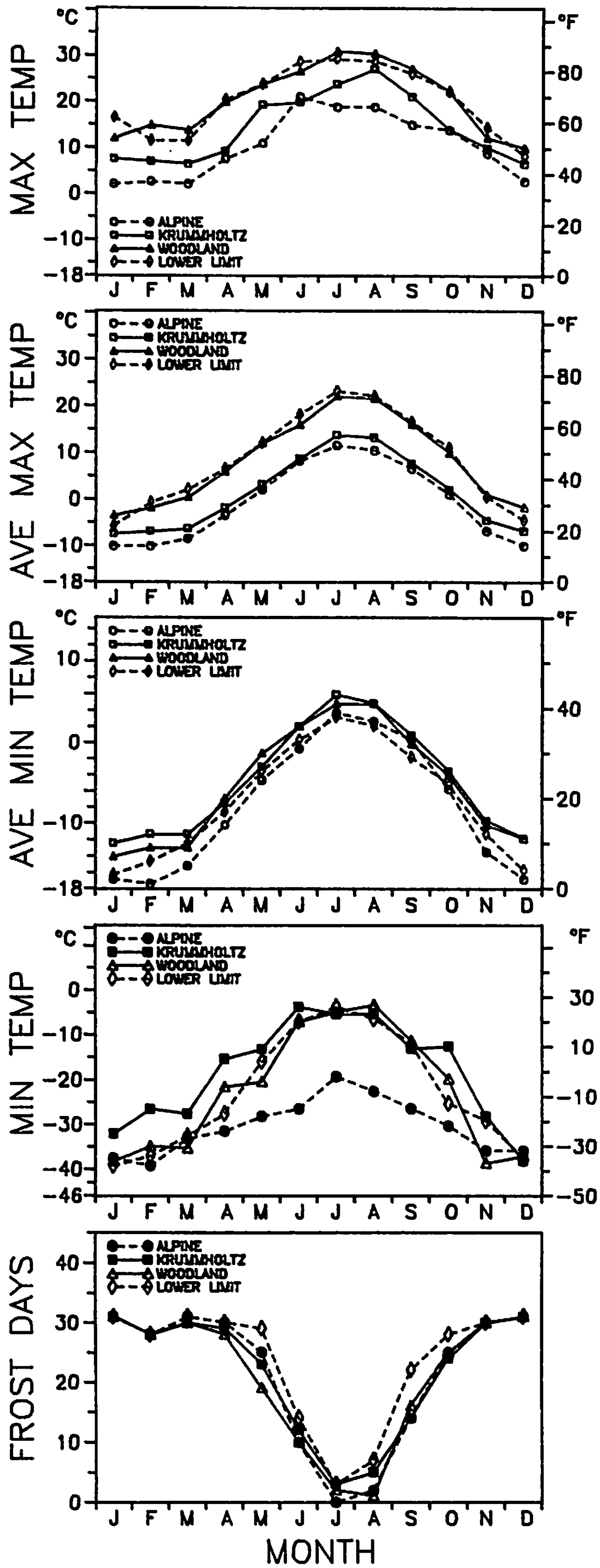

Figure 1—Comparison of temperature data from tundra, timberline, woodland, and high subalpine forests. Monthly data are summarized over a 10-year period and plotted against time. The data plotted come from the Niwot Ridge, Old Glory Mountain, King's Hill, and Cooke City weather stations; data from other comparable stations appear in table 1.

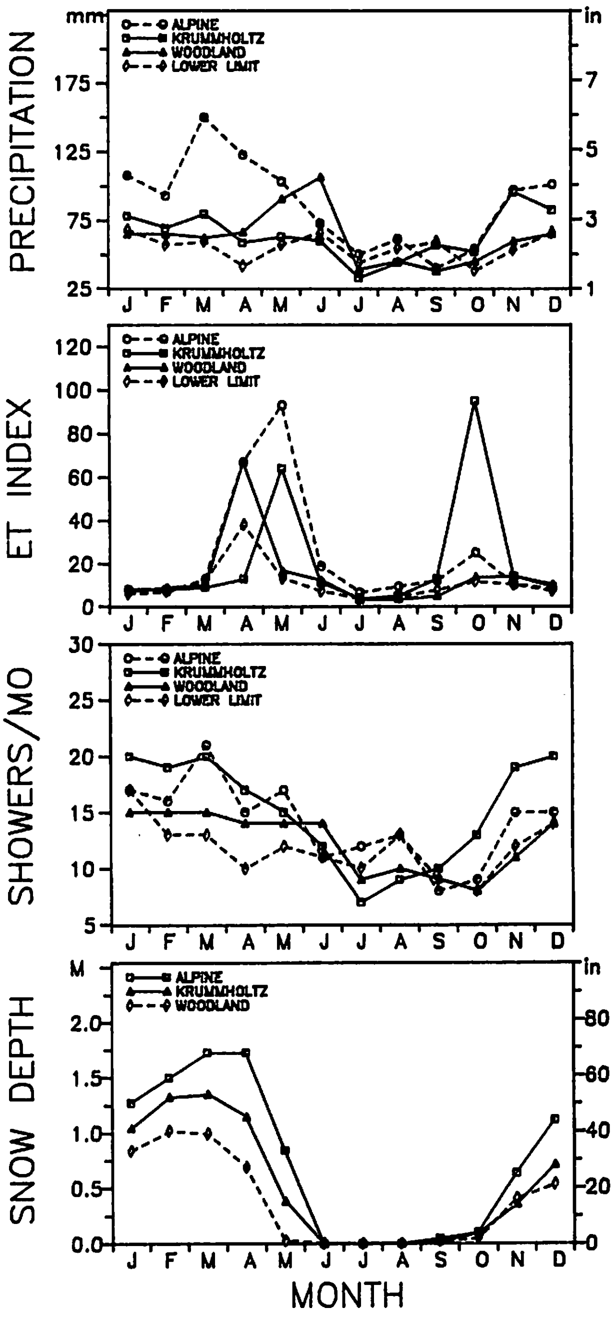

Figure 2—Comparison of precipitation data from tundra, timberline, woodland, and high subalpine forests. Monthly data are summarized over a 10-year period and plotted against time. A P/T index value of 1 indicates a relatively droughty season (Daubenmire 1956; Walter and others 1975); no alpine point falls below 5; timberline and fir types have 2 near-droughty (I = 2 to 5) months, and the woodland had 3 near-droughty months. The data plotted come from the Niwot Ridge, Old Glory Mountain, King's Hill, and Cooke City weather stations; data from other comparable stations appear in table 1.

Table 2—Climate[1] of stone pine communities of North America and Eurasia

	Species and location			
	P. albicaulis **North America**	***P. cembra*** **Euro-Alps**	***P. sibirica*** **Siberia**	***P. pumila*** **N. China**
Temperature[2] (°C)				
Abs. min	–34 ± 2	–23 ± 1	–55 ± 2	–52 ± 4
May min	–16 ± 2	–10 ± 1	–18 ± 2	–21 ± 2
Jan. mean min	–14 ± 2	–8 ± 0	–27 ± 2	–30 ± 8
Jan. mean max	–5 ± 3	–1 ± 1	–19 ± 2	–24 ± 9
July mean min	4 ± 1	5 ± 1	12 ± 1	8 ± 0
July mean max	18 ± 1	14 ± 1	21 ± 1	15 ± 2
Abs. max	29 ± 1	27 ± 2	37 ± 1	33 ± 1
Precipitation[3] (mm)				
Total	[2]931 ± 229	939 ± 9	432 ± 21	[2]407 ± 137
Summer	102 ± 14	323 ± 36	187 ± 11	143 ± 43
Summer dry month	4 ± 4	45 ± 16	8 ± 2	4 ± 2
Summer wet month	116 ± 16	214 ± 15	181 ± 8	165 ± 25
June-Sept. showers (No.)	8 ± 1		14 ± 1	1 ± 1

[1] Values presented are mean ± one standard error. Sample size is 4 for *P. albicaulis* (except average max and mins for January and July, *n* = 5), 3 for *P. cembra*, 8 for *P. sibirica*, except for average max and mins for January and July, *n* = 4), and 8 for *P. pumila* (except for average max and mins for January and July, *n* = 4).

[2] Temperature data (°C) are the mean ± one standard error. Absolute temperatures are recorded for 10 years in *P. albicaulis* and *P. cembra*; records for the Asian pines are longer (and unspecified).

[3] Precipitation (mm) data are total (sum of all months), summer (July, August, plus September), driest summer month (July to September) recorded, wettest summer month (July to September) recorded, and average number of showers in June toSeptember. High variances in total precipitation for *P. albicaulis* and *P. pumila* are reduced to 705 ± 51 mm and 274 ± 37 mm by omission of the Crater Lake and Petropavlovsk stations, respectively.

one, the annual course of nine factors at Cooke City, MT (subalpine fir with seral whitebark), Kings Hill, MT (woodland), Old Glory Mountain, BC (treeline = upper krummholz), and Niwot, CO (alpine). The reader should refer to table 1 to become convinced that the stations presented do reasonably represent other stations in their zones and, thus, that the comparison of data from these sites accurately represents climatic changes that would occur on a gradient across a whitebark pine woodland at any single location.

In the following discussion the climates of high-altitude vegetation zones will be related primarily to whitebark pine performance. A reader wishing to relate the data to other organisms or phenomena can do so by using community characteristics (for example, seral whitebark, whitebark woodland, whitebark krummholz, or above whitebark's range) as indicators of the position of a different phenomenon (for example, performance of another organism) in the climatic gradient.

Whitebark pine is most likely excluded from low-altitude grasslands and forests by high temperatures or scarcity of water. While temperatures at lower altitudes are warmer [average July maxima are 28, 26, 25, and 20 °C in foothill grasslands, Douglas-fir forests, low subalpine fir forests, and whitebark woodlands, respectively (Weaver 1980) (table 1)], high seedling photosynthesis at temperatures as high as 30 to 35 °C (Jacobs and Weaver, this proceedings) as well as the survival of specimen trees in lawns in the foothill grassland zone argue against temperature control. Lesser precipitation [380, 580, and 755 mm in foothill grasslands, Douglas-fir forests, and whitebark woodlands (Weaver 1980 and table 1)] and longer droughts [drought indices of 1.8, 0.3, and 0.0, respectively (Weaver 1980)] probably exclude whitebark pine from the grassland and Douglas-fir zones.

It seems unlikely that whitebark pine is excluded from lower parts of the subalpine fir zone by drought, since warmer (25 versus 20 °C) and perhaps rainier (82 versus 60 to 75 mm) conditions in the lower subalpine zone compensate to produce an equally drought-free condition (0.0 month drought index, Weaver 1980). If drought stresses and substrates are, in fact, similar, it seems likely that the lower limit of whitebark pine forests is set by competition rather than by climate (Arno and Weaver, this proceedings).

We reason, from the preceding, that the lower limit of whitebark dominance is set by conditions that limit the performance of its competitors upslope. The expectation that low temperatures probably eliminate whitebark competitors from the higher subalpine woodland zone is supported by the observation that whitebark pine and spruce range farther down into cold-air pockets than do lodgepole pine or subalpine fir. Two climatic differences between whitebark woodlands and subalpine forests below them seem contrary to this expectation: average minimum temperatures are higher and frost days are fewer in the higher altitude forest (fig. 1). I believe that the conclusion suggested—that whitebark woodlands require warm nights—is spurious and that the data result from a correlation between the presence of the tree, coincidental climatic data, and topographic-edaphic conditions which actually control locally. In the high subalpine zone the tree often grows on steep, rocky ridges from which cold air drains (yielding the warm night condition) and on which excessive drainage occurs (causing drought better tolerated by whitebark pine than subalpine fir). A scan of the other climatic data available (figs. 1 and 2) shows no differences—in either "killing factors" (absolute maximum or minimum temperatures) or factors likely to affect growth and competitiveness (average maximum temperatures, average mean temperatures, or drought months)—between the climates of climax whitebark woodlands and subjacent subalpine fir forests with whitebark subclimates.

Above the whitebark pine woodlands the tree gives way, via krummholz, to alpine tundra. The low stature of tundra vegetation makes the possibility of its competitive domination of forest trees seem unlikely. One therefore hypothesizes that one or more physical factors control tree distribution (Arno 1984; Tranquillini 1979) and looks to climatic data to clarify some possibilities. First, temperature effects. On our synthetic temperature gradient the small drop—relative to the temperature range observed within whitebark pine communities—in absolute high, average maximum, and average minimum temperatures from whitebark to alpine sites is so small that control by high or average temperatures (heat sums) seems unlikely (fig. 1). The far larger drop in absolute lows across the woodland-alpine gradient—and especially so in summer—suggests that growing season frosts could be an important factor in the final elimination of whitebark from high-altitude sites (fig. 1). This conclusion is supported by the absence of whitebark pine from the depths of frost pockets. As to mechanism, Tranquillini (1979) argued that, while early summer frosts may deform them, trees are more likely killed by winter desiccation, desiccation due to a cuticle inadequacy attributed to a short growing season. The climatic feature controlling cuticle development may be frosting (correlated with lows) rather than inadequate heat sums (correlated with averages) since opening and closing of the photosynthetic season is largely induced by frosts (Tranquillini 1979). Second, neither precipitation nor a drought index that ignores wind flow, become more unfavorable as one ascends from whitebark pine woodland to the tundra above. Third, other factors—such as high wind [contributing to desiccation through blasting and water transports (Hadley and Smith 1986; 1987)] and bleaching radiation (Tranquillini 1979)—for which we add no data, may contribute, in concert, to the disappearance of trees. Fourth, whether one factor or several acting in concert prohibit trees, the fact that timberline vegetation changes faster on the altitudinal gradient than any postulated climatic factor is nicely explained by the observation that, until the canopy begins to open, trees provide mutual shelter (Tranquillini 1979). This explanation applies to all factors from frost damage to frost-free period, degree days, wind blasting, desiccation, UV damage, or other factors considered by Tranquillini (1979) and Arno (1984).

Snow data (fig. 2) show that snow depth and duration generally increase with altitude. While the shielding of roots from hard frosts is probably important to trees, I doubt that the small differences observed control tree distribution. On the other hand, deep, long-lying snow undoubtedly benefits low organisms (for example, seedlings including those of whitebark pine, low plants, decomposers, and small animals) by shielding them from frost or predators—and may hinder them by crushing or supporting snow mold. It simultaneously affects large animals by covering their foodstuffs. Benefits and disbenefits are magnified on wind scour and wind deposit sites both above and below timberline.

Rain shower numbers in the Rockies range from 20 per month in winter to 10 per month in summer (fig. 2); summer showers are half as common on the Sierra-Cascade axis (table 1). Summer shower numbers vary little with altitude (Weaver 1985) and vary little between high-altitude types. About half of the showers at this altitude deposit less than 2.5 mm (table 1). While showers less than 5 mm may be important to mosses, lichens, and small animals ranging from insects to squirrels, their shallow penetration and rapid evaporation from both plants and soil render them largely ineffective to most vascular plants (Weaver 1985).

STONE PINE CLIMATE

Two stone pines (*Pinus sibirica* and *Pinus pumila*) dominate vast areas in northern Eurasia and two stone pines appear in high-altitude woodlands in the Alps (*Pinus cembra*) and the Rocky Mountains (*Pinus albicaulis*) (Crichfield and Little 1966). Their close relationships and ecological similarities (Mirov 1967) invite comparison of their climates as a test of the hypothesis that similar communities indicate similar climates.

While winter temperatures are especially low in stone pine communities of northern Eurasia, summer temperatures are similar in areas dominated by all four trees. Since the trees are dormant at midwinter, transplanted *Pinus albicaulis* and *Pinus cembra*, which normally experience absolute lows of only –21 to –38 °C, might tolerate the –34 to –67 °C lows experienced by their near-relatives of northern Eurasia. Frost danger is much more similar during the growing season; for example, at a hypothetical bud break in May absolute lows are all in the –10 to –21 °C range. Absolute highs are higher on Eurasian plains than in subalpine woodlands (table 2). Average maximum temperatures in July are slightly warmer in pine communities of the Eurasian plains (15 and 21 °C) than in pine communities of more southerly mountains (14 and 18 °C). Average minimum temperatures in July are also higher on the Eurasian plains (8 and 12 °C) than in subalpine woodlands (4 and 5 °C).

Although precipitation regimes differ considerably among stone pine habitats, the water regimes are apparently equivalent. In contrast to whitebark pine's winter wet/summer dry climate, all the Eurasian pines experience a winter dry/summer wet climate. In all four regions, however, snow accumulates over winter, melting snow saturates the soil, and excesses run off. Thus, wherever soil water-holding and drainage properties are similar, runoff should eliminate any effect of the large differences in October-June precipitation (603 to 829 mm for *Pinus albicaulis*, 616 mm for *Pinus cembra*, 245 mm for

Pinus sibirica, and 264 mm for *Pinus pumila*) and provide similar starting conditions. Stored soil water must provide survival water during occasional summer months in which rainfall provides as little as 0 to 13 mm, regardless of the region and community type. To the extent that moss-lichen-insect biotas are controlled by temperature and superficial moisture (numbers of June to September showers) these biota may differ little between stone pine communities.

Comparison of production data among these forests should suggest the degree to which growth—as opposed to survival—is limited by water availability. While growing season water availability differs considerably among regions (July to September precipitation for *Pinus albicaulis*, *Pinus pumila*, *Pinus sibirica*, and *Pinus cembra* is 102 mm, 143 mm, 187 mm, and 323 mm, respectively), there is probably little difference in other factors likely to control growth. Temperatures are similar (table 2). Nutrient availabilities are unlikely to differ systematically among regions so large. And underlying genetics (as suggested by taxonomic status) are similar.

I conclude that, while stone pine woodlands in one region indicate very similar climatic conditions, the degree of climatic similarity may decline with increases in the distance between the regions considered. Climatic differences increase as one compares stone pine climates in Montana with others in Montana, Oregon, and Eurasia. The climates appear, however, to be equivalent for stone pines; that is, effective growing season temperatures and water availabilities seem so similar as to permit success in transplanting. These equivalences should apply to other species with similar requirements, but they deteriorate for very different organisms: a person moving from a stone pine community in Montana to one in Eurasia will have to buy a warmer coat and a bigger umbrella. Indicator organisms are, then, good indicators of equivalencies for their near relatives, but relatively poorer indicators of conditions needed for the success of increasingly different species.

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REFERENCES

Arno, S. 1984. Timberline: mountain and arctic forest frontiers. Seattle, WA: The Mountaineers. 304 p.

Baker, F. 1944. Mountain climates of the western United States. Ecological Monographs. 14: 223-254.

Billings, D. 1989. [Personal communication.] Durham, NC: Duke University.

Callison, J.; Harper, K. 1982. Temperature in relation to elevation in the Uinta mountains, Utah. Encyclia. 59: 21-27.

Canadian Department of Transport. 1961-1970. Monthly record of meterological measurements in Canada. Toronto, ON: Canadian Department of Transport, Meterological Branch.

Clements, F. 1916. Plant succession: an analysis of the development of vegetation. Publ. 242. Washington, DC: Carnegie Institute of Washington. 512 p.

Crichfield, W.; Little, E. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

Daubenmire, R. 1956. Climate as a determinant of vegetation distribution in eastern Washington and northern Idaho. Ecological Monographs. 26: 131-154.

Despain, D; Rankin, R. 1989. [Personal communication]. October. Yellowstone National Park, Mammoth, WY.

Gumbel, E. 1954. Statistical theory of extreme values and some practical applications. National Bureau of Standards Applied Mathematics Series #33. Washington, DC: U.S. Government Printing Office. 51 p.

Hadley, J.; Smith, W. 1986. Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology. 67: 12-19.

Hadley, J.; Smith, W. 1987. Influence of krummholz mat microclimate on needle physiology and survival. Oecologia. 73: 82-90.

Harper, K.; Woodward, R.; McKnight, K. 1980. Interrelationships among precipitation, vegetation, and streamflow in the Uinta Mountains, Utah. Encyclia. 57: 58-86.

Holdridge, L. 1947. Determination of world plant formations from simple climatic data. Science. 105: 367-368.

Leeson, B. 1989. Banff meterological records from several winters and one summer, 1978. Unpublished records on file at: Parks Canada, Natural History Research, Calgary, AB.

Lieth, H. 1988. [Personal communication]. December. Onsabrück, West Germany: University of Onsabrück.

Losleben, M. 1983. Climatological data from Niwot Ridge, East Slope, Front Range, Colorado (1970-1982). Boulder, CO: University of Colorado, Institute of Arctic and Alpine Research. 193 p.

Marr, J. 1961. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies in Biology. 8: 1-134.

Mirov, N. 1967. The genus *Pinus*. New York: Ronald Press. 602 p.

Muller, M. 1982. Selected climatic data for a global set of standard stations for vegetation science. The Hague: Junk. 306 p.

Price, R.; Evans, R. 1937. Climate of the west front of the Wasatch Plateau in central Utah. Monthly Weather Review. 65: 291-301.

Schimper, A. 1903. Plant geography on a physiological basis. Oxford: Clarendon Press.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps. Berlin: Springer-Verlag. 137 p.

Tranquillini, W. 1989. [Personal communication]. January. Innsbruck, Austria: University of Innsbruck.

U.S. Department of Commerce. 1951-1980. Climatological data. Washington, DC: U.S. Department of Commerce.

Walter, H. 1973. Vegetation of the earth in relation to climate and ecophysiological conditions. New York: Springer-Verlag. 237 p.

Walter, H.; Harnickell, E.; Mueller-Dombois, D. 1975. Climate-diagram maps of the individual continents and the ecological climatic regions of the earth. Berlin: Springer-Verlag. 36 p. and 9 maps.

Weaver, T. 1980. Climates of vegetation types of the Northern Rocky Mountains and adjacent plains. American Midland Naturalist. 103: 392-398.

Weaver, T. 1985. Summer showers: their sizes and interception by surface soils. American Midland Naturalist. 114: 409-413.

Whittaker, R. 1975. Communities and ecosystems. New York: MacMillan. 385 p.

Speakers answered questions from the audience following their presentations. Following are the questions and answers on this topic:

Q. (from R. Brown)—Is summer or winter desiccation more limiting to the distribution of whitebark pine?

A.—My study is correlative and therefore generates hypotheses rather than testing them. Altitudinally, I speculate that whitebark is excluded from grasslands, but not from subalpine forests and alpine tundra, by summer drought. Tranquillini (1979) argued that the upper limit of *Pinus cembra* is set by winter desiccation, possibly because of inadequate cuticle; a similar explanation for whitebark's distribution is not inconsistent with the data presented. Geographically, I speculate that whitebark's dominance declines to the north and west when more water-demanding competitors are supported, to the east when mountain sites with climates cool enough to exclude competitors or moist enough to support the tree disappear, and to the south when high-altitude sites become too dry, probably in the summer (Arno and Weaver, this proceedings).

Q. (from L. McHargue)—Is summer rainfall important to whitebark pine and, if so, would you expect especially resistant ecotypes in the summer-dry Sierra Nevada?

A.—Whitebark must maintain a minimal water content in the summer. Its dominance is greatest in summer-dry regions, and in these regions it must depend for survival water on soil water stored during the winter. Near and north of the Canadian border (Arno and Weaver, this proceedings) summer rainfall becomes more plentiful; since ecotypes (ecoclines) develop along most environmental gradients, I would expect some ecotypic variation with respect to late-season activity across the north-south range of the tree.

Q. (from M. Merigliano)—Might the near-absence of whitebark pine on interior Great Basin ranges—as opposed to the Cascade-Sierra axis—be due to the clear, sunny rather than more overcast winter days?

A.—Tranquillini suggests that upper timberline is controlled by winter desiccation. On this basis, one might expect the timberline in a region with clear, sunny winter days to be lower than that of a cloudier region. If timberline were pushed down to levels with summer warmth great enough to support competing trees, whitebark might be squeezed out.

Q. (from R. Krebill)—You have described the present climates of sites now occupied by whitebark pine. Are those climates the same as the climates the stands established in? Are whitebark stands "in sync" with today's environment?

A.—Weather varies from day to day and year to year; climate (average weather) varies from decade to decade and century to century (consider the little ice age, the hypsithermal, and the Wisconsin glaciation); and the difference between the two depends on the life span of the observer. In the Northern Rocky Mountains, I see reproduction throughout the altitudinal range of whitebark pine and I presume it exists throughout the geographic range of the species. If so, from the viewpoint of whitebark pine, the regional climate has not changed significantly and the tree is "in sync." Global warming of 1 to 5 °C, predicted by some (not all) current climatic models, may be comparable to that which occurred during the hypsithermal, and while it might not drive the tree from the region, it would surely induce a redistribution.