# Vegetation Distribution and Production in Rocky Mountain Climates—with Emphasis on Whitebark Pine

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# VEGETATION DISTRIBUTION AND PRODUCTION IN ROCKY MOUNTAIN CLIMATES—WITH EMPHASIS ON WHITEBARK PINE

**Tad Weaver**

**Abstract**—The distribution and production of vegetation on the altitudinal gradient (grassland-forest-alpine) was plotted against climatic parameters to evaluate hypothetical controlling factors. (1) Whitebark pine (*Pinus albicaulis*) is likely excluded from higher zones by a cool growing season or wind-induced drought. It is probably not excluded by low temperatures occurring during its hardening, hard, or dehardening seasons. (2) While the lower physiological limit of whitebark pine is probably set by drought, its lower realized limit is directly set by subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) competitors and indirectly set by factors that control their distribution. (3) The upper limits for most other dominant species are probably set by growing season temperature. The lower limits are likely set by competition down to the cedar-hemlock (*Thuja plicata*/*Tsuga heterophylla*) zone and by drought in drier areas. (4) Production is strongly correlated ($r^2 = 0.86$) with growing season length (soil thawed season minus dry soil days). Multiplying season length by average temperature did not improve the growing season predictor, perhaps because vegetation at each altitude is especially adapted to temperatures in its zone.

Vegetation composition and structure vary along gradients of temperature and precipitation whether the condition changes with altitude (Daubenmire 1956; Gams 1931; Weaver 1980) or geography (Holdridge 1967; Walter 1973; Whittaker 1975). Graphical devices based on simple parameters such as average annual temperature and total annual precipitation (Holdridge 1967; Whittaker 1975) are workable predictors of the vegetation growing in particular climates. It seems obvious, however, that these devices succeed, not because the climatic parameters used are causal, but because the parameters are correlated with causal climatic factors.

Production of vegetation is largely determined by climate and is therefore expected to be highest where temperature, moisture, and nutrients are simultaneously favorable. In Rocky Mountain vegetation one therefore expects production to be highest in low-altitude (warm) moist forests (*Thuja-Tsuga*) and to decline both with increasing altitude (because of cooling and reduced nutrient availability) (Weaver 1979) and with decreasing altitude (because of decreasing water availability). While it is rarely done, vegetation production should also be successfully plotted in a Hutchinsonian (1958) hyperspace with axes that are either physiologically meaningful or surrogates well correlated with physiologically meaningful axes.

The object of this paper is to correlate vegetation performance—survival and production—with physiologically meaningful aspects of temperature and moisture. Study of the distribution of species on these presumptively causal axes will eliminate some hypotheses of cause and sharpen others for experimental tests. While whitebark pine (*Pinus albicaulis*) is the primary subject of this paper, the approach could be applied to other species, as well.

## METHODS

Impacts of climatic factors on vegetation distribution were evaluated by comparing factor levels among segments on a vegetational gradient. In essence, the method allows one to deduce (1) that a presumptive factor that does not vary between vegetation types is not controlling the vegetation changes observed, and (2) that a presumptive factor that does change between vegetation types deserves further discussion as directly controlling, indirectly controlling, or a noncausal correlate. The method is illustrated here with discussion of whitebark pine, but it could be applied to many other species as well.

### The Data

Environmental zones were identified by climax vegetation occupying them (Daubenmire 1943; Daubenmire and Daubenmire 1968; Huschle and Hironaka 1980). They included, from low to high altitude, desert shrub, dry grassland, warm forest, cool forest, and alpine ecosystems. Specific zones are listed with their Kuchler (1964) type numbers and representative stations in table 1.

Climates of the environmental zones were characterized by using climatic statistics from approximately five stations in each environmental-vegetation zone. To maintain the integrity of the data, raw data are plotted wherever possible. When necessary, medians were used to represent "typical" sites; use of medians deemphasizes sites with conditions intermediate between modal conditions of adjacent types. The stations chosen include most available stations and may thus be considered as a "complete sample." The sample may not be entirely random because weather stations must be accessible; in higher types, for example, the sites may be relatively low.

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Table 1—Weather stations representative of major Northern Rocky Mountain environmental zones.[1] Zones are listed from high to low altitude

| Zone | Station locations |
|---|---|
| Alpine[2] | White Mountain, CA; Niwot Ridge, CO |
| Whitebark pine[2] | Old Glory, BC; Kings Hill, MT; Ellery Lake, CA; Crater Lake, OR |
| Subalpine fir | High: Summit, MT; West Yellowstone, MT; Lake Yellowstone, MT; Low: Burke, ID; Seeley Lake, MT; Hungry Horse, MT |
| Douglas-fir | East: Hebgen Lake, MT; Lakeview, MT; Lamar, WY; Palisades Dam, ID; Dixie, ID; West: Libby, MT; Lincoln, MT |
| Cedar-hemlock | West Glacier, MT; Sandpoint, ID; Pierce, ID; Avery, ID; Priest, ID |
| Ponderosa pine | West: Garden Valley, ID; Polson, MT; Potlatch, ID; Kooskia, ID; East: Melstone, MT; Busby, MT; Colstrip, MT; Lame Deer, MT; Roundup, MT |
| Idaho fescue | Gallatin Gateway, MT; Virginia City, MT; Mystic Lake, MT; Wisdom, MT; Bozeman MSU, MT; White Sulphur Springs, MT |
| Bluebunch wheatgrass | Browning, MT; Belgrade, MT; Kalispell, MT; Ennis, MT; Dillon, MT; Augusta, MT; Crow Agency, MT; Billings, MT |
| Grama grass | Ekalaka, MT; Jordan, MT; Malta, MT; Rock Springs, MT; Rapelje, MT; Chester, MT; Great Falls, MT; Fairfield, MT |
| *Atriplex* spp. | Lovell, WY; Worland, WY; Basin, WY; Powell, WY; Deaver, WY |

[1] The vegetation types, with their Kuchler (1964) type numbers (KTXX), are: *Deschampsia caespitosa*-Carex (KT52), *Pinus albicaulis* (KT15), *Abies lasiocarpa* (KT15), *Pseudotsuga menziesii* (KT12), *Thuja plicata*/*Tsuga heterophylla* (KT2), *Pinus ponderosa* (KT11,16), *Festuca idahoensis* (KT63), *Agropyron spicatum* (KT63), *Bouteloua gracilis* (KT64), *Atriplex* (KT40). *Abies* types from higher and lower altitudes, *Pseudotsuga* types from east and west of the mountains, and ponderosa pine types from east and west of the Rockies are separately presented to emphasize possible differences.

[2] The White Mountain alpine site (10,150 ft) is unusually dry. The Ellery Lake whitebark pine site has only precipitation data; temperature data were therefore taken from a similar altitude at a nearby White Mountain site (9,645 ft).

## Killing Temperatures

The hypothesis that extreme temperatures might exclude a plant (for example, whitebark pine) from an adjacent zone was tested by determining whether the condition is more extreme in the unoccupied than in the occupied zone; if it is not, the hypothesized factor is considered unlikely to be lethal. This test was used on temperatures of early fall frosts, midwinter extreme lows, midwinter average lows, late fall frosts, midsummer average highs, and midsummer extreme highs. Midwinter lows and midsummer highs were tested because these temperatures might exceed the potential tolerances of a plant; fall and spring frosts were considered because they might kill partially hardened plants. Fall frost temperatures were measured as the absolute low in the month in which average temperature first fell below 0 °C; where no month had an average temperature of 0 °C, the values were interpolated to 0 °C from adjacent months. Spring frost temperatures were estimated similarly for the month in which average temperatures first rose above 0 °C. I argue later (see growing season) that average temperatures below 0 °C restrict water and nutrient uptake and therefore open and close the growing season; the use of 0 °C is in contrast to the 5 °C used by many phenologists (for example, Chang 1968). "Absolute" temperatures were the lowest (or highest) seen in the period of record—10 years or more.

## Starvation Temperatures

The plant might be excluded from a zone free from killing events if (temperature) conditions failed to support net photosynthesis on an annual basis. Two indices of growing season temperature were used to test the possibility of such starvation. First, temperatures were averaged across all growing season (defined later) months. Despite its common use in predicting growth (Chang 1968; Larcher 1975), this index is expected to underestimate the benefits of warmer temperatures because chemical reaction rates increase exponentially with increasing temperature. An alternate index of temperature was therefore tested. In the second index temperatures were replaced with growth support units (gsu) and these were averaged across the season. On the assumptions that $Q_{10} = 2$, that very slow growth begins at 1 °C, and that native plants tolerate normal high temperatures of their zones, the growth support unit curve was constructed by interpolating between 0 growth rate units (gsu) at 0 °C, 1 gsu at 1 °C, 2 gsu at 11 °C, 4 gsu at 21 °C, 8 gsu at 31 °C, and 16 gsu at 41 °C. That is, we expect no growth at 0 °C or below, 1 unit at 1 °C, 2 units at 11 °C, 4 units at 21 °C, etc.

## Killing Drought

Evaporation equals roughly 2 mm/°C x month (Daubenmire 1956; Nielson 1986; Stephenson 1990; Thornthwaite 1948; Walter 1973). As a result, one might index drought duration by counting months when average precipitation (mm/2) is less than average temperature (C) or drought intensity by summing, across growing season months, precipitation deficits below the calculated balance.

A count of months registering drought on the Walter index may overestimate drought duration where the deficit is small because drought may open late or close early in the month. To minimize this effect I have normalized drought duration from a scatter diagram of duration against deficit: 0-5 mm = 0 months, 6-15 mm = 1 month, 16-35 mm = 2 months, 36-50 mm = 3 months, and 51-85 mm = 4 months.

I have used the sum of warm-season (average temperature above 0 °C) water deficits as an index of drought magnitude. I do so with the recognition that, due to exclusion of important factors (for example, wind, Penman 1949, and exponential temperature effects, Stephenson 1990), this index usually underestimates water deficit.

## Water Starvation

"Water starvation" should occur where plants are not desiccated, but where water supplies do not support net photosynthesis on an annual basis. For example, starvation would occur if water were continually available, but evapotranspiration equaled or exceeded uptake rates. Such starvation would select for organisms with lower ET rates: Mesophytic leaves would be replaced by xerophytic leaves and leaf exposure might be reduced by reduction of stature even to the point where plants existed only at the ground surface or under transparent rock.

## Growing Season

For sensitive introduced plants, frost-free season is often recorded as an indicator of season length (Burke and others 1976; USGS 1971).

Since cool region plants normally tolerate growing season frosts, I argue for a different index. Growth requires both leaf activity (photosynthesis) and root activity (water and nutrient absorbtion). For plants with frost-insensitive leaves (Burke and others 1976), midday temperatures should be high enough for photosynthesis long before soils are thawed. Root activity extends (maximally) from spring soil thaw to the fall refreeze, so this period should be a better index of growing season length. Thus I open and close the growing season with 0 °C average monthly air temperatures. So represented, initial activity in grasslands begins at spring soil temperatures (0-25 cm) near 0 °C and activity ceases in the fall with soil temperatures as high as 5 °C (Weaver, in preparation). In, or adjacent to, the subalpine fir (*Abies lasiocarpa*) zone the growing season may exceed this period because deep snow cover may prevent the freezing of soil water.

While the temperature-bounded season probably applies at high-altitude sites, at low-altitude sites soil drying may close the growing season before frost does. Thus, one may better index growing season as warm season months minus any drought months included in the warm season. While the Northern Rocky Mountain drought season comes at summer's end (Weaver 1980), this index will also apply to regions where the warm season opens with dry months. It is conceivable that other periodic factors, for example nutrients or pest attack, might affect growing season length.

## Production

Production estimates for each series were drawn from the literature (table 2). These are correlated with climatic conditions that might control them: warm season length, warm moist season length, and the product of warm soil season length and temperature. For the latter, two temperature expressions were tested: average temperature minus 5 °C and Q (the $Q_{10}$-based average). The third (product) indices were expected to be best because they assume that plants grow when soils are unfrozen-moist and that their growth rate is proportional to temperature (over 5 °C for the first linear index and over 1 °C for the second exponential index).

# RESULTS AND DISCUSSION

In the Northern Rocky Mountains vegetation changes from grass-shrub (*Atriplex*, *Bouteloua*, *Agropyron*, and *Festuca*) to conifer (*Pinus ponderosa*, *Thuja-Tsuga*, *Pseudotsuga*, and *Abies*) to alpine graminoid with increasing altitude. Subzones listed parenthetically are described by Daubenmire (1943) and mapped by Kuchler (1964). This paper compares weather data gathered in these zones to test hypothesized controls of distribution and production. The method is illustrated with whitebark pine.

## Upward Limits

I speculate that the upward limits of whitebark pine might be determined by lethal factors (winter low temperatures, spring-fall frosts, or desiccation) or production deficits (starvation) due to inadequate water or heat units. These hypotheses are considered in the following paragraphs.

If winter lows are lower in the alpine than in the pine zone below, winter cold might be the excluding factor, otherwise not. Contrary to my expectation, neither absolute lows nor average January minima are lower in the alpine than in the pine (or most other) vegetation zone(s) (fig. 1). The failure of low temperatures to develop at higher altitudes may be due to the high density of cold air: Cold air entering from the north stays low like mercury poured under water and air cooled by exposure to cold alpine ground runs off (Geiger 1965). Since extreme temperatures are not lower at high than low altitude, I deduce that neither whitebark pine, nor most other native dominants, are excluded from high sites by extreme low temperatures of winter. An exception to this generalization seems to appear in high- or low-altitude frost pockets, where accumulating cold air may kill trees in winter or spring (Weaver 1990).

For natives of an area, I suggest that frost damage is more likely when plants are partially hardened (fall) or partially dehardened (spring) than at midwinter. I expect (1) winter to be delimited approximately by the fall month in which surface soils fall below 0 °C and the spring month in which they rise above 0 °C, (2) winter to be a season of low root activity, low water, and low nutrient uptake, and (3) 0 °C soil temperatures to be approximately coincident with 0 °C air temperatures (Weaver, in preparation). I therefore (1) compare, across vegetation types, observed temperature lows in these spring-fall seasons of incomplete frost hardness (fig. 2), (2) discover no difference, and (3) conclude that frosts probably do not partition vegetation native to the region. The preceding discussion depends on the assumption that plants harden and deharden in phase with air/soil temperatures. This argument would be fallacious if day length were the primary controller of the hardening/dehardening process. However, since both temperature and correlated day length triggers are important (Salisbury and Ross 1992), I expect frosts to exclude plants from environmentally distant, but not environmentally adjacent, vegetation types.

While frosts and winter freezes probably do not exclude whitebark pine from the alpine (or other plants from the vegetation zone immediately above), a lack of heat units

Table 2—Productivity in grams per square meter per year and aboveground standing crop (Abvegr std crp) of major Rocky Mountain vegetation types

| Vegetation type | Productivity[2] | Abvegr std crp | Source |
|---|---|---|---|
| | *g/m$^2$/yr* | *t/ha (age,yr)* | |
| *Alpine* | 135 | 1.35 | Thilenius and others 1974 |
| | 100-200 | 1.00-2.00 | Scott and Billings 1964 |
| *Pinus albicaulis* | [1]60 | [1]140 (300-500) | Weaver and Dale 1974 |
| | [1]25-75 (53) | | Pfister and others 1977 |
| | 200-700 | 350 (300-500) | Forcella and Weaver 1977 |
| *Abies lasiocarpa* | 100-200 | 160 (300-700) | Aplet and others 1989 |
| | 860 | 357 (106 yr) | Whittaker and Niering 1975 |
| | [1]95-180 (137) | | Pfister and others 1977 |
| | | 100-250 (old) | Weaver and Forcella 1977 |
| | | 150-250 | Landis and Mogren 1975 |
| *Pseudotsuga menziesii* | 1,550 | 438 (252) | Whittaker and Niering 1975 |
| | [1]30-170 (150) | | Pfister and others 1977 |
| | | 100-350 (350+) | Weaver and Forcella 1977 |
| *Thuja plicata-Tsuga heterophylla* | 870 | 290 (105) | Hanley 1976 |
| | 550 | 316 (250) | Hanley 1976 |
| | 1,380 | 504 (103) | Hanley 1976 |
| | [1]150-330 (240) | | Pfister and others 1977 |
| *Pinus ponderosa* | [1]188 | | Clarey and others 1975 |
| | [1]30-150 (168) | | Pfister and others 1975 |
| | 490-570 | 150-250 (150) | Whittaker and Niering 1975 |
| | | 50-250 (350+) | Weaver and Forcella 1977 |
| *Festuca idahoensis* | 235 | 2.35 | Collins and Weaver 1978 |
| | 195 | 1.95 | Weaver and Collins 1977 |
| | 147 | 1.47 | Daubenmire 1970 |
| *Festuca scabrella* | 152 | 1.52 | Willms and others 1986 |
| *Bouteloua gracilis* | 103 | 1.03 | Weaver 1983 |
| | 53-95 | 0.5-1.0 | Hunt and others 1988 |
| *Atriplex spp.* | 28 | | West 1983 |

[1] Since merchantable production and standing crop are emphasized in these studies, one might expect the figures to be 50 to 66 percent of those reported in studies of total production (Weaver and Forcella 1977).

[2] Where production and standing crop are expressed volumetrically, masses were calculated using specific gravities of ABLA=0.38, PIAL=0.40, PIEL=0.35, PSME=0.45, PIPO=0.43, PICO=0.38, THPL=0.33, TSHE=0.41 (U.S. FPL 1974).

(starvation) may exclude, from an altitudinal zone, plants of lower zones. Average growing season temperatures in the alpine (and for most zones below it) are distinctly lower than temperatures in the vegetation zone below (fig. 3). This correlation suggests the possibility of—but does not prove—significant effects of growing season temperature. In support of this hypothesis, production-temperature relations (discussed below) suggest that the vegetation of each altitudinal zone is especially adapted to temperatures occurring in its zone. In this regard, it is satisfying to see that optimum temperatures for whitebark pine photosynthesis (20-25 °C, Jacobs and Weaver 1990) are similar to summer maximum temperatures (10-25 °C, Weaver 1990).

Graphs of estimated soil water availability against vegetation type (fig. 4) indicate little or no stress in alpine, whitebark, subalpine fir, and Douglas-fir zones. On this basis one might exclude drought as a factor determining whitebark's upslope limit. Due to two modifying factors, this conclusion seems premature. First, as one moves upslope from forest to alpine (or mountain meadow), winds increase and, with increasing wind, drought increases due to reduced water availability—snow may be blown off site (Daubenmire 1981) and water in uninsulated soils freezes—and increasing water loss—through abrasion of cuticle (Hadley and Smith 1987) and thinning of the leaf's boundary layer (Gates and Papian 1971; Nobel 1983). I see winter wind effects as probable controllers because trees invading (or planted into) mountain meadows are more often desiccated in winter than summer. The wind effect hypothesis is consistent with the fact that groups of trees sometimes invade sites that individuals cannot invade alone (Armand 1992; Tranquillini 1979). In such situations adjacent trees are more likely sheltering each other from drying wind than from lethal low temperatures. Second, as one moves upslope the average soil becomes progressively better drained (Weaver 1979), and thus effective precipitation is a smaller fraction of total

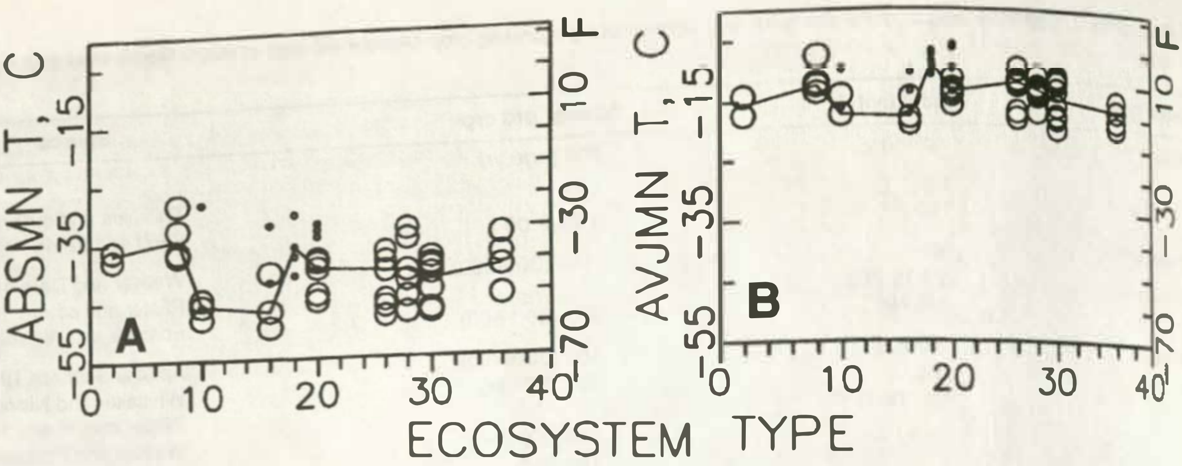

**Figure 1**—Midwinter low temperatures in 10 Rocky Mountain ecosystems. Low temperatures (°C and °F) are represented by absolute winter minimums (A, ABSMN) and average January minima (B, AVJMN). Ecosystem types range altitudinally from alpine (2), down through forests (8-20) to grass and shrublands (26-36); specifically, they are alpine (2), whitebark pine (8), subalpine fir (10), Douglas-fir (16), cedar-hemlock (18), ponderosa pine (20), Idaho fescue (26), bluebunch wheatgrass (28), gramagrass (30), and desert shrub (36). Large and small circles represent data gathered east and west of the Rockies, respectively. Lines connect median values.

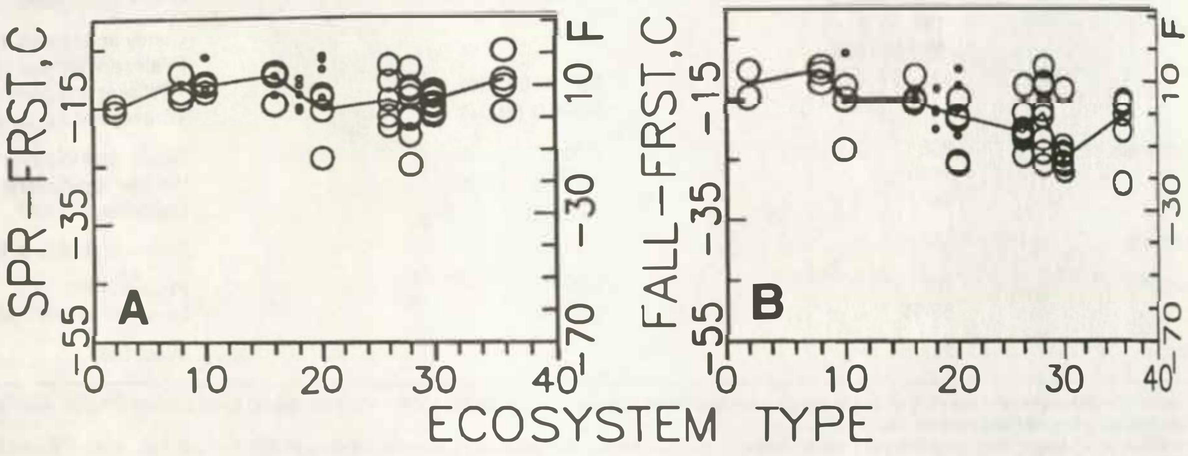

**Figure 2**—The coldest early spring (A, SPR-FRST) and late fall (B, FALL-FRST) frosts (°C and °F) in 10 Rocky Mountain ecosystems. Ecosystems, symbols, and lines are as in figure 1.

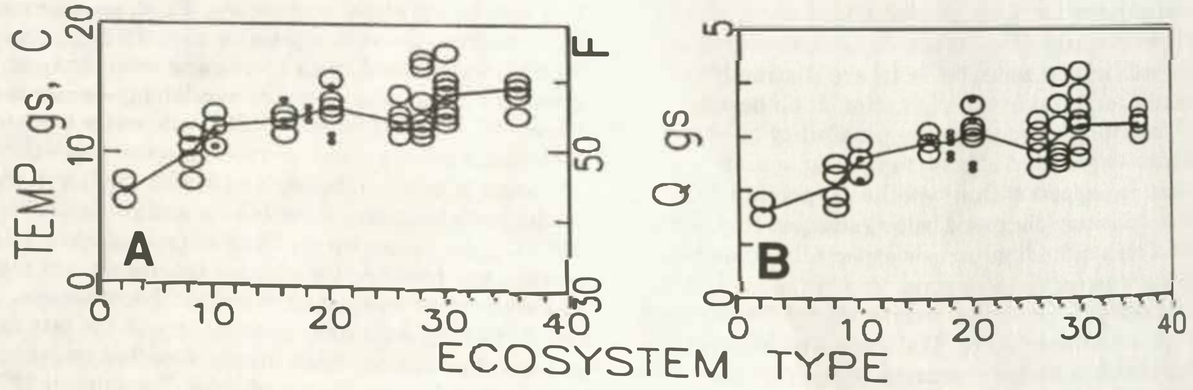

**Figure 3**—Average growing season temperatures in 10 Rocky Mountain ecosystems. The first graph (A, TEMP gs) gives the average growing season temperature (°C and °F). Q gs in the second graph (B) considers the exponential response of physiological processes to increasing temperature ($Q_{10}$). Ecosystem types, symbols, and lines are as in figure 1.

precipitation at higher than lower altitudes; that is, the Walter drought indices presented in figure 4 probably overestimate water availability on (high-altitude) thin-soil sites.

## Downward Limits

I speculate that downward limits of whitebark pine might be determined by heat, drought, or competition. The following paragraphs consider these hypotheses.

As one moves downslope maximum temperatures (fig. 5) rise. That this correlate of tree disappearance is not controlling is suggested by three facts. Summer averages in vegetation zones below whitebark pine (10-15 °C, fig. 3) are well below the whitebark pine optimum (20-25 °C, Jacobs and Weaver 1990), so downward migration might actually improve production. July maxima (20-27 °C, fig. 5) in zones below are near the whitebark pine optimum temperature (20-25 °C, Jacobs and Weaver 1990) and thus should not be damaging. Long-term maxima (30-42 °C, fig. 5) in zones below do not eliminate net photosynthesis (Jacobs and Weaver 1990) and thus are probably not lethal. In addition, if whitebark pine trees are well watered, they grow well as lawn trees in the *Agropyron spicatum* zone (for example, Belgrade, MT) where temperatures are far higher than those found on sites whitebark naturally occupies.

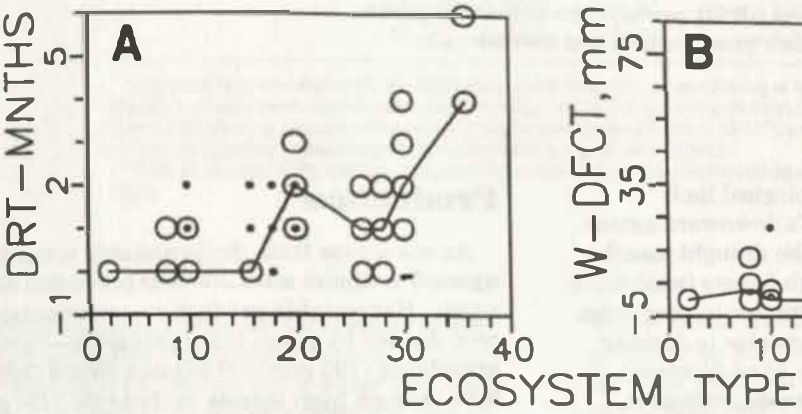

Figure 4—Drought severity in 10 Rocky Mountain ecosystems. The first graph (A) gives the number of dry months (DRT-MNTHS). The second (B) indexes the annual water deficiency (W-DFCT, mm). Both were calculated after Walter (1973). The ecosystem types, symbols, and lines are as in figure 1.

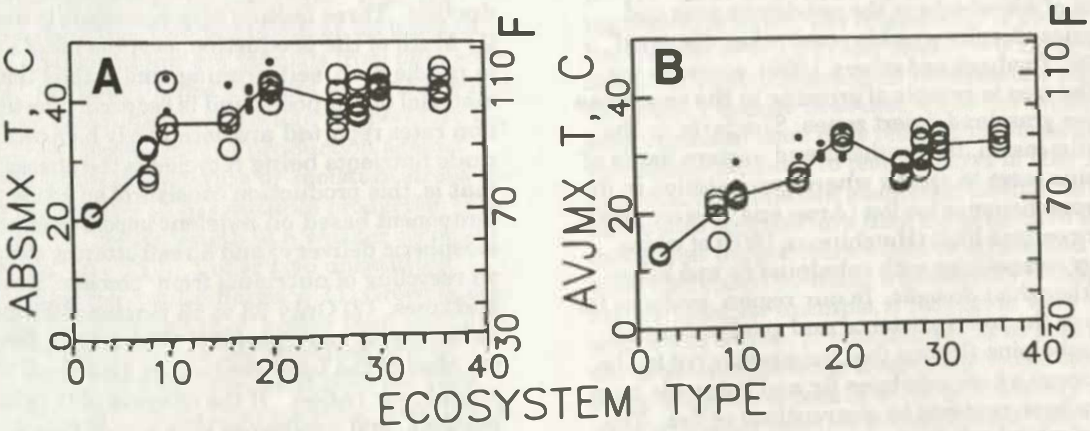

Figure 5—High temperatures (°C and °F) recorded in 10 Rocky Mountain ecosystems. The first graph (A) represents absolute summer highs (ABSMX). The second (B) gives average July maxima (AVJMX). The ecosystem types, symbols, and lines are as in figure 1.

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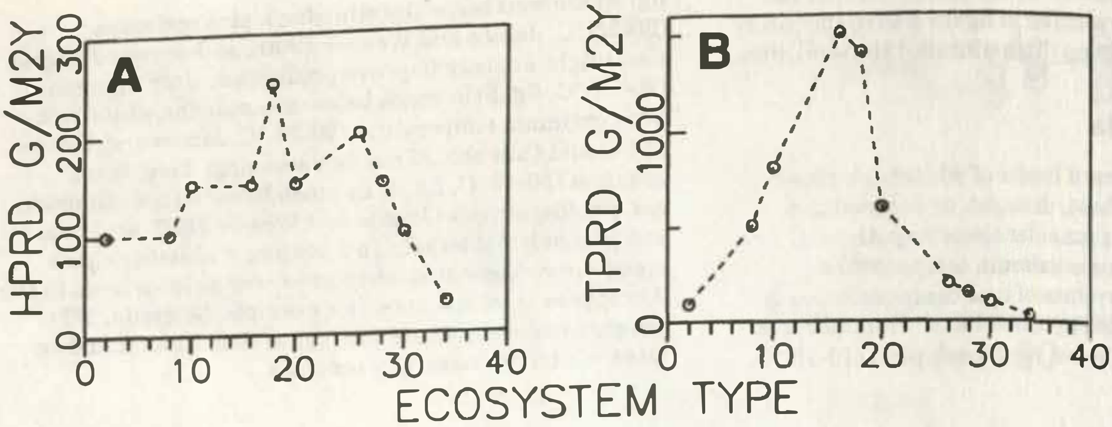

**Figure 6**—Biomass production in 10 Rocky Mountain ecosystems (see also table 2). The first graph (A) presents harvestable production (HPRD, g/m²/yr). The second (B) gives total production (TPRD, g/m²/yr). The ecosystem types, symbols, and lines are as in figure 1.

Drought likely sets the lower physiological limit (Hutchinson 1958) for whitebark pine's downward extension. Walter's (1973) index suggests the drought months and water deficits are near zero in high forests (whitebark pine, subalpine fir, and Douglas-fir), greater in ponderosa pine forests and grasslands, and still greater in *Atriplex* shrublands (fig. 4). If (as noted above) wind decreases and waterholding capacity of soils increases downslope, water conditions for whitebark production improve as one moves downslope; this is consistent with the fact that whitebarks growing in the subalpine fir zone can be stately timber producers (Pfister and others 1977; Weaver and Dale 1977). Water deficits remain slight down through the subalpine fir and possibly the Douglas-fir zones. The complete absence of whitebarks in the ponderosa pine and grassland zones, despite possible nutcracker dispersal (Lanner 1990; Tomback and others 1990), supports my doubt that the tree is capable of growing in the ponderosa pine and drier grassland-desert zones. Similarly, in the geographic dimension, the southern and eastern limits of whitebark pine seem to appear where precipitation in its altitudinal zone becomes too low (Arno and Weaver 1990).

The lower realized limit (Hutchinson 1958) of whitebark is set by competition with subalpine fir and lodgepole pine rather than drought. In our region, evidence for this fact lies in the tree's existence and good growth on sites in the subalpine fir zone (but apparently not in the Douglas-fir zone) where subalpine fir and lodgepole competition have been removed by clearcutting or fire. The lower limit of whitebark is, then, set by those factors—likely drought (thin soils and wind) and low summer temperature—that exclude subalpine fir and lodgepole pine from higher sites. In the geographic dimension, to the north and west where rainfall is higher, whitebark is also unable to form pure stands or disappears (Arno and Weaver 1990). (European foresters ask why we don't eliminate competitive "natives" [subalpine fir and lodgepole pine] from their zone to allow expansion of whitebark pine and increased production of quality white pine lumber.)

## Production

As one moves from dry grasslands to moist forests and upward to alpine sites one sees production rise and fall again. Harvestable production—merchantable standing crop divided by years in its production—rises from dry grasslands (100 g/m²/yr) to moist forests (300 g/m²/yr) and falls through high forests to the alpine (100 g/m²/yr, fig. 6, table 2). Available data suggest that total aboveground production (total increment g/m²/yr) also increases from dry grass and shrublands (50-100 g/m²/yr) to warm forests (over 500 g/m²/yr) and falls to the alpine (100 g/m²/yr, fig. 6, table 1). The trend is parallel, but—at least in forests—total production is far higher than harvestable production. Three factors may contribute to this difference: (1) Much of the production, over the life of a stand, is lost to needle drop, self pruning, and natural thinning; this material decomposes and is recycled. The total production rates reported are deceptively high because they include nutrients being recycled to the atmosphere and [illegible] that is, this production consists of an actual production component based on nutrient import (weathering and atmospheric delivery) and a restructuring component based on recycling of nutrients from "obsolete" leaves, branches, and trees. (2) Only 33 to 50 percent of the material extant at harvest is merchantable (Weaver and Forcella 1977). (3) Most of the total production data comes from areas outside our region. If the climates of Douglas-fir, cedar-hemlock, and ponderosa pine stands from which production data are reported are moister or warmer than the Montana stands in which the harvestable productivity data were gathered, somewhat higher productivities might be expected.

I expect productivity to be controlled, like vegetation distribution, by climate. In the following paragraphs I will explore the hypothesis that production depends on growing season length and the warmth of that season

Growing season length might be indexed as the number of months where daily average temperatures are above

Table 3— Relationship of production (g/m²/yr) to climatic factors

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Harvestable production[1] | | | | | | | |
| HP | = | 66.00 | + | 12.8000 | WS | $p = 0.50$ | $r^2 = 0.05$ |
| | | −171.00 | + | 70.0000 | GS | $p = 0.00$ | $r^2 = 0.86$ |
| | | 34.00 | + | 1.7700 | GSxT | $p = 0.04$ | $r^2 = 0.44$ |
| | | −38.00 | + | 14.4000 | GSxQ | $p = 0.01$ | $r^2 = 0.58$ |
| Log HP | = | 0.78 | + | 0.3000 | WS | $p = 0.00$ | $r^2 = 0.78$ |
| | | 1.75 | + | 0.0060 | GSxT | $p = 0.12$ | $r^2 = 0.27$ |
| | | 1.44 | + | 0.0530 | GSxQ | $p = 0.03$ | $r^2 = 0.44$ |
| Total production[2] | | | | | | | |
| TP | = | −880.00 | + | 32100000 | GS | $p = 0.16$ | $r^2 = 0.22$ |
| | | 50.00 | + | 8.3200 | GSxT | $p = 0.32$ | $r^2 = 0.12$ |
| | | −398.00 | + | 77.0000 | GSxQ | $p = 0.19$ | $r^2 = 0.20$ |
| Log TP | = | 0.40 | + | 0.4700 | GS | $p = 0.03$ | $r^2 = 0.45$ |
| | | 1.96 | + | 0.0086 | GSxT | $p = 0.32$ | $r^2 = 0.12$ |
| | | 1.47 | + | 0.0820 | GSxQ | $p = 0.22$ | $r^2 = 0.22$ |

[1] Harvestable production (HP, top diameter greater than 10 cm) and the log of harvestable production (log HP) are regressed against warm season (WS), warm-moist growing season (GS), the product of warm-moist growing season and average growing season temperature (GSxT), and the product of warm-moist growing season and $Q_{10}$-based growth support units (GSxQ).

[2] Total production (TP) and log total production (log TP) are also regressed against GS, GSxT, and GSxQ.

0 °C. The rationale is that, unless air temperatures are above 0 °C, exposed soils will be frozen (Weaver, in preparation) and frozen soils will deliver little water and nutrients. Because a regression of production against this index of growing season is so loose ($r^2 = 0.05$, table 3, fig. 7), the hypothesis that warm-season length controls production is inadequate.

The previous index may fail because, at least at lower altitudes, growing season is limited in late summer by a lack of soil water, rather than temperature. If so, the growing season index would be improved as an index of production by subtracting soil-dry months from total soil-warm months. As above, I index drought as periods when precipitation (mm/2) is less than average temperature (C, after Walter 1973). Regressions of production against months without either temperature or moisture stress explain most of the variance in harvestable production ($r^2 = 0.86$, table 3, fig. 7). Season length is a weaker correlate of total production ($r^2 = 0.22$). I offer two unsatifying hypotheses for this important difference: (1) Growing season predicts harvestable production better than total production because photosynthates are allocated first to canopy maintainence (so this component does not vary much among types) and second to supporting structure; if so, the relationship between season length and trunk production is clarified by omitting the common leaf-twig production. (2) If total production were measured in slightly more favorable segments of the environmental types than harvestable production, the understatement of season length would weaken the relationship.

If all vegetation—grassland to forest to alpine—had a single temperature response curve, we would expect production in "warm moist soil days" to rise exponentially with increasing temperature. This expectation is based on the rise in chemical reaction rates with rising temperature, on the resultant physiological response curves (Larcher 1975), on degree-day prediction of plant phenology (Chang 1960), and on the prediction that degree-day formulae might be improved by use of temperature averages computed from a nonlinear $Q_{10}$ relationship (Larcher 1975). Thus, we expect production to be better correlated with the product of growing season days x temperature than with growing season days alone. In fact, whether we use our average growing season temperature or growing season Q index, the relationship is poorer for both harvestable ($r^2 = 0.44$) and total ($r^2 = 0.12$) production. Since the basic physiological response is a physiochemical necessity, I deduce first that, while the vegetation of each environmental zone does respond to temperature, it is specifically adapted to temperatures in that zone and, second, that temperature adaptation distinct to each zone eliminates temperature from the predictive equation. I doubt that temperature would be eliminated if adaptation were eliminated by using a genetically homogeneous vegetation type; for example, if the region were vegetated with a single crop, production would be best predicted by the product of growing season length and temperature. Since competitiveness of a tree undoubtedly depends on its productivity relative to competitors, this conclusion supports earlier speculation that growing season temperature adaptation provides at least one basis for the existance of different vegetation zones.

While I have argued that production in a zone is best predicted from the length of its warm moist growing season, I expect the standing crop of mature accumulative (woody) vegetation (table 2) to be largely determined by site fertility. Accumulation—slow or fast—depends on photosynthesis minus respiration. Synthesis depends on light, warmth, water (open stomates), and nutrients. In the absence of stand destruction, annual inputs of light, warmth, water, and elements with atmospheric cycles (for example, C, H, O, N) should support eternal accumulation. Limited supplies of nutrients with geologic cycles (for example, P, K, Ca) will halt accumulation (Weaver 1978). It is also argued (Odum 1969) that accumulation is halted when respiration equals production. Thus, in young trees net production is high because the ratio of photosynthetic mass to respiratory mass is high, in longer stemmed trees efficency declines as the respiratory load increases, and growth ceases when respiration equals gross production; heartwood's contribution to this relationship is in proportion to its inertness. While the respiratory factor undoubtedly contributes to observed declines in production with stand height (and age) (Weaver and others 1990), I see nutrient supplies as more limiting in high forests because the trees are far shorter (and therefore more efficient) than productive trees of lower altitudes. In contrast, standing crops in less accumulative (herbaceous) vegetation are determined by production occurring in one growing season, and while it could be determined by supplies of a geologically cycling nutrient, standing crop is more likely determined by a bulk resource like light (unlikely), warmth, water, or an atmospheric nutrient like nitrogen.

# CONCLUSIONS

Whitebark pine vegetation is likely excluded from the alpine zone by cool growing season temperatures or droughts occurring most likely in winter. It seems unlikely that freezes of late fall, midwinter, or early spring exclude the tree from higher sites.

The lower physiological limit of whitebark pine is likely set by drought. Its lower realized limit is likely due to competition with lodgepole pine or subalpine fir.e By control of competition, managers could probably extend whitebark's range downslope.

The distribution of other dominant plants on the temperature water gradient may be similarly controlled.

Annual production is strongly related ($r^2 = 0.86$) to the number of growing season days. The lack of correlation with temperature suggests that plants of any vegetation zone are adapted to temperature conditions peculiar to that zone. Mature standing crops of woody vegetation are more likely determined by nonatmospheric nutrients than temperature and precipitation. Potential standing crops of herbaceous vegetation, on the other hand, are more likely limited by bulk resources such as warmth, water, carbon, or nitrogen.

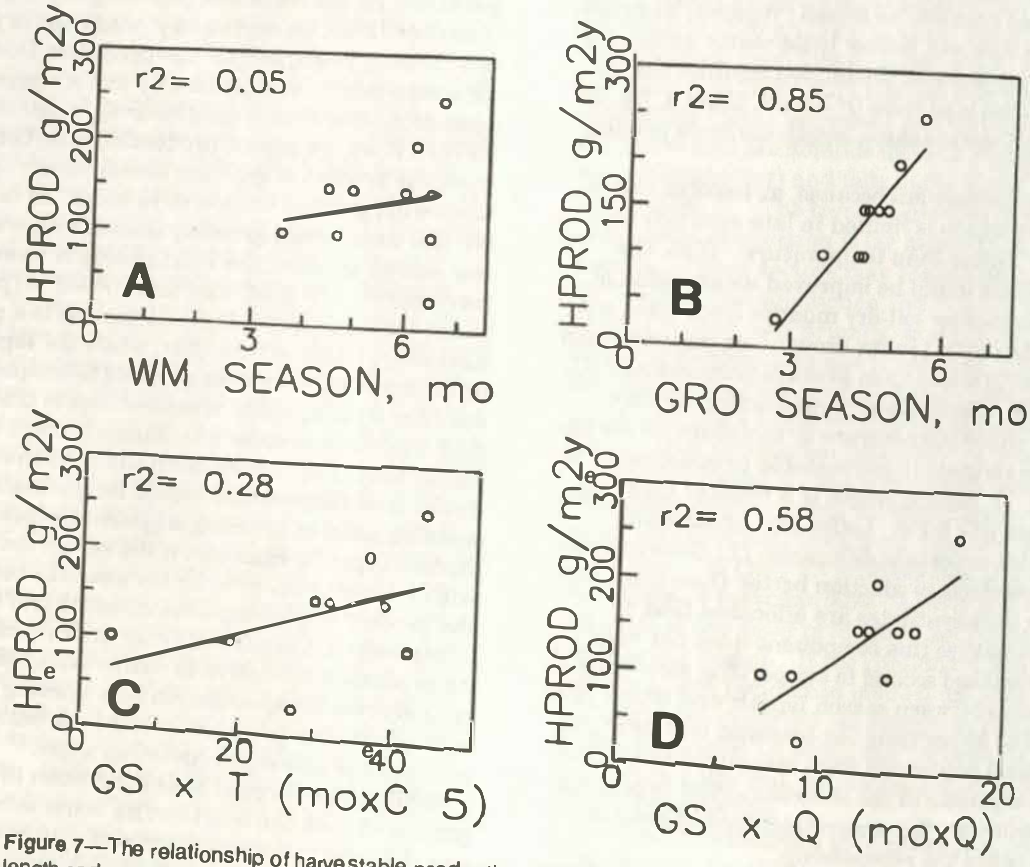

**Figure 7**—The relationship of harvestable production (HPROD, g/m²/yr) to season length and temperature: (A) production vs. warm season (WM-SEASON), (B) production vs. warm-moist season (GRO-SEASON), (C) production vs. warm-moist season (GS) x average summer temperature above 5 °C (C-5), (D) production vs. warm moist season (GS) x growth support units ($Q_{gs}$). The ecosystem types are as in figure 1.

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