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CLIMATES WHERE STONE PINES GROW, A COMPARISON

Tad Weaver

Abstract—While stone pine climates are similar, species adapted to relatively moderate climates may be excluded from the ranges of congeners by more severe climates, and species with longer warm-moist growing seasons are probably more productive than congeners. Absolute low/summer average/absolute high temperatures for stone pines listed in order of increasing absolute low temperature are *Pinus sibirica* (−55/13/37 °C), *P. pumila* (−52/9/36 °C), *P. koraiensis* (−42/14/36 °C), *P. albicaulis* (−34/9/29 °C), and *P. cembra* (−23/8/27 °C). The Walter drought index shows little stress in stone pine forests despite large differences in summer/winter precipitation: in order of increasing summer rainfall, precipitation is *P. albicaulis* (102/829mm), *P. pumila* (142/264mm), *P. sibirica* (187/245mm), *P. cembra* (323/616mm), *P. koraiensis* (394/242mm). Estimated thawed-soil growing season increases from *P. albicaulis* (4.5mo), through *P. pumila* (4.6mo), *P. sibirica* (5.5mo), and *P. cembra* (6.3mo) to *P. koraiensis* (7.8mo); growing seasons of the first three trees could be shortened by drought.

Stone pines grow in most of the boreal zone (fig. 1) (Fullard and Darby 1964; Lanner 1990; Mirov 1967). *Pinus pumila* and *P. sibirica* occupy vast far-northern (50 to 70° N. latitude) areas in northeastern Asia; *P. sibirica* ranges from just west of the Urals (55° E. longitude) halfway to the Pacific (115° E. longitude) and *P. pumila* ranges from 115° E. longitude to the Pacific (165° E. longitude). *P. koraiensis* grows at the boreal-deciduous forest transition in eastern China (120 to 150° E. longitude and 45 to 55° N. latitude with outliers to 35° N. latitude at high altitude). Paralleling *P. koraiensis*, *P. albicaulis* occupies the Rocky-Cascade-Sierra Mountain chains of North America from 55° N. latitude southward to 45° N. latitude with outliers to near 35° N. latitude. *Pinus cembra* appears in the Alps at approximately 45° N. latitude. Glaciated parts of the conifer forest zone—both in northern Europe and North America—lack stone pines (fig. 1).

Due to their common ancestry and common boreal forest habitat, one expects the trees to occupy similar climates. This paper tests that hypothesis by comparing climates occupied by the trees with respect to 20 factors that may be important in determining the ranges and productivities of the species. The information may be especially useful for predicting the success of introductions—from one region to another—of stone pines, their tree associates,

and to some degree, even their herb, cryptogam, and animal associates. Such introductions might be of interest as either producers or pests.

METHODS

Climates of environments dominated by closely related stone pines (Lanner 1990; Mirov 1967) were compared. The comparisons are nonstatistical, since the objective was to discuss biological responses rather than the climates themselves.

The climates were characterized by choosing three to four stone pine stands at which temperature and precipitation were regularly measured (a complete sample of accessible data); summarizing the data for periods of 10 years (*P. albicaulis* and *P. cembra*) or longer (unspecified); and calculating means for selected parameters. The stations studied are listed here—from west to east—each with its approximate latitude, longitude, and altitude (m). Note that *P. albicaulis* and *P. cembra* grow significantly higher than, and to the south of, the Asian pines. Asterisked Siberian stations lack most temperature data. Scientists who helped identify weather stations in stone pine climates are listed in the acknowledgments.

Pinus albicaulis stations (USDC 1961–80) were Crater Lake, OR (43° N., 122° W., 1,990m), Ellery Lake, CA (38° N., 119° W., 2,940m), Old Glory, BC (49° N., 119° W., 1,008m), and Kings Hill, MT (46° N., 110° W., 2,225m). *Pinus cembra* stations (contributed by W. Franquillini) were Hagen (47° N., 11° E., 1,800m), Obergurgl (47° N., 11° E., 2,070m), and Patscherkofel (48° N., 11° E., 1,952m). *Pinus sibirica* stations (Muller 1982) were Serov (60° N., 61° E., 132m*), Surgut (61° N., 73° E., 40m), Kolpasevo (58° N., 83° E., 76m*), Jenisejsk (58° N., 92° E., 78m*), Krasnojarsk (56° N., 93° E., 15m), Tura (64° N., 100° E., 130m*), Irkutsk (52° N., 104° E., 468m), and Kirensk (58° N., 108° E., 256m). *Pinus pumila* stations (Muller 1982) were Vitujsk (64° N., 122° E., 107m*), Jakutsk (62° N., 130° E., 100m*), Verchojansk (68° N., 133° E., 137m), Ochotsk (59° N., 143° E., 6m), Zyranka (65° N., 151° E., 43m*), Petropavlovsk-Kamcaskij (53° N., 159° E., 32m), Apuka (65° N., 170° W., 10m*), and Anadyr (65° N., 178° E., 62m). *Pinus koraiensis* stations (contributed by Luo Ju Chun and Zhao Shidong) were AnTu (43° N., 128° E., 591m), Chagbei-ShenYang (42° N., 128° E., 738m) and YiChun (48° N., 129° E., 231m).

Parameters studied describe climates with respect to temperature, precipitation, and growing season. The following three paragraphs list these parameters and outline the rationales for their choice; the rationales are developed further in Weaver (1993) and in the following discussion.

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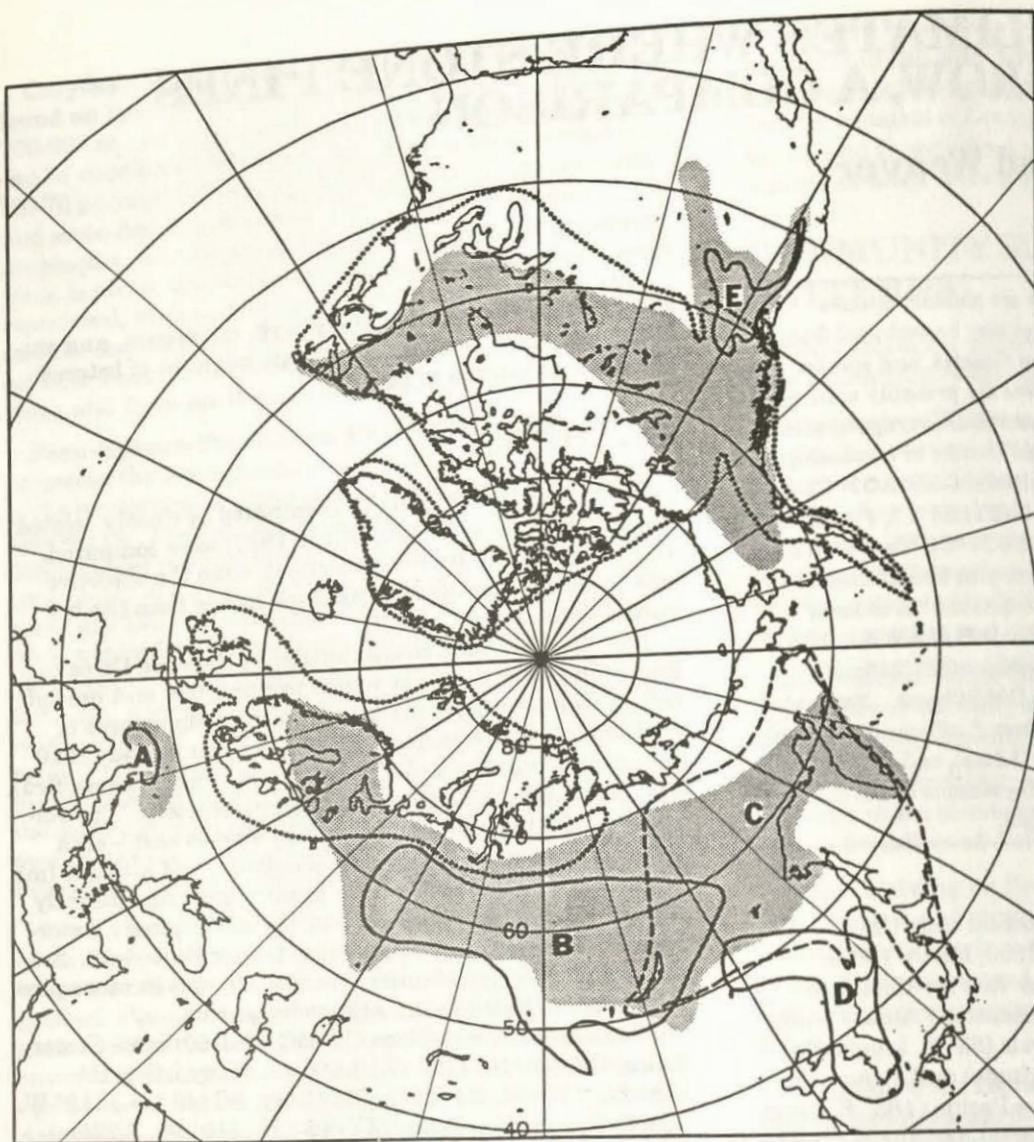


Figure 1—Distribution of stone pines in relation to space, conifer forests, and pleistocene glaciation. North America and Eurasia are seen from a polar view. Shading locates the conifer zone on the two continents (Fullard and Darity 1964). Areas within the dotted lines received pleistocene glaciation (Denton and Hughes 1981). Ranges of the stone pines (Mitsch 1967) are outlined by solid or dashed lines: A = *Pinus contorta*, B = *P. sibirica*, C = *P. murrayana*, D = *P. koraiensis*, E = *P. abies*. The absence of stone pines in the conifer zone of northwestern Eurasia and parts of North America could be due to glaciation.

Ten temperature parameters were compared. Midwinter frost danger was described by the long-term minimum temperature (the absolute low), the average January minimum, and the average January maximum. Extreme fall and spring frosts are represented by the absolute lows in the first and last months of winter (that is, the absolute lows in the months with 0°C average air temperature; Weaver 1994). The average growing-season temperature was calculated across those months when average air temperatures were above 0°C. This average was recalculated using "temperature growth support units = Q" to account for the rise in rates of metabolic processes with rising temperature; these points lie on a curve defined by 0°C = 0, 1°C = 1, 11°C = 2, 21°C = 3, 31°C = 4, and 41°C = 5 (Weaver 1994). Summer highs were represented by the average July minimum, average July maximum, and long-term high.

Seven precipitation parameters were compared. October-June precipitation was measured to determine whether soil was moist in winter and at the opening of

the growing season. Summer precipitation was indexed by July-September precipitation and by precipitation in the wettest and driest month in that period. Since plants require water, not precipitation, months with a positive water balance were estimated with the Walter index (Nielson 1986; Walter 1973), which assumes that for every 2°C rise in average temperature 1 mm of precipitation will be evapotranspired. Two derivatives were studied: drought months (duration of periods with a negative water balance) and drought magnitude (total estimated deficit). While the Walter index tends to underestimate drought (Stephenson 1990), it may be adequate in these cool climates. Poikilohydric (Larcher 1975) organisms may be more dependent on a number of growing hours than by the number of (rain days than on total precipitation; rain days per month were therefore recorded.

Four growing-season parameters were compared. Length of the growing season was indexed first as the number of months when air temperature is above 0°C, that is, the approximate number of months when the soil is thawed

(Weaver 1994). Second, drought months (none according to the Walter index) were subtracted from the warm-season index to create a better warm-moist season index. Despite contrary observations (Weaver 1994), growth is expected to be indexed by the integral of temperature over growing season. Thus two indices of growing season productivity (Weaver 1994) were calculated: [growing season \times (average growing season temperature -5°C) (Chang 1968)] and, considering the Q_{10} effect, [growing season \times average growing season Q].

WINTER TEMPERATURES

Average winter (January) temperatures in northeastern Asia are the world's coldest and they warm southward (Fullard and Darby 1964). Normal daily lows in regions occupied by the trees are *Pinus pumila* (-30°C), *P. sibirica* (-27°C), *P. koraiensis* (-27°C), *P. albicaulis* (-14°C), and *P. cembra* (-8°C), respectively (table 1). Daily highs in winter average 8°C higher (table 1).

Absolute lows experienced by *Pinus sibirica* (-55°C) and *P. pumila* (-52°C) rise to *P. koraiensis* (-42°C), *P. albicaulis* (-34°C), and *P. cembra* (-23°C) (table 1). *Pinus albicaulis* and *P. cembra* may be protected from extreme low temperatures by the drainage of cold air from their mountaintop sites. Becwar and Burke 1982 show that timberline conifers of the Colorado Rockies do not survive temperatures below -40°C ; thus *P. sibirica* and *P. pumila* may be the only stone pines tolerant of -50°C .

Frosts of early fall and late spring may catch trees in partially hardened states. Absolute lows in the first and last months of winter were -21°C for *P. koraiensis*, -17°C for *P. sibirica*, and -10°C for the remaining trees. Why are absolute lows for fall-winter-spring frosts lower in the *P. koraiensis* and *P. sibirica* regions than in the *P. pumila* regions where average temperatures are lower (table 1; Fullard and Darby 1964)?

SUMMER TEMPERATURES

Continentality allows northeastern Asia to warm in summer more than less continental parts of the polar region. Thus absolute maximum temperatures of *Pinus sibirica* (37°C) and *P. pumila* (33°C) are considerably higher than those of *P. cembra* (27°C) and *P. albicaulis* (29°C) (table 1). Absolute summer highs in the *P. koraiensis* forest at the boreal-deciduous forest transition are as high (36°C) as in interior forests. Average July highs in *P. sibirica* and *P. koraiensis* forests are like those in Rocky Mountain Douglas-fir (*Pseudotsuga menziesii*) forests, a vegetation zone below the Rocky Mountain stone pine zone (Weaver 1994).

Daily growth rates are determined by average temperature conditions in the growing season. (1) Temperature conditions are represented most simply by average temperature; this is 13°C for *Pinus sibirica*, 11°C for *P. koraiensis*, and 8 to 9°C for *P. pumila*, *P. albicaulis*, and *P. cembra*. Like July highs, 13°C average temperatures, are similar to those found in the Douglas-fir/ponderosa pine forests of the Rocky Mountains (Weaver 1994). (2) Because growth rises exponentially with increasing temperature (Q_{10} ; Larcher 1975), a better index of temperature on growth may be a cross-season average of growth support units (Weaver 1994), which give greater weight to high than low temperatures. With this index climates cool from *P. sibirica* to *P. albicaulis* to *P. pumila*-*P. koraiensis* to *P. cembra* (table 1).

PRECIPITATION

Winter-spring precipitation is high in *Pinus albicaulis* (829 mm) and *P. cembra* (616 mm) and lower (about 250 mm) in northeastern Asia (table 2). Since the lower amounts will saturate most mountain soils (Weaver 1978), the excess is expected to run off, to have little effect on water supplies in forest stands during the growing season,

Table 1—Temperatures¹ in stone pine communities of the world. Climates are listed in order of increasing winter temperatures

Temperature data	Species, location, number of stations ²				
	<i>P. pumila</i> N. China 4+	<i>P. sibirica</i> Siberia 4+	<i>P. koraiensis</i> Korea-China 3	<i>P. albicaulis</i> N. America 4	<i>P. cembra</i> Euro-Alps 3
Winter Temperature					
Jan. mean min	-30.0 ± 8.0	$-27.0(\pm 2.0)$	$-27.0(\pm 2.0)$	-14.0 ± 2.0	-8.0 ± 0.0
Jan. mean max	-24.0 ± 9.0	-19.0 ± 2.0	-11.0 ± 2.0	-5.0 ± 3.0	-1.0 ± 1.0
Abs min	$-52.0(\pm 4.0)$	-55.0 ± 2.0	-42.0 ± 1.0	-34.0 ± 2.0	-23.0 ± 1.0
Frost spring	-11.0 ± 8.0	-18.0 ± 2.0	$-26.4(\pm 0.2)$	-11.0 ± 1.0	-10.0 ± 1.0
Frost fall	$-11.0(\pm 3.0)$	-16.0 ± 2.0	-27.6 ± 0.7	-11.0 ± 1.0	-10.0 ± 1.0
Summer Temperature					
July mean min	$8.0(\pm 0.0)$	$12.0(\pm 1.0)$	$14.0(\pm 1.0)$	4.0 ± 1.0	$5.0(\pm 1.0)$
July(mean)max	$15.0(\pm 2.0)$	21.0 ± 1.0	26.0 ± 0.0	18.0 ± 1.0	14.0 ± 1.0
Abs max	33.0 ± 1.0	37.0 ± 1.0	36.0 ± 2.0	29.0 ± 1.0	27.0 ± 2.0
T_{gs}	9.0 ± 1.0	13.0 ± 1.0	11.3 ± 1.2	9.0 ± 1.0	8.0 ± 1.0
Q_{gs}	1.9 ± 0.2	$2.4(\pm 0.1)$	1.9 ± 0.1	2.1 ± 0.2	$1.7(\pm 0.1)$

¹Temperature data ($^\circ\text{C}$) are the mean \pm one standard error. Absolute temperatures are recorded for 10 years in *P. albicaulis* and *P. cembra*; records for the Asian pines are unspecified (presumed longer). T_{gs} and Q_{gs} are growing season averages defined in the text.

²Sample size is four for *P. albicaulis* (except average max and min for January and July, $n = 5$), three for *P. cembra*, and for both *P. pumila* and *P. sibirica* eight, except for January max-min, July max-min, and spring-fall frost temperatures where $n = 4$.

and, thus, to have little effect on production. Large snowfalls in the *P. albicaulis* and *P. cembra* forests, relative to those in the Asian forests, surely result in greater snowpacks, which shelter ground-level plants and animals less frost tolerant than the trees.

Summer precipitation is lower where moisture carrying air masses cross mountains (northeastern Asia and the Rocky Mountains) than where they do not (Alps and eastern China). Thus summer rainfall increases from *Pinus albicaulis* (102 mm) to *P. pumila* (187 mm), *P. sibirica* (187 mm), *P. cembra* (323 mm), and *P. koraiensis* (394 mm). Precipitation in the driest month parallels summer rainfall (table 2).

Soil water may be adequate in spite of low rainfall if evapotranspiration is low. If we assume that 1 °C degree evaporates 2 mm per month (Nielson 1986, 1992; Walter 1973), we see that stone pines do not experience drought in any month (table 2). In addition, some buffering against drought occurs because snowmelt water stored in the soil provides a supplement to summer showers. However, even at boreal temperatures Walter's index may understate evaporation (Stephenson 1990), so there is probably less summertime restriction of growth by drought (stomate closure) in *Pinus cembra* and *P. koraiensis* than in *P. albicaulis*, *P. sibirica*, and *P. pumila* forests.

Organisms without water reserves—such as lichens, mosses, and invertebrates—are more sensitive to summer drought and may distinguish wetter and drier forests. These organisms are surely inhibited in *Pinus pumila* and *P. albicaulis* forests (one to eight rain days/month) relative to *P. cembra* and *P. koraiensis* forests (16 to 18 rain days).

GROWING SEASON

Survival depends on photosynthetic provisioning for winter respiration and the outcome of competition may depend on excesses above this basic provisioning. One expects production to be correlated with the number of warm-moist days, with the warmth of those days (Q_{10} , Larcher 1975), and thus with their product.

If water stress never occurs, the length of the warm-moist season increases from *Pinus albicaulis* (4.5 mo) to *P. pumila* (4.6 mo), *P. sibirica* (5.5 mo), *P. cembra* (6.3 mo), and *P. koraiensis* (7.8 mo) (table 3). And if temperature conditions were identical in these forests, one would therefore expect production in *P. cembra* and *P. koraiensis* forests to be half again as great as in *P. pumila* and *P. albicaulis* forests. Actual differences could be even larger because the temperature-defined growing season may overstate stand productivity in drier regions. For example, while subsoils remain moist all summer in higher (J. Brown, personal communication) and lower (Weaver 1974) parts of the *P. albicaulis* zone, drying of surface soils apparently causes tree water stress at lower (B. Keane, personal communication), but not higher (J. Brown, personal communication), sites. Similar droughty periods probably occur in warmer *P. pumila* and *P. sibirica* forests.

Production is expected to rise exponentially with rising temperature, and thus productivity might be better correlated with the product of season length and temperature "growth supporting units." While this production hypothesis was rejected in a cross-vegetation zone analysis (Weaver 1994), the genetic similarity of stone pines might allow it to operate here. If so, and if water deficits in Siberia do not shorten the growing season, *P. koraiensis* and *P. sibirica* will be promoted to the most productive stone pines (table 3).

CONCLUSIONS

From a tree's point of view, average conditions in the stone pine zones are similar: water stress is slight or nonexistent and growing season temperatures average 9 to 13 °C. Seasonal extreme conditions may, however, prevent reciprocal transplantation. Winter or fall-spring frosts in the *Pinus sibirica*/*P. pumila*/*P. koraiensis* region may exclude the other pines. And weak droughts in the *P. albicaulis*/*P. pumila*/*P. sibirica* regions might exclude *P. cembra* or *P. koraiensis*.

Table 2—Precipitation¹ in stone pine forests of the world. Climates are listed in order of increasing summer precipitation

Precipitation data	Species, location, number of stations ²				
	<i>P. albicaulis</i> N.(America) 4	<i>P. pumila</i> N. China 4+	<i>P. sibirica</i> Siberia 4+	<i>P. cembra</i> Euro-Alps 3	<i>P. koraiensis</i> Korea-China 3
Total	931 ± 229	407 ± 137	432 ± 21	939 ± 9	636 ± 68
Oct.-June	829 ± 234	264 ± 76	245 ± 22	616 ± 43	242 ± 62
July-Sept.	102 ± 14	143 ± 43	187 ± 11	323 ± 36	394 ± 17
Wettest summer month	116 ± 16	165 ± 25	181 ± 8	214 ± 15	346
Driest summer month	4 ± 4	4 ± 2	8 ± 2	45 ± 16	32
Summer drought months	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Summer water deficit	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Summer rain days, average number	8 ± 1	1 ± 1	14 ± 1	16 ± 1	18

¹Precipitation (mm) data are total (sum of all months), winter, summer (July, August, plus September), driest summer month (July-September) recorded, wettest summer month (July-September) recorded, and average number of showers in June-September. 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.

²Sample size is four for *P. albicaulis*, three for *P. cembra*, three for *P. Koraiensis*, and eight for both *P. pumila* and *P. sibirica* (except for summer drought months and deficit, where it is only four).

Table 3—Stone pine productivity correlates: growing season,¹ growing season temperature,² and their products. Climates are listed in descending order by one estimate of productivity, warm moist season

	Species, location, number of stations				
	<i>P. koraiensis</i> Korea-China 2	<i>P. cembra</i> Euro-Alps 3	<i>P. sibirica</i> Siberia 4	<i>P. pumila</i> N. China 4	<i>P. albicaulis</i> N. America 4
Warm season	7.8 ± 0.1	6.3 ± 0.2	5.5 ± 0.2	4.6 ± 0.4	4.5 ± 0.3
Summer drought months	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Warm-moist season	7.8 ± 0.1	6.3 ± 0.2	5.5 ± 0.2	4.6 ± 0.5	4.5 ± 0.3
T _{gs}	11.3 ± 1.2	8.0 ± 1.0	13.0 ± 1.0	9.0 ± 1.0	9.0 ± 1.0
Q _{gs}	1.9 ± 0.1	1.7 ± 0.1	2.4 ± 0.1	1.9 ± 0.2	2.1 ± 0.2
GS x T _{gs} -5 °C	56.5	18.9	44.0	18.4	18.0
GS x Q _{gs}	15.6	10.7	13.2	8.7	9.5

¹Warm-season and warm-moist season are two indices of growing season. Warm-season months occur after average monthly air temperature rises above 0 °C and before it falls below 0 °C. The warm-moist season is the warm season minus any months in which T/2 is greater than P (mm). Walter 1978.

²Walter drought does not occur in stone pine regions. Two indices of growing-season temperature are provided. T_{gs} is the average temperature in growing season months. T_{-5C} is used as one index of growth support on the assumption that growth does not occur below 5 °C (Chang 1968). Q_{gs} is the average of temperatures weighted for their growth-supporting capacity: 0 °C = 0, 1 °C = 1, 11 °C = 2, 21 °C = 4 (Weaver 1993).

Organisms filling other niches might find the climates dissimilar (Weaver 1990). Poikilohydric organisms and humans would react differently to the relatively summer-rainy climates of the *P. cembra* and *P. koraiensis* regions than to the other stone pine climates. And organisms wintering under snow—small mammals, insects, plants of small stature—are more protected from the extremes of winter cold in the *P. cembra* and *P. albicaulis* regions than in the other climates.

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