The ecology of whitebark pine (Pinus albicaulis Engelm.) was studied for two summers on Bachelor Butte, a volcanic peak in the Cascade Range of central Oregon. The pine grows primarily within the timberline zone which separates the closed forest from the alpine zone. Whitebark pine occurs principally on ridges radiating from the summit, with younger trees on the highest vegetated ridges, and the oldest trees (more than 700 years old) in the lowest part of the timberline zone. Whitebark pine groves were divided into four types according to trunk diameter and tree height distribution.

Eleven whitebark pine trees from 1980-2500 m elevation were studied to determine morphological variation within and between the pines. Significant differences in growth potential and general vigour were found between branchlets producing seed cones (seed branchlets) and those never producing seed cones (pollen branchlets); seed branchlets elongated more, produced longer needles, and were stouter than pollen branchlets. Needles, branchlets, and buds generally decreased in size with increasing elevation; growth was most vigorous near the butte's base, and was least on the highest ridges. Mature cones were produced only in summer 1979.

Phenological studies for the same 11 trees in 1979 showed that the lower the elevation, the sooner growth commenced in spring and the sooner it finished in late summer. Seed branchlet growth was significantly suppressed during July, when needles and cones were rapidly increasing in size on the same branchlet. Seed branchlets achieved
maximum elongation before pollen branchlets on the same tree.

Influences on the growth, morphology and distribution of the pine were studied. Annual variation in needle and branchlet elongation was related to environmental factors by correlation and regression analysis. Needle growth was more effectively related to climate (R²=0.61 for needles on pollen branchlets and 0.65 for seed branchlets) than was branchlet growth (R²=0.18 for pollen branchlets and 0.22 for seed branchlets). Climate of both the year of elongation and the previous year was significantly related to the growth of the pine's organs. Needles were affected by summer temperatures of the current year, whereas branchlet growth was not. Cone production was significantly related to temperature of the previous year (R²=0.38).

The pre-dawn xylem pressure potential for 20 trees in the timberline zone during the summer drought was -10.1 bars. At mid-day, it averaged -15.9 bars for the same trees. Readings were significantly lower on the leeward side of the trees than on the windward side.

Most of the whitebark pine tree crowns on Bachelor Butte were somewhat misshapen. This asymmetry is due primarily to the effect of prevailing winter winds from the southwest, which flow around the peak in a definite pattern. The winds appear to affect tree form both through desiccation of exposed branchlets and the accumulation of snow and ice. Whitebark pine distribution on the peak is primarily dependent upon the distribution of snowdrifts. Pines grow only where snow-melt occurs earliest, viz. atop ridges and other areas swept nearly snowless by winter winds.

Effects on the trees of wind during the growing season are minimal. Trees show no significant difference in needle or branchlet length on the side of the tree facing the prevailing wind and the side away from it. Needle longevity is also relatively consistent on different sides of the tree.
ECOLOGY OF PINUS ALBICAULIS
ON BACHELOR BUTTE, OREGON

by

DENNIS LUECK

A THESIS

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Typed by Whitey Lueck for Dennis Lueck
ACKNOWLEDGEMENT

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The realization of this short novel would have been impossible, were it not for the encouragement and support of many friends and colleagues. Life on the mountain was sweetest when I was able to persuade companions to spend a week with me in the wild. They braved hailstorms, lightning, summer snows, and MORE! just to stay at my timberline camp with its magnificent view of lakes and snow-capped peaks. And then there were those clear summer evenings when, from Pine Marten Knob, we could watch the full moon rise over central Oregon's desert... But I digress! I wish to express my sincere gratitude to Don Zobel, for his advice and counsel, and for his understanding of my propensity to be incessantly distracted by autres choses. Employees of Mount Bachelor Ski Corporation were always very helpful, too, providing me with ski lift rides up the mountain, and giving me refuge when the worst of storms drove me from my tent. I appreciated, as well, Frank Smith's assiduous review of the thesis text, and his useful suggestions. I also thank my parents who, after all, made this entire study possible, and who threatened me with a severe case of boils should I not have completed it.
Frontispiece. Bachelor Butte, Oregon (2763 m elevation), seen from the east. Pine Marten Knob (2378 m) is visible on the lower right flank of the peak, as is Tot Mountain (2294 m) on the lower left flank.
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Throughout the western part of North America, whitebark pine (Pinus albicaulis Engelm.) is common at and below the timberline of many of the higher mountains. Because of the inaccessibility of many of the regions where whitebark pine grows, and its slow growth rate, historically there has been little interest in harvesting the tree. Consequently, the zone where it grows is one of those least disturbed by the impact of man. Another result of the pine's inaccessibility is that very little is known about its ecology. Since the pine grows mostly near the elevational limit of tree growth, it is probably relatively sensitive to minor fluctuations in weather from one year to the next, and thus might be useful in determining past weather patterns. It often has a misshapen crown which may be directly or indirectly caused by wind. If the tree's gross morphology were indeed influenced by wind, morphology might serve as an indicator of wind patterns and perhaps even velocities. Thus, observation of tree morphology might be an inexpensive screening technique for the siting of electricity-generating wind turbines.

The natural range of whitebark pine extends southward from British Columbia through the southern Sierra Nevada of California and eastward atop isolated mountain peaks and into the Rocky Mountains, as far south as Wyoming. The pine usually grows at elevations between 1350 and 3650 m (Mirov, 1967), and in central Oregon is most common between 1800 and 2500 m. It is most important in the subalpine zone and rare below 1500 m. It occasionally grows in abundance on relatively level terrain, but is most noticeable on exposed ridges. The biology of whitebark pine is much like that of other pines (Mirov, 1967), yet there are salient differences, especially concerning the pine's reproduction.

Pinus albicaulis was first described in 1851 by John Jeffrey, a
Scottish botanist sent to western North America to collect the seeds of native plants which might be useful as ornamenals. He called the tree he discovered near the Fraser River in southwestern British Columbia *Pinus flexilis*. In 1863, Engelmann, in the Transactions of the St. Louis Academy, named it *Pinus albicaulis* (Sargent, 1897).

Bachelor Butte, an isolated volcanic peak, was chosen as the primary study site for whitebark pine for two reasons. First, it is accessible year-round, a factor of great importance in reaching the whitebark pines which usually grow far from the nearest road. A ski resort is operated on the lower north flank of the peak, and ski lifts reach into the lower part of the whitebark pine zone. Second, Bachelor Butte is a nearly symmetrical volcanic cone, allowing winds to flow smoothly around the peak, an ideal situation for studying effects of wind on trees.

Bachelor Butte is located in central Oregon 30 km west-southwest of Bend (Figure 1). The summit lies 15 km southeast of the top of South Sister. The butte has been known to Caucasians since the 1820's when the first explorers penetrated central Oregon. It was first known as Brother Jonathan, the Methodist missionaries from Salem having named it as part of a "family" of peaks (viz. the Three Sisters, the Husband, the Wife, and the Brother). In the late nineteenth century, however, the peak became known simply as Bachelor Butte, in contradistinction to the Three Sisters peaks, from which it stands apart (Brogan, personal communication, 1978).

Studies were carried out primarily during the summers of 1978 and 1979, although monthly visits were made during winter, as well. I established a camp at 2330 m on the north flank of the peak, from which I carried out daily excursions in summer.

There apparently has been no description of the flora or fauna of Bachelor Butte. During my excursions, I studied plant community composition in an effort to provide a base-line for further ecological studies, as well as to indicate what rôle other plants may play in the ecology of the pine. I also observed the animals.

The growth and development of needles, branchlets, and cones of
Figure 1. Location of study site in the state of Oregon.
whitebark pine were closely monitored during two summers. The pine's morphology was also studied in detail, with particular attention given to gender-influenced differences. Lastly, a detailed examination was made of possible environmental influences on the distribution and gross morphology of whitebark pine trees.
II. ENVIRONMENT OF BACHELOR BUTTE

GEOLOGY

Bachelor Butte is one of a series of majestic peaks of volcanic origin which punctuate the western horizon of central Oregon and rise high above the high lava plains to the east. The southernmost of a chain of eight peaks beginning at Mount Jefferson, 80 km to the north, Bachelor Butte rises abruptly more than 800 m above the surrounding terrain, attaining a height of 2763 m with a base six kilometers in diameter.

Early workers believed that the platform upon which the High Cascades were formed was initiated in Pliocene time. Broad shield volcanoes were formed of olivine basalt and basaltic andesite, capped by steeper cones of pyroclastic debris (Williams, 1944). Taylor (1970) suggests that the present peaks are entirely of Pleistocene and Holocene age.

Structural weaknesses in the Cascades are typically aligned north to south (Oregon Department of Geology and Mineral Industries, 1976). As seen from the top of Bachelor Butte, there is a very obvious alignment of Tot Mountain, the summit of Bachelor Butte itself, Pika and Pine Marten Knobs, and the cinder cone at the base of the butte's north side (Figure 2).

The oldest Cascade peaks suffered profoundly from glacial erosion during the Pleistocene. However, the large basaltic cone of Bachelor Butte developed during and since the closing stages of the Pleistocene. Within the last few millennia, floods of blocky basalt erupted and numerous basaltic scoria cones arose above widely scattered vents on Bachelor Butte. Another relatively recent phenomenon is the cinder cone at the base of the north side of the mountain (Oregon Department of Geology and Mineral Industries, 1976). The flows and scoria that erupted most recently from fissures on the flanks of Bachelor Butte are dark gray to black vesicular lavas rich in glass.

I came upon a heretofore undiscovered lava tube on the lower south
Figure 2. Schematic cross-sections (to scale) through the summit of Bachelor Butte.
side of Bachelor Butte, on the north flank of "Tot Mountain." It is about 20 m long and 2-3 m in diameter, and only slightly inclined; trees growing atop it conceal it well. It can be entered from either end, the south entrance being widest and the north one but a slit.

The nearly symmetrical cone of Bachelor Butte has been weathered very little as compared to older Cascade peaks. Nonetheless, glaciation on its northeast flank left a prominent terminal moraine 80 m high at 2400 m elevation. This moraine results from what Taylor (1970) termed the neoglacial "Little Ice Age," less than 2500 years ago. Such moraines are common in the High Cascades between 2100 and 2500 m elevation.

The present substrates on Bachelor Butte vary according to altitude and aspect. On the lower flanks of the cone, the blocky lava has been covered by volcanic ash and other debris. From circa 2100 m to the summit, most of the surface is composed of lava blocks ranging in size from a few centimeters to more than a meter in diameter. On the cone's upper half, most of the vegetation grows on lava ridges which radiate downward from the summit.

The substrate of the Pinus albicaulis groves ranges from very rocky (greater than 80% rock cover) to quite loamy (less than 20% rock cover). The highest groves tend to have the least developed soils, while lower and older groves typically have acquired a modest loam layer.

Erosion of the butte has been caused mostly by snow and wind. Rainfall is negligible here and is usually rapidly absorbed by the porous ground. The heavy snowpack which accumulates above 2000 m is, however, a great erosive force. There are few flat areas larger than a few hundred square meters and most of the butte's flanks have slopes of 10-40%. After snow reaches a depth of several meters it begins to creep, transporting rock downslope and resulting in a constantly changing topography.

Snow melt, greatest during early summer afternoons, results in only minor erosion. At treeline, running water persists from late morning until early evening; melting at other times of the day is
easily absorbed by the soil.

Wind redistributes dust and ash particles, as well as snow, around the mountain. Above 2200 m, the greatest accumulation of fine particles dropped by the prevailing westerly winds occurs just east of the lateral moraine on the northeast flank.

CLIMATE

INTRODUCTION

The climate of the High Cascades, like that of the entire Pacific Northwest, is maritime in nature, with the majority of the storms coming from the southwest during the winter months. The moisture-laden winds move first across the Coast Range and the Western Cascades before finally encountering the High Cascades. East of the Cascades a more continental climate prevails with hotter summers, colder winters, and low annual precipitation except in the mountains. Bachelor Butte is the easternmost peak of the High Cascades, but is nevertheless greatly influenced by marine air, especially in winter.

Seasonal variation in weather is great. A cyclonic flow of air, most typical during winter, generally connotes frequent storms, rising air, clouds and precipitation. Most precipitation above 2000 m falls during winter as snow. However, at such elevations snowfall can occur during any month. From late October until early June, humidity remains high and persistent, cold, dry winds are uncommon. Temperature extremes are infrequent; minima are seldom below -20 C, even in the higher mountains. Snowfall consequently has a high moisture content and becomes well compacted.

Anti-cyclonic air flow is most common during summer and results in infrequent storms, high pressure, descending air, and little precipitation. Rainfall is usually limited to showers or thunderstorms often accompanied by hail. Above 2000 m, summertime temperatures may infrequently reach 25 C. Summer winds are typically from the north and east and are very dry and neither particularly strong nor persistent.
TEMPERATURE

Temperatures at treeline on Bachelor Butte were measured with a recording thermometer placed in a grove of mature whitebark pine trees at 2350 m on the northwest flank of the mountain. The thermometer's sensor was 2 m up in one of the trees and was suspended 15 cm below a white, insulated, wooden shade which shielded the sensor from above and from the sides. Temperature data were obtained from June until September, 1978 and 1979.

In order to obtain some idea of temperature regimes in the High Cascades at other times of the year, data were obtained from a National Weather Service recording station. The nearest station with a climate analogous to that of Bachelor Butte is Santiam Pass (1450 m), located at the crest of the High Cascades, 45 km north of Bachelor Butte. The Santiam Pass station provides data for more years than other stations in the vicinity and still reflects conditions in the High Cascades.

Mean daily temperatures were calculated for Bachelor Butte as the mean of each day's maximum and minimum. Five-day means of daily maxima and minima were plotted to show the temperature pattern at the 2350 m level of Bachelor Butte during summer (Figure 3).

Between 23 June and 18 September, 1978, freezes occurred three nights in June, two in August, and six in September. In 1979, during the same period, ten freezes occurred: once at the end of June, five times in July, and four times in September. Both summers, a period of extended high pressure with high daily means lasted from mid-July until mid-August, maxima being 26 C in 1978 and 23 C in 1979. Summer minima were -5.5 C in June 1978 and -7.2 C in early July, 1979.

Mean monthly temperatures at Santiam Pass for 1964-78 show the typical annual temperature pattern in the High Cascades (Figure 4). Annual monthly temperatures vary little from the 15-year mean, with one standard deviation ranging from 1.2-2.1 C°.

For comparable periods at Bachelor Butte and Santiam Pass during the summers of 1978-79, monthly means ranged from 2.5-7.9 C° lower at Bachelor Butte. Daily maxima at Bachelor Butte remain much lower than at Santiam Pass in summer, due mostly to the decrease in temperature.
Figure 3. Five-day means of summer temperature for the lower Timberline Zone of Bachelor Butte, measured during the study. Solid lines are the average maximum temperature, dotted lines are the average minimum temperature, and the ends of the vertical lines indicate the extreme maximum and minimum for the five-day period.
Figure 4. Mean monthly precipitation (bars) and temperature (line) at the Santiam Pass station of the National Weather Service (1964-78).
with increasing elevation. However, on summer nights, Bachelor Butte typically has warmer temperatures than Santiam Pass, especially from mid-July to mid-August, when day as well as night temperatures are warmest. This reversed nighttime temperature difference is due to the local topography of the two recording stations. Cool night air tends to flow down to the base of Bachelor Butte, leaving the upper slopes with much warmer temperatures. Santiam Pass, on the other hand, is located in a low area which collects the cool air draining from the surrounding terrain. As a result, vegetation on the upper slopes of Bachelor Butte is exposed to less daily temperature variation in the summer than is the vegetation at Santiam Pass, which is at a much lower elevation. In spite of the depressed summertime minima at Santiam Pass, most daily means remain higher than those at Bachelor Butte.

PRECIPITATION

Information regarding summer precipitation was obtained from the Santiam Pass station. No data were available for Bachelor Butte itself. Measurements were available from a snow course maintained by the Soil Conservation Service of the United States Department of Agriculture at Dutchman Flat (elevation 1940 m), a clearing at the base of the butte's northern flank. Measurements were made since the 1930's at the first of each month from January until June.

The annual precipitation pattern at Santiam Pass resembles patterns throughout the High Cascades. Most precipitation falls between October and April, with maximum amounts in December and January (Figure 4). Although rain is not infrequent at Santiam Pass during the winter, it only rarely falls at Bachelor Butte due to the latter's higher elevation.

The Dutchman Flat snow course data show a great variability in annual snow accumulation (Figure 5). Maximum snow depth typically occurs around the first of April, and can range from as much as 4.8 m (1974) to as little as 1.4 m (1977). Mean monthly depths are nearly identical to those obtained from snow course measurements as far back as 1931. Snow depth usually decreases beginning sometime in April,
Figure 5. Mean monthly snow depth (and extreme maxima and minima) at Dutchman Flat, elevation 1940 m (1966-79).
but snow may remain on the ground at the base of Bachelor Butte as late as mid-July.

At higher elevations on Bachelor Butte, snow is very unevenly distributed because of the strong wintertime winds. Ridges above treeline are generally free of snow even in the middle of winter, whereas the depressions between the ridges acquire deep drifts. More snow accumulates on the peak's east and northeast sides where the only extensive permanent snowfields exist. This is due to the prevailing southwest-erly winter winds (see next section) and to relatively low insolation.

Closed forest below treeline has a fairly even snow cover, indicated by the lower limit of epiphytic lichens (Alectoria sarmentosa and Sphaerophorus globosa) on the tree trunks (Denison, personal communication, 1980). These lichens will not survive below the snow line.

Above the closed forest, considerable wintertime precipitation occurs as rime, which can attain a thickness of nearly one meter on the windward sides of larger trees, causing considerable mechanical damage.

Records show low summertime precipitation at Santiam Pass, which is likewise true for Bachelor Butte. In 1978-79, the June precipitation on Bachelor Butte generally resulted from thunderstorms which developed south of the peak between mid-morning and late afternoon, and eventually covered the mountain. They were often accompanied by pea-sized hail which attained depths of 10-20 cm in less than an hour. Between mid-July and mid-August a drought persisted, broken only in late August by moderate storms typically arriving from the southwest. The only other precipitation during the early and late parts of summer was from fog-drip.

WIND

Information concerning the wind régime at Bachelor Butte was acquired from several different sources. A simple wind-run anemometer was erected at 2350 m on the north flank of the mountain during the summer of 1978. The sensor was 3 m above the canopy of a grove of
Pinus albicaulis. Data were recorded daily for the entire summer except when the anemometer malfunctioned.

Another anemometer was erected by the United States Forest Service just east of Pine Marten Knob in autumn 1978. It measured wind velocity and direction periodically from October 1978 until February 1979.

The Lower Atmospheric Handbook for the Columbia Basin States (Pacific Northwest River Basins Commission, 1975) provides much information about wind. Eugene, Oregon, was chosen as the station whose high-altitude winds would best represent the winds at Bachelor Butte. Eugene is 105 km west of Bachelor Butte at an elevation of 129 m in the Willamette Valley. Readings were made at 2000 m altitude at 10 a.m. local time.

Employees of the United States Forest Service and of Mount Bachelor Ski Corporation also provided valuable information about the winds on Bachelor Butte. For insight regarding the region’s seasonal atmospheric circulation, the Atlas of the Pacific Northwest (Highsmith and Kimerling, 1979) was consulted.

The anemometer on the north flank of the mountain indicated that summer winds were light and variable. During the warmest part of the summer, observations showed that winds were typically from the east and northeast during the day. At night, the air was often calm except for a strong downslope breeze which developed shortly after sunset and continued for about one hour.

In late summer and early fall, winds at Bachelor Butte acquire a strong westerly to southwesterly component that persists until the next summer. Enormous snowdrifts to the east of ridges and massive accumulation of rime on the westward sides of trees are clear indicators of the direction of these prevailing winter winds.

Information acquired during winter from the United States Forest Service anemometer was scanty. October and November 1978 were atypically warm and dry; winds then were primarily from the northeast with a mean velocity of 22 km per hour. In January and February 1979, when winter storms finally began to arrive, winds were primarily from the west, with mean velocity of 11 km per hour.

Annual wind patterns at 2000 m above Eugene correspond very well
with observations made at Bachelor Butte. The Eugene data may, in fact, underestimate the total wind run at Bachelor Butte, since the topography of the High Cascades may cause an increase in the velocity of winds passing over the high peaks. Wintertime winds should not be significantly diminished when passing over the low Western Cascades southwest and west of Bachelor Butte.

The Eugene data indicate that from early fall the southwesterly component of winds does indeed become increasingly dominant until winds from the west and southwest constitute nearly 70% of the total wind run in December (Table I). December and January produce more than twice the total wind run of July and August.

Seasonal differences in wind are especially remarkable when winds of the "growing season" are compared to those of the "non-growing season." The former is generously considered here to last from June through September. Nonetheless, these four months account for scarcely 24% of the total annual wind run as measured above Eugene (Figure 6).

When the direction from which the wind blows is examined, an even greater difference between the two seasons is found. Winds with a north to northeast component account for 41% of the total wind run during the growing season, whereas winds from the south-southwest to west-southwest contribute approximately 20% of that total (Figure 6). During the non-growing season, winds from the north to northeast account for only 16% of total wind run, and those from the southwest for 50%. On an annual basis, the winds from the southwest and northeast octants account for more than 60% of all wind.
TABLE I. ANNUAL WIND REGIME AT 2000 M ABOVE EUGENE, OREGON (DATA COMPiled FROM THE LOWER ATMOSPHERIC HANDBOOK OF THE COLUMBIA BASIN STATES).

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</tr>
</tbody>
</table>

Percent of Annual Wind Run

<table>
<thead>
<tr>
<th></th>
<th>12</th>
<th>11</th>
<th>9</th>
<th>8</th>
<th>6</th>
<th>6</th>
<th>5</th>
<th>7</th>
<th>8</th>
<th>10</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>100%</td>
</tr>
</tbody>
</table>
Figure 6. Wind stars for 2000 m above Eugene, Oregon. The length of the line for each direction is proportional to the total wind run from that direction for the entire season. 1 cm = 5000 km wind run.
Bachelor Butte, like other peaks of the High Cascades, does not have a clearly defined timberline. Instead, the closed forest cloaking its lower slopes gives way only gradually to the treeless alpine expanses toward the summit (Figure 7). Numerous ridges radiating from the summit permit trees to ascend higher than would otherwise be possible since strong winter winds reduce snow accumulation there. The trees growing on the ridges benefit from precocious snowmelt, as it allows them an adequate growing season, even though snow may remain in adjacent depressions throughout the summer.

Franklin and Dyrness (1973) define two high-elevation zones in the High Cascades. The lower one they call the *Tsuga mertensiana* Zone, consisting of a closed forest subzone and an upper parkland subzone. The closed forest around the base of Bachelor Butte fits the description of their lower subzone. Higher on the butte (2200-2300 m), the forest opens somewhat, creating a variation of their upper parkland subzone. Because of Bachelor Butte's steep flanks, this subzone never develops as it does on more even terrain. Instead of islands of trees separated by fairly extensive alpine meadows, the groves of trees here occupy more or less parallel ridges above the closed forest.

Above the *Tsuga mertensiana* Zone, Franklin and Dyrness recognize only the Alpine Zone. On Bachelor Butte, however, there exists yet another band of vegetation between the upper part of the *Tsuga mertensi-
ana* Zone and the lower part of the Alpine Zone (Figure 8). In this band, whitebark pine (*Pinus albicaulis*) is the predominant tree, and mountain hemlock (*Tsuga mertensiana*) is only a minor component of the stands. The groves of pines grow from 2350-2530 m atop ridges which ascend toward the summit (Figure 9). This pine-dominated zone can be further divided into two subzones which are distinguishable by the size of the trees in the groves and by the vegetation, or lack of it, in the depressions separating adjacent ridges.
Figure 7. Aerial photograph of Bachelor Butte (north is at top). Dots represent sampled white-bark pine groves described in Chapter III. Tot Mountain is a bottom center and Pine Marten Knob is just to the right of top center.
Figure 8. Diagrammatic representation of vegetation zones on the north flank of Bachelor Butte.
Figure 9. Whitebark pine groves atop ridges on the south flank of Bachelor Butte. Photograph taken from Tot Mountain, looking northwest.
Above the zone dominated by whitebark pine is the true Alpine Zone. As elsewhere in the High Cascades, the Alpine Zone is poorly developed, the unstable, coarse, porous volcanic debris on steep slopes being unsuitable for the formation of extensive alpine communities typical of many mountains.

The flora of youthful Bachelor Butte is depauperate compared to that of the older Three Sisters peaks just 10 km to the northwest. Van Vechten (1960) cites nearly twice as many herbaceous species in the Alpine Zone of those peaks as for similar elevations on Bachelor Butte. Much more weathering and erosion have occurred on the Three Sisters, resulting in more extensive soil development which has permitted the establishment of more complex plant communities.

METHODS

During the summers of 1978-79, observations regarding the vegetation were recorded. Locations were pinpointed on an aerial photograph and a Brunton compass and a Lufft altimeter were used to verify locations.

In early June, 1979, an aerial reconnaissance flight was made around the peak soon after snowmelt had begun. Photographs obtained during the flight were later examined to provide insight into snowdrifting and snowmelt patterns, and facilitate study of some of the less accessible parts of Bachelor Butte.

Twenty-five groves of whitebark pines were selected for study. The sample plots ranged in size from 100 to 300 m² and were evenly distributed around the mountain (Figure 7). Sample groves included both the lower and upper parts of the Timberline Zone. To determine stand density and size distribution, whitebark pine trunks greater than 5 cm diameter were counted. As Pinus albicaulis tends to grow in clumps, the number of stems in each clump was counted. Diameters were measured with a diameter tape at one meter height. Heights were either estimated, or a meter tape was dropped to the ground from the top of trees in the grove.
To facilitate comparison of tree densities of different groves, the number of stems (greater than 5 cm diameter) per 100 m² was calculated. The 25 groves were then grouped according to density as well as to height and diameter of trees within the grove.

Whitebark pine reproduction was also noted. Young trees with a trunk diameter of less than 5 cm at 1 m height were counted and their density per 100 m² was calculated. Also, groups of pine seedlings (and, less frequently, single pine seedlings) less than 25 cm tall were counted.

Cores were obtained from about 50 trees within the sample groves, to provide an idea of the age range of the whitebark pine trees on Bachelor Butte. Cores were made with an increment borer, entering the trees from the east side of the trunk at circa 1 m height. Since most trees were at least slightly inclined to the east, the annual rings were wider on that side and counting them was easier.

Each core was placed in a plastic straw and frozen upon return to the laboratory. Cores were examined before they began drying out. The core was cut transversely along its entire length with a single-edge razor blade. The exposed surface was tilted toward the light source so it was being viewed at a 45° angle, and examined under a dissecting microscope. Only then were the very thin rings visible.

Study of the herbaceous flora of Bachelor Butte was mostly carried out in the field, with the aid of Flora of the Pacific Northwest (Hitchcock and Cronquist, 1973). Some specimens were collected and compared with herbarium sheets. Field notes and dried specimens were supplemented by colour photographs of the plants in flower. A list of species was prepared (Appendix A). I also identified birds and mammals observed near and above timberline (Appendices B and C).

RESULTS AND DISCUSSION

CLOSED FOREST ZONE

The Closed Forest Zone extends from the base of Bachelor Butte's north side (1950 m) to an elevation of about 2250 m. On the south side
of the butte, closed forest scarcely reaches the base, which is higher (2250 m) than on the north side (Figure 2). In its natural state, the zone is unbroken except for occasional small meadows and a narrow avalanche track extending from below the terminal moraine on the north-east flank all the way to the base of the mountain. However, on the peak's north flank, many breaks now occur in the forest where Mount Bachelor Ski Corporation has cleared extensive areas of the forest to create open ski runs.

Mountain hemlock predominates in the Closed Forest Zone. The trees are relatively uniform in age (300-400 years), based on ring counts of hemlock stumps along the ski runs. On the lower north flank, the trees attain a height of more than 25 m. However, at the top of the zone, they rarely exceed 15 m. Some whitebark pine, subalpine fir (Abies lasiocarpa), and lodgepole pine (Pinus contorta) also occur in this zone, though none accounts for more than 5% of the total cover. Lodgepole pine occurs mostly toward the base of the butte, although occasional trees may grow in open areas at higher elevations. Both lodgepole pine and whitebark pine attain heights of 15 m and trunk diameters of about 50 cm within this zone.

Few herbs grow in the dense shade produced by the hemlocks. Nonetheless, in slightly more open areas, sedges (Carex spp.) and rushes (Juncus spp.) are common, as well as Lupinus spp., Polygonum newberryi, and Luzula hitchcockii.

TIMBERLINE ZONE

Between 2300 m and 2530 m, vegetation occurs primarily on ridges radiating from the summit, which alternate with depressions of varying character and size. This Timberline Zone can be subdivided into two parts. The lower part consists of groves of older trees growing on gently domed ridges which are separated by shallow depressions in which herbaceous plant communities have developed. The upper part consists of younger groves on narrow ridges which are separated by extensive, deeper depressions with blocky lava where snow may remain year-round.

In the old groves of the lower part of this zone, whitebark pine
predominates, but mountain hemlock is still a significant component. In some groves here, subalpine fir forms a dense carpet about 1 m thick beneath the larger pines and hemlocks, with occasional small trees developing on the east edge of the groves. Lodgepole pine is rare and is usually restricted to open areas between groves.

The largest whitebark pines here are nearly 15 m tall and almost one meter in diameter. Many trees are over 300 years old and some of the largest trees are certainly more than 700 years old, though their exact ages are difficult to ascertain since their trunks are typically hollow. In one tree, the trunk measured 8 dm in diameter and the outer 5 cm of trunk alone had nearly 100 annual rings.

The frequency of pines in each of the four height classes is similar in all the old groves (Types I and II, Figure 10). Diameter distribution, however, is somewhat different and can be used to distinguish two types among the older groves. In Type I, 19% of the trees have diameter 5-15 cm and 38% are 30-45 cm, and the mean number of trees per 100 m$^2$ is 13.6. The second type of old grove (Type II) contains an average of 54% of trees 5-15 cm and only 12% of them 30-45 cm. Tree density in Type II is 20.5 trees per 100 m$^2$. These figures probably reflect the age distribution of the trees in each grove, since trunk diameters seem to be proportional to age. Type II groves, where nearly three times as many trees have diameter 5-15 cm, can be considered younger than those in Type I. The two types of old groves do not show any particular pattern of distribution on the mountain.

Few herbs actually grow within these old groves, although many grow on the edges and in the depressions between groves. However, Luzula hitchcockii and Vaccinium scoparium create extensive carpets in about one fourth of the groves and Penstemon davidsonii, sedges, and grasses are also common, though not abundant, within the groves. Intergrove depressions support poorly developed plant communities consisting mostly of sedges, Antennaria alpina, Lütkea pectinata, Aster alpigenus, and Eriogonum marifolium. Outwash areas at the lower end of many of these depressions have a very fine substrate eroded during the peak snowmelt. Here, communities are composed almost entirely of sedges in
Figure 10. Distribution of tree heights (shaded bars) and trunk diameters (open bars) for whitebark pines in the four grove types of the Timberline Zone on Bachelor Butte. Types I and II are dominated by older, larger trees than types III and IV. See text.
the open areas, and *Saxifraga tolmiei* adjacent to larger rocks.

In the upper part of the Timberline Zone, subalpine fir and mountain hemlock grow only occasionally on the east sides of ridges. Lodgepole pine is absent. The younger groves here are composed of much smaller trees than those in the old groves below, with a maximum height of about 6 m and greatest trunk diameter of 30 cm. Most trees grow upright, at least during the summer, and true krummholz whitebark pines develop only atop the lateral moraine east of the glacial cirque.

Above the highest groves of living trees, no islands of all dead trees exist to indicate a retreating timberline. Most of the upright trees in the highest groves are about 100 years old, and well-decayed trunks can be found in some of these high groves. Perhaps these groves are the result of a timberline advance after the Little Ice Age about 350 years ago.

As in the older groves, the frequency of pines in each height class within the young groves is fairly consistent (Figure 10). It is possible to distinguish two types of groves within this part of the Timberline Zone, again based solely on differences in trunk diameter. In Type III, 76% of the trees have diameter 5-15 cm and 23% are 15-30 cm. In Type IV, however, nearly 100% of the trees have a trunk diameter of less than 15 cm and only 2% have trunks of diameter greater than 15 cm. Tree densities are also different, with Type III having 43.1 stems per 100 m$^2$ and Type IV with 50.5. Type III groves appear to be older than Type IV groves, having a higher frequency of larger diameter trees. The two types of young groves also show no pattern as to where they occur within their elevation zone.

Flowering plants associated with pines in the upper Timberline Zone include *Anemone drummondii*, *Penstemon davidsonii*, *Vaccinium scoparium*, and *Castilleja applegatei*. Hummingbirds (Appendix B) and whitelined sphinx moths (*Hyles lineata*) were frequently observed visiting both *Penstemon* and *Castilleja* flowers. In the lava-filled depressions separating these groves, plants such as *Oxyria digyna*, *Saxifraga tolmiei*, and *Cryptogramma crispa* grow. At the lower end of many of these depressions, outwash areas up to several hundred meters square support
simple sedge meadows, on the outer edges of which grow *Eriogonum marifolium* and *Calyptridium umbellatum*.

Fewer saplings (trunk diameter less than 5 cm) occur in the lower Timberline Zone than in the upper part (Table II). On the other hand, the lower groves contain more seedlings (height less than 25 cm) than do the higher groves. This distribution may reflect both differences in reproductive potential and age of the two parts of the Timberline Zone. The upper part is younger and produces fewer cones, whereas the lower part contains older trees which produce far more cones, resulting in more groups of seedlings. The seedlings, however, do not presently appear to mature as successfully in the older groves.

In summary, the lower, older groves of the Timberline Zone contain fewer and larger trees, and the higher, younger groves more numerous smaller trees. Height class changes little within the grove types described above, but height decreases at high elevations.

The most extensive vegetated area in the upper Timberline Zone occurs to the east of the cirque on the northeast flank. Sand, ash, and plant debris accumulate here on the leeward side of the lateral moraine and provide a fine substrate for plants. More than 1000 m² are covered with *Phyllodoce empetriforis*, *Lütkea pectinata*, *Eriogonum pyrolifolium*, and *Penstemon davidsonii* are more abundant here than anywhere else on the mountain at this elevation.

**ALPINE ZONE**

The scree slopes and lava-block fields which cover the top third of Bachelor Butte comprise the Alpine Zone. They extend down like fingers into the depressions between the upper groves of the Timberline Zone. The substrate here is very unstable and is constantly shifting position due to alternate freezing and thawing, high winds, and erosion caused by snowpack movement and snowmelt.

The only woody plants that survive in the Alpine Zone are severely deformed whitebark pines, few reaching over 5 dm in height. They are widely scattered throughout the Alpine Zone, but occur most frequently on the south and west flanks. On the east flank, snow accumulations are
TABLE II. DENSITY (NUMBER PER 100 M$^2$) OF WHITEBARK PINE SAPLINGS AND SEEDLINGS IN THE FOUR TYPES OF TIMBERLINE ZONE GROVES (N=NUMBER OF GROVES SAMPLED).

<table>
<thead>
<tr>
<th>Grove Type</th>
<th>n</th>
<th>Saplings$^1$</th>
<th>n</th>
<th>Seedlings$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>5</td>
<td>3.2 ± 1.7</td>
<td>4</td>
<td>4.2 ± 3.1</td>
</tr>
<tr>
<td>II</td>
<td>5</td>
<td>5.3 ± 2.6</td>
<td>3</td>
<td>4.4 ± 2.8</td>
</tr>
<tr>
<td>III</td>
<td>9</td>
<td>6.3 ± 3.0</td>
<td>7</td>
<td>1.9 ± 0.7</td>
</tr>
<tr>
<td>IV</td>
<td>6</td>
<td>12.0 ± 5.3</td>
<td>3</td>
<td>1.7 ± 0.7</td>
</tr>
</tbody>
</table>

1 trees less than 5 cm diameter at one meter height
2 single tree or group of trees less than 25 cm tall
much greater than elsewhere on the mountain, and this seems to preclude the establishment of pines there. The glacial cirque on the northeast side of Bachelor Butte, with its very steep and crumbly upper walls, has virtually no vegetation.

In the relatively stable lava-block fields of the Alpine Zone, crevices where adequate soil has accumulated are occasionally occupied by Oxyria digyna, Cryptogramma crispa, Saxifraga tolmiei and Cardamine bellidifolia. On the more open and considerably more unstable scree slopes grow Eriogonum pyrolifolium, Draba aureola, Polemonium pulcherrima, and Hulsea nana, with some sedges in the more stable areas. Both Eriogonum pyrolifolium and Hulsea nana seem remarkably adapted to their constantly eroding substrate, having very long, thick taproots which are sometimes exposed for 25 cm or more. The plant remains alive and produces leaves and flowers at the crown. No plant on the scree slopes is taller than 10-12 cm.

At the gently domed summit of Bachelor Butte, a plant community composed primarily of Erigeron compositus, Arabis platysperma, and Calyptridium umbellatum exists on the south-facing side. Elsewhere on the summit are simple sedge communities, mostly adjacent to snowmelt pools.
IV. MORPHOLOGY

INTRODUCTION

It is difficult to ascribe a particular growth form to Pinus albicaulis, as it varies greatly in different locales. The pine's general appearance is influenced most by the elevation at which it grows, its age, and its exposure to wind and snow.

Although whitebark pine is monoecious, it bears its seed cones on branchlets which are easily distinguished from other branchlets of the same tree. This distinction will henceforth be recognized by calling those branchlets which bear seed cones "seed branchlets" and those that never bear seed cones "pollen branchlets."

METHODS

Eleven whitebark pine trees were selected from four different elevation zones on Bachelor Butte's north flank, and six branchlets in the crown of each were examined to compare their morphology. Three were pollen branchlets (i.e. did not produce seed cones) and three were seed branchlets.

The lowest elevation at which sample trees were located was 1980 m at the base of the butte (Table III). In the lower Timberline Zone, sample trees were all within 150 m of Pine Marten Knob. Some of the trees were isolated, and others were one of a group of several trunks growing together. Two trees were chosen from the upper Timberline Zone just below Pika Knob. The fourth group of trees was located on the highest vegetated ridge on the mountain, on the lateral moraine just east of the cirque. Here, all the trees were very deformed, and none attained a height greater than three meters. Height, trunk diameter, and age of all the sample trees are presented in Table III.

At the end of summer 1979, all study branchlets were removed, and the needles of each separated according to the year during which they were produced. Branchlet diameter at the base of the oldest whorl of
TABLE III. CHARACTERISTICS OF THE ELEVEN WHITEBARK PINE TREES SAMPLED FOR MORPHOLOGICAL CHARACTERISTICS.

<table>
<thead>
<tr>
<th>Elevation Zone</th>
<th>Number of Trees</th>
<th>Height (m)</th>
<th>Trunk Diameter at Breast Height (cm)</th>
<th>Age (yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base of Butte (1980 m)</td>
<td>2</td>
<td>10-12</td>
<td>24-44</td>
<td>64-126</td>
</tr>
<tr>
<td>Lower Timberline Zone (2300-2355 m)</td>
<td>4</td>
<td>6.5-10.8</td>
<td>34-80</td>
<td>200-700+</td>
</tr>
<tr>
<td>Upper Timberline Zone (2410 m)</td>
<td>2</td>
<td>3.2-4.1</td>
<td>12-13</td>
<td>79-90</td>
</tr>
<tr>
<td>Highest Vegetated Ridge (2500 m)</td>
<td>3</td>
<td>2-3</td>
<td>22-28(^1)</td>
<td>150-320</td>
</tr>
</tbody>
</table>

\(^1\) at "thigh height" (0.5-1.0 m); no trunk at breast height
needles was also measured for 10 pollen branchlets and 10 seed branchlets per sample tree. Needle length is considered to be the distance from the tip of the needles to the top of the bud scales from which they emerged. Twig length for a given year is the distance between successive series of bud-scale scars. Twig diameters, needle length, and annual twig elongation were measured with a caliper. Some needles were preserved in FAA solution and later sectioned transversely for anatomical study.

Seed cones which matured during 1979 were harvested in mid-August and seeds were removed, air-dried, and weighed in lots of 100.

RESULTS AND DISCUSSION

GENERAL TREE MORPHOLOGY

A whitebark pine can be a severely deformed mass of crooked stems less than a meter high, or a nearly symmetrical tree with a broad, diffuse crown atop a straight bole. The tallest and most symmetrical trees occur in the more protected areas near the base of the butte. The tree attains a maximum height of about 15 m on Bachelor Butte, though it is known to grow to 33 m in Alberta (Day, 1967). Larger diameter, though shorter, trees occur in the lower Timberline Zone. There, trunk diameters may attain nearly one meter, whereas at lower elevations, diameters rarely exceed 50 cm.

In the Timberline Zone on Bachelor Butte, the pines typically grow in clumps of from 2-10 trees, whereas at lower elevations single trees are more frequent. Whitebark pine does not naturally fork near its base, but rather retains a single leader for up to 100 years after germination. Excavation of several clumps of trees 1-3 m tall showed that, indeed, all the trunks were separate. The clumping appears, instead, to be the result of pine seed caching by animals.

The bark of whitebark pine is very light in colour (hence, the tree's name) and very thin, rarely more than 1 cm thick, even at the base of older tree trunks. Elsewhere on the tree, the bark is usually
3-5 mm thick. It is quite smooth, except toward the base of some older trees, where it is broken by narrow fissures into small plates which, upon falling, reveal the reddish inner bark (Sargent, 1897).

The wood of *Pinus albicaulis* is light in colour, soft, and very close-grained. It is presently of little economic importance, primarily because of its inaccessibility and slow rate of growth.

**BRANCHLET MORPHOLOGY**

Young whitebark pine trees have regular whorls of branches at right angles to the main stem, which give them a narrow conical form. Until trees attain an age of about 100 years, or a breast-height trunk diameter of about 15 cm, they remain very resilient and bend under the first heavy snows of winter. Most remain under the snow until late the following spring.

Older trees at all but the highest elevations acquire a relatively broad crown with many long, ascending, stout branches which remain almost vertical at lower elevations. In the Timberline Zone, these branches become swept to one side of the trunk, while still remaining more or less parallel to one another. The lower branchlets in the crown are much shorter and more slender than those higher in mature trees.

The branchlets are very tough and flexible, and can be bent 180° from their normal direction of growth without breaking. Such capabilities permit them to withstand strong winds and the great accumulations of rime, ice, and snow during the winter.

During favourable years, the stout upper branchlets produce seed cones at their tips, and the slender, lower branchlets develop pollen cones. Branchlet type is most easily determined by examining its diameter just below the oldest whorl of needles. Of 86 seed branchlets measured, diameters ranged from 1.09-1.93 cm (mean=1.38, s.d.=0.17) with no great difference in diameter due to elevation. One hundred and ten pollen branchlets from the same set of sample trees had diameters from 0.44-0.69 cm (mean=0.55, s.d.=0.06). Here, there was some relation between elevation and branchlet diameter. The higher
the elevation, the thicker the branchlet \((r^2 = 0.31)\).

The same results were indirectly obtained by Pravdin (1950) in his study of the sexual dimorphism of *Pinus sylvestris*. He found that shoots bearing ovulate cones (i.e. seed branchlets) had a greater growth potential and hence greater dimensions than did staminate (pollen) shoots. Shimanyuk et al. (1963), in their studies of *Pinus sibirica* in the Soviet Union, established that the diameter of branchlets can serve as a valuable index of cone production and that the number of cones produced is proportional to the diameter of the branchlet.

Annual branchlet elongation is also dependent upon branchlet type. It varies considerably from one year to the next, yet mean annual growth for 1973-79 for the 11 sample trees was 1.05 cm for pollen branchlets and 3.06 cm for seed branchlets.

Branchlet elongation is also related to elevation. Pollen branchlet growth decreases with increasing elevation. Seed branchlets, too, are longer at the butte's base than at higher elevations (Table IV).

Winter branchlet buds are ovate, with acuminate tips, and are covered by light brown scales. Buds of seed branchlets tend to decrease in length with increasing elevation (Table IV). On seed branchlets, the mean length of 24 winter buds measured in early September was 1.32 cm (s.d. = 0.24). Winter buds at the tips of pollen branchlets had a mean length of 0.90 cm (s.d. = 0.22), their length being less related to elevation.

**NEEDLE MORPHOLOGY**

*Pinus albicaulis* is most easily distinguished from its closest allies (*P. cembra* and *P. koraiensis*) by its entire (i.e. untoothed) needles and by the presence of both ventral and dorsal stomata on the needles (Shaw, 1914). The stomata are generally in 3-4 rows on the two ventral sides of the needle, and in one or two rows on the dorsal side.

The needles of whitebark pine usually occur in fascicles of five, the latter densely clustered at the ends of the branchlets. They are
TABLE IV. NEEDLE LENGTH, BRANCHLET ELONGATION, BUD LENGTH, AND REPRODUCTIVE POTENTIAL OF SAMPLE TREE POLLEN BRANCHLETS AND SEED BRANCHLETS FOR FOUR DIFFERENT ELEVATION ZONES ON BACHELOR BUTTE.  

<table>
<thead>
<tr>
<th>Elevation Zone</th>
<th>Number of Trees</th>
<th>Mean Needle Length (^2) Pollen (cm)</th>
<th>Mean Needle Length (^2) Seed (cm)</th>
<th>Mean Branchlet Length (^3) Pollen (cm)</th>
<th>Mean Branchlet Length (^3) Seed (cm)</th>
<th>Mean New Bud Length (^4) Pollen (cm)</th>
<th>Mean New Bud Length (^4) Seed (cm)</th>
<th>Percent of Years With Cone Scars</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base of butte (1980 m)</td>
<td>2</td>
<td>4.9 (0.58)</td>
<td>5.9 (0.83)</td>
<td>1.5 (0.16)</td>
<td>6.1 (1.56)</td>
<td>0.88 (0.25)</td>
<td>1.74 (0.08)</td>
<td>100%</td>
</tr>
<tr>
<td>Lower Timberline Zone (2300-2355 m)</td>
<td>4</td>
<td>3.8 (0.55)</td>
<td>4.0 (0.90)</td>
<td>1.2 (0.34)</td>
<td>3.1 (1.01)</td>
<td>1.01 (0.22)</td>
<td>1.34 (0.20)</td>
<td>65</td>
</tr>
<tr>
<td>Upper Timberline Zone (2410 m)</td>
<td>2</td>
<td>3.7 (0.51)</td>
<td>4.4 (0.88)</td>
<td>1.0 (0.34)</td>
<td>3.0 (0.73)</td>
<td>0.88 (0.07)</td>
<td>1.31 (0.06)</td>
<td>55</td>
</tr>
<tr>
<td>Highest Vegetated Ridge (2500 m)</td>
<td>3</td>
<td>3.2 (0.68)</td>
<td>4.4 (0.79)</td>
<td>0.9 (0.36)</td>
<td>3.2 (1.02)</td>
<td>0.71 (0.10)</td>
<td>1.14 (0.23)</td>
<td>27</td>
</tr>
</tbody>
</table>

1 parenthesized numbers indicate standard deviations in cm
2,3 1973-79
4 1979
5 1973-78
dark green, with deciduous light brown sheaths at their bases. On Bachelor Butte, the needles range in length from 2-8 cm, and the basal sheaths are typically about 1 cm long.

Each needle possesses three resin canals, two dorsal and one ventral. A single vascular bundle occurs in the center of each needle, surrounded by transfusion tissue and a well-developed endodermis.

Needle length on both types of branchlets varies considerably from year to year on Bachelor Butte. However, needles on pollen branchlets are, for any given year, much shorter than are those on seed branchlets (Figure 11). Mean needle length on pollen branchlets for 1973-79 is 3.72 cm and on seed branchlets is 4.79 cm.

Regardless of branchlet type, needle length decreases with increasing elevation (Figure 11 and Table IV). Needle length can also vary considerably within a single tree, with the longest needles generally being farthest from the crown's perimeter.

The number of needles produced each year on a branchlet varies somewhat. Seed branchlets, perhaps due to their greater length, always have more needles than do pollen branchlets. The maximum number of needle fascicles produced in any one year was 60 for seed branchlets and 28 for pollen branchlets.

The needles can remain on the branchlet for as long as 12 years, during which secondary growth can occur (Rickson, personal communication, 1979). Needle drop is very irregular, however, some falling off after only four or five years.

Needle longevity is surprisingly consistent for both types of branchlet. Needles were retained on pollen branchlets for an average of 6.9 years and for 7.0 years on seed branchlets. Within each of the four elevational zones, needle longevity was also nearly identical for both types of branchlet, except in the high ridge trees, where seed branchlets tended to keep their needles for one year longer than did pollen branchlets.

MORPHOLOGY OF REPRODUCTIVE ORGANS

Both staminate (pollen) and pistillate (seed) cone initials in
Figure 11. Mean needle length for needles produced in six different years at three elevations on Bachelor Butte, for branchlets which produced seed cones (seed branchlets) and for those which did not (pollen branchlets).
whitebark pine develop late in the summer, when the next year's buds are being formed. The following summer, during branchlet elongation, the staminate cones are produced along the proximal part of the new growth. The magenta staminate cones are about 5 mm long and release their pollen in mid-summer. The likewise magenta pistillate cones develop at the tip of the expanding shoot and are about 1 cm long. After fertilization, the young cones grow very little. By late autumn, they are scarcely more than 15 mm long and are erect, surrounding the next year's bud.

The following summer, as the new twig elongates, the cones become horizontal and increase rapidly in size (Figure 12). The number of cones produced on a single seed branchlet ranged from one to five on Bachelor Butte, although as many as eight occurred on pines in the central Sierra Nevada (Tomback, 1977). The cones are oval to sub-globose, sessile, and have very thick scales, on each of which two seeds may be borne. At the tip of each scale is a small, chestnut brown umbo which represents the part of the seed cone which was exposed at the time of fertilization the preceding year. The cones are deep purple and secrete viscous resins which, beginning in mid-July, ooze from the developing cones in fat, glistening droplets. Only in mid-to late-August do the cones finally begin to dry. Seeds are about 1 cm long and 7 mm thick and have a dark brown, hard and thick seed-coat with a very thin wing attached to it. The wing remains attached to the seed-bearing scale when the seed is forcibly removed from the cone.

In *Pinus sibirica*, there is a direct correlation between cone size and seed number (Shimanyuk, 1963). Likewise, the number of seeds per whitebark pine cone can easily be estimated by counting the number of full-size scales, then multiplying by two, presuming that complete fertilization occurred the previous summer. Verified seed numbers per cone ranged from 70 to over 100. The mean weight of six lots of 100 air-dried seeds was 12.1 g (s.d. = 0.44) per lot.

Estimates of cone production during past years can be made by counting the cone scars which remain on the seed branchlets (Pravdin,
Figure 12. Seed cones at the tips of whitebark pine branchlets in late July 1979 on Bachelor Butte (2350 m).
1950). These scars indicate only the potential for seed production the year the cones matured, as many cones which begin developing during the first summer will either abort, or be destroyed, and leave a scar. During 1971-79, trees in the Timberline Zone on Bachelor Butte had the potential for big seed crops in 1974, 1976, 1977, and 1979.

Cone production in a given year can vary considerably from one area to another. During summer 1978, trees at the summit of Black Butte (1963 m elevation) 37 km north of Bachelor Butte, produced many cones. The same summer, only two deformed cones were found in the entire Timberline Zone of Bachelor Butte.

The production of staminate cones also appears to be irregular and coincides with that of pistillate cones. Thus, during summer 1978 on Bachelor Butte, both staminate and pistillate cones were abundant, whereas in summer 1979, few new seed cones and no pollen cones were observed.

Cone scar records also indicate a decreasing potential for cone production with increasing elevation. Some of the trees on the highest ridge east of the cirque showed no cone scars since at least 1967, whereas trees near the butte's base had cone scars every year for the same period.

The youngest tree found producing cones during summer 1979 was in the lower Timberline Zone of the butte's south flank. The tree, 4 m tall with a trunk diameter of 12 cm, had 45 rings at a height of 1 m. In most groves, however, trees do not begin bearing cones until they are nearly 100 years old.
V. PHENOLOGY

INTRODUCTION

Various plant organs develop at different times of the growing season and at varying rates. Phenology is the study of the periodicity of this development. The timetable of growth and development varies from year to year, depending on environment. Most data presented below represent only one growing season, 1979. These data probably typify developmental patterns during other years, but the particular dates will vary from one year to the next.

The climate of Bachelor Butte, as discussed in Chapter II, is one of extremes. A long, moderately cold, snowy winter accompanied by strong and persistent winds is generally followed by a very short, warm, dry summer. These climatic factors, which play a principal role in determining the phenology of the mountain's vegetation, change with elevation. Trees growing atop the highest ridges have only a very short period in which to produce new growth and then prepare buds for the next year.

METHODS

The eleven trees in four elevation zones described in Chapter IV were used to study phenology. Branchlet and needle elongation were monitored at 7-14 day intervals from early June until mid-September on three pollen branchlets and on three seed branchlets of each tree. Branchlet measurements were made from the site of attachment of the winter bud scales to the apex of the newly developing bud. Needles were measured as soon as they broke through their protective sheath, and their length was considered to extend from the top of the bud scales to the needles' tips. Three fascicles per new branchlet were measured with a vernier caliper to the nearest tenth of a millimeter.

The lengths of needles and branchlets attained by the growing season's end (late August) were considered to be the "final" lengths
for those organs. The date at which 90% of that final length was achieved on the curve showing elongation was determined (see Figure 13 for example). That date was used to compare trees and branchlets with one another to determine if, indeed, varying patterns existed in the development of these organs during the course of the summer.

Winter survival of 49 first-year conelets formed during summer 1978 was followed on 22 seed branchlets of three mature whitebark pines in the vicinity of Pine Marten Knob. Each branchlet had from one to four cones. The branchlets were tagged 1 October 1978 and then examined again 5 June 1979 to determine how many cones had been lost during the winter.

The development of 44 second-year cones was followed on 16 seed branchlets of six trees in the Timberline Zone. Very few cones could be found on trees near the butte's base. Likewise, live cones were absent on the highest vegetated ridge at the beginning of summer 1979. Cone length (from base to apex) was measured at approximately weekly intervals from early June until early August with a caliper. None of the 44 cones was purposefully destroyed; however, many disappeared due to natural disturbances during the course of the summer. The mean cone length for each date was calculated for all the cones which eventually reached maturity.

Within the same groves, but in different trees, developing cones were randomly sampled five times from late June until mid-August. Each time, five to eight cones which appeared to be developing normally were removed, placed in airtight containers, and weighed and measured. They were oven-dried at 70 C for 72 hours and the percent dry matter for each cone was calculated.

As with needle and branchlet length, the dates at which 90% of maximum cone length was achieved were compared.

RESULTS AND DISCUSSION

BUD PHENOLOGY

Buds which gave rise to branchlets and needles in summer 1979
Figure 13. Sample needle and branchlet elongation for four trees (12 branchlets of each type) in the lower Timberline Zone.
were initiated during summer 1978. The primary factor determining the date of bud-opening the next spring is temperature (Kramer and Kozlowski, 1979), but it is probably also affected by photoperiod and endogenous rhythms within the plant (Tranquillini, 1979; Vaartaja, 1962). Bud-opening in 1979 occurred in late May in the Timberline Zone, and during the second week of June on the highest vegetated ridge. The snowpack was at that time still one to two meters deep around some of the sample trees. Soil temperatures at 15 cm below the surface were slightly above freezing (0.5 °C) near those trees where snow had melted away enough to expose the ground.

As the buds opened, branchlet and needle elongation began almost simultaneously. The needles remained, however, within a translucent white sheath (the inner bud scales) for several weeks after the bud opened. Soon after expansion of each new shoot began, the following year's developing bud was visible among the young needles at the tip of the branchlet. Development of the next year's bud occurred throughout much of the summer. In 1979, bud length stopped increasing in mid- to late-August, at which time it was assumed that bud formation was complete.

**NEEDLE PHENOLOGY**

The date at which needles broke through their protective sheaths varied at different elevations. On the trees at the butte's base, it occurred during the first several days of July. In the Timberline Zone, needles broke out of their sheaths between 8 and 15 July, and on the highest vegetated ridge, the new needles were not visible until the last week of July. Tranquillini and Unterholzer (1968) found, too, that needles of larch (Larix sp.) began growing later at higher elevations. At the time that Bachelor Butte whitebark pine needles broke through the sheath, they were 0.6-1.0 cm long on pollen branchlets and 0.8-1.4 cm long on seed branchlets.

Needle maturity, like bud-opening and sheath-splitting, appears to occur later with increasing elevation (Table V). The greatest difference exists between those trees near the base of the butte, and
TABLE V. DATES WHEN NEEDLES AND BRANCHLETS OF PINUS ALBICAULIS AT FOUR DIFFERENT ELEVATIONS ON BACHELOR BUTTE ATTAINED 90% OF THEIR FINAL LENGTH IN 1979.

<table>
<thead>
<tr>
<th>Location</th>
<th>Total Number Of Branchlets Monitored</th>
<th>Needle (Mean of Dates for Pollen and Seed Branchlets)</th>
<th>Branchlet Type Seed</th>
<th>Pollen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base of Butte (1980 m)</td>
<td>4</td>
<td>29 July</td>
<td>(23 August)</td>
<td>(30 July)</td>
</tr>
<tr>
<td>Lower Timberline Zone (2300-2350 m)</td>
<td>24</td>
<td>9 August</td>
<td>12 August</td>
<td>9 August</td>
</tr>
<tr>
<td>Upper Timberline Zone (2410 m)</td>
<td>8</td>
<td>11 August</td>
<td>11 August</td>
<td>5 August</td>
</tr>
<tr>
<td>Highest Vegetated Ridge (2500 m)</td>
<td>12</td>
<td>13 August</td>
<td>1 September</td>
<td>16 August</td>
</tr>
</tbody>
</table>

1 Parenthesized dates represent only two data points
the ones in the Timberline Zone and higher. Trees in upper and lower parts of the Timberline Zone vary little, and in fact differ by only a few days from those trees on the highest vegetated ridge. There was little difference, only two to four days, between maturation of needles of pollen branchlets and those on seed branchlets at similar elevations.

In his study of subalpine fir (Abies lasiocarpa) in Washington, Fonda (1976) found that timberline firs and those at an elevation 300 m lower all started growth more or less simultaneously, but the lower trees continued growing for about four weeks longer. On Bachelor Butte, however, whitebark pines both begin and end growth later at the highest elevation.

BRANCHLET PHENOLOGY

Branchlet elongation and needle elongation commence almost simultaneously in Pinus albicaulis. Seed branchlets attain 90% of their final length from several days to as many as three weeks before pollen branchlets have reached a similar point in their development (Table V). This difference may be related to the position of the reproductive organs on the respective branchlets. On the seed branchlet, they are produced at the very tip of the shoot, whereas reproductive organs develop at the base of the new growth on pollen branchlets. Thus, if the pistillate cones are to be receptive when the staminate cones are producing pollen, the seed branchlet must develop faster.

Data obtained from the trees near the base of the butte are not dependable, as only two branchlets of each type were studied. Of the remaining trees studied, those in both parts of the Timberline Zone all had similar dates of 90% maturity, whereas branchlets of trees on the highest ridge did not reach a similar stage until one and one-half to three weeks later (Table V).

In the lower Timberline Zone, where cone production was most abundant in summer 1979, seed branchlet elongation slowed significantly during July (Figure 13). During the same period, there was a great increase in cone size, which may have tied up most of the available
carbohydrates. Needle elongation, though, continued rapidly in the same month. Seed branchlets resumed elongation in August, when cones had nearly reached their maximum size.

PHENOLOGY OF REPRODUCTIVE ORGANS

Seed production in whitebark pine is determined by the successful completion of three distinct stages, each of which is closely related to environmental factors. The first stage is the inception and development of embryonic reproductive organs in the bud (year 1). Stage two is the opening of the buds and pollination (year 2). And the third stage (year 3) involves fertilization and the development and maturation of the cones and seeds. If environmental conditions are unfavourable at any point in this series, the trees may produce fewer cones, cones of inferior quality, or none at all. The entire cycle, from the initiation of embryonic organs until ripe seeds are produced, lasts 27 months in whitebark pine, as in most pines (Mirov, 1967).

In summer 1978, pollen cones and first-year seed cones were produced in abundance. That summer, the development of the magenta pollen cones occurred during July and closely followed that of pollen cones in the occasional lodgepole pine trees in the Timberline Zone. Pollen fly occurred most intensively between 8-11 August, when the mountain was literally enveloped in clouds of pollen.

On 15 August 1978, temperatures dipped just below freezing and several centimeters of snow fell. The expended pollen cones began dropping soon afterwards. Few of the just-pollinated pistillate cones seemed adversely affected; by late August 1978, they were nearly 15 mm long and 10 mm in diameter, and cone production the following summer (1979) was unusually high.

Of the 49 conelets examined in spring 1979, only six (ca. 12%) were dead, as indicated by their tawny colour and diminutive size compared to the other larger, deep purple cones. The dead conelets still remained on the tree. Shimanyuk (1963), in his study of Pinus sibirica (a close relative of Pinus albicaulis), found that the fall of young conelets began in the year of pollination, and intensified the
following spring. Conelet drop is due primarily to the lack of pollination the previous season, and weather during the flowering period. Severe winter weather does not appear to cause any physical damage to the conelets. Late spring freezes may have an effect on the conelets (Kramer and Kozlowski, 1979) in either their first or second summer of growth. Although several trees on the highest ridge produced conelets in 1978, none survived through the winter.

In early June, the cones which aborted later during the summer had an average length of 2.10 cm (s.d.=0.23). Those cones which eventually produced seeds, however, averaged 2.35 cm in length (s.d.=0.17).

Of the 44 cones followed, only two were wider than long. These lopsided cones had been only partially fertilized, and thus grew abnormally. They were not included in calculations of normal cone elongation. Most cones were 5-8% longer than wide at maturity.

Cone enlargement began in late spring and early summer while snow still lay deep around tree trunks, and coincided with bud opening; i.e., it occurred in late May or early June in the Timberline Zone. The greatest increase in length for the cones which matured normally was during July (Table VI). As length increased, so did the variation (s.d.) among cones. Seventy-six percent of these cones reached 90% of their final length between 20 and 26 July.

Cones varied slightly in their dimensions, depending on the weather and the time of day they were measured. Such fluctuations are apparently due to water relations within the cone itself. Kozlowski (1971) found diurnal changes in cone size, with a decrease during the day when water stress was greatest, and an increase at night. I found that, toward the middle of August, as cones began to dry, their dimensions decreased.

During years of abundant seed production, there may be a concomitant decrease in vegetative growth (Kramer and Kozlowski, 1979; Eis et al., 1965). During good cone years, the tree uses large amounts of its carbohydrates for the rapidly developing cones and vegetative growth may be somewhat retarded. On trees at Bachelor Butte, there
TABLE VI. CONE ELONGATION FOR THE TWENTY-ONE CONES OF THE LOWER TIMBERLINE ZONE WHICH EVENTUALLY REACHED MATURITY.

<table>
<thead>
<tr>
<th>Date</th>
<th>Number of Cones Sampled</th>
<th>Mean Length (cm)</th>
<th>Standard Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>6 June</td>
<td>16</td>
<td>2.37</td>
<td>0.17</td>
</tr>
<tr>
<td>13 June</td>
<td>21</td>
<td>2.50</td>
<td>0.22</td>
</tr>
<tr>
<td>25 June</td>
<td>21</td>
<td>2.69</td>
<td>0.24</td>
</tr>
<tr>
<td>7 July</td>
<td>21</td>
<td>3.07</td>
<td>0.28</td>
</tr>
<tr>
<td>18 July</td>
<td>21</td>
<td>3.64</td>
<td>0.42</td>
</tr>
<tr>
<td>30 July</td>
<td>21</td>
<td>4.49</td>
<td>0.73</td>
</tr>
</tbody>
</table>
was a good cone crop in 1979 and in 1974, 1976, and 1977 (the latter three years were deduced from cone scars; see Chapter IV). In three out of four of these years, the needle length on seed branchlets was much below normal (Figure 11). Moreover, in years when branchlets produced no cones, needles were longer (greater than 5.0 cm). Only in 1975 and 1978 (both years of generally low cone production) did needles on those few branchlets which did produce cones exceed needles on coneless branchlets. Branchlet length also appeared to be shorter in three of the four abundant cone years (1974, 1977, and 1979) and longer in 1978 and 1975, when few cones were developing.

Most of the study cones which aborted during summer 1979 had already begun decreasing in size during June, although they did not fall off until between 7 and 31 July. Cones died earliest and in greatest numbers in the upper part of the Timberline Zone. Many cones also died in the lower part of the Timberline Zone, but because of a greater abundance of cones in that part of the zone, losses were not as apparent.

The seasonal pattern of increase in dry weight of second-year cones in whitebark pine (Figure 14) appears very similar to that of red pine (Pinus resinosa) described by Kramer and Kozlowski (1979). Wet weight increased sharply from June until early August and then leveled off. Dry weight increased at a much slower rate, which continued into late August. Dry weight of the cones did not begin to increase substantially until August, when it went from 27% to 39% during a two-week period.

Increase in dry weight was accompanied by a drying of the maturing cones' resinous coating. Harvest of the cones by natural consumers then began. Animals avoid tampering with the cones before this stage, apparently because the resins impede the extraction of the seeds, which do not ripen anyway until the cone starts to dry.

Most of the seed harvest on Bachelor Butte was carried out by Clark's nutcrackers (Nucifraga columbiana), small, gray members of the crow family. The remainder of the harvest was accomplished by chickarees (Tamiasciurus douglasii) in the Timberline Zone, and least
Figure 14. Change in cone weight and percent dry matter in the lower Timberline Zone (each data point represents 5-8 cones).
chipmunks (*Eutamias minimus*) and golden-mantled squirrels (*Spermophilus lateralis*) at lower elevations. Although many animals (e.g. woodpeckers, bears, martens, and numerous rodents) are known to prey upon the seeds of whitebark pine and its relatives, only the four mentioned above were seen harvesting or consuming whitebark pine seeds on Bachelor Butte.

Twenty-three cones (including two lopsided ones) remained after 21 of the original 44 cones aborted and dropped off during the summer. Of these 23, 12 had been partly destroyed by nutcrackers by mid-August, and completely emptied of their seeds by the last week of August. The last 11 cones were entirely removed by chickarees during the last week of August. Thus, within a three-week period (9-30 August), the total summer production of cones in the Timberline Zone of Bachelor Butte was annihilated. By the first week of September, not a single mature cone with whole seeds in it could be found. Shimanyuk (1963) reported even more rapid stripping of cones from a forest of *Pinus sibirica* in western Siberia: within a nine-day period in late August, all cones had been removed or their seeds harvested by Eurasian nutcrackers.

The speed with which the nutcrackers harvest the seeds is, of course, dependent upon their numbers. Tomback (1977) found that the nutcrackers of the Sierra Nevada in central California, usually dispersed throughout subalpine forests, tend to converge in the whitebark pine belt when the pine seeds begin ripening. Thus, seed harvest can proceed with incredible speed. The manner in which animals harvest the pine seeds, and the effect the harvest has on the pines, are more thoroughly described in Chapter VI.
VI. INFLUENCES ON GROWTH, MORPHOLOGY, AND DISTRIBUTION OF PINUS ALBICAULIS

INTRODUCTION

Whitebark pine dominates the upper elevational limit of tree growth in the Cascades. This timberline ecotone has severe environmental extremes which appear to prevent the spread of the pine to higher elevations. Trees living in such a precarious ecotone are especially sensitive to relatively minor fluctuations in annual temperature or other environmental factors such as soil moisture, snow accumulation, and annual wind régime. This sensitivity may be indicated by differences in annual growth, which can also have a long-term effect on the overall morphology of the tree (Tranquillini, 1979). I examined the possible relationship between needle and branchlet growth and the annual climatic variation.

Where strong, predominantly unidirectional winds persist throughout much of the year, trees may acquire a misshapen or asymmetrical crown as a result of the wind (Barsch and Weischet, 1963; Grace, 1977; Holtmeier, 1971). The two sides of such a crown typically differ noticeably in volume. The windward side consists of relatively dense, clipped branches. The more voluminous leeward side often has longer, less compact branches which trail off to the lee, away from the trunk.

The two different sides of the tree may possess other distinguishing features. Holtmeier (1971) suggested that the needles of the windward side of conifers might be significantly shorter than those of the leeward side. The two sides of a tree may also differ in needle longevity.

The degree of crown asymmetry can vary considerably. Some trees are only slightly misshapen, whereas others have a distinctly one-sided crown, with no branches on the windward side. I examined the distribution of these varying degrees of deformation in an effort to better understand their relation to the microclimate of different parts of the peak.
Water balance of timberline conifers in the Alps is rarely critical during the summer as there is adequate soil moisture and most subalpine trees have relatively low transpiration rates (Tranquillini, 1979). Osmotic pressures in timberline conifers do not usually exceed 24 bars (Pisek, 1935) during the growing season. Water content of needles also remains above the critical value at which desiccation may begin (Larcher, 1974). Conditions in the subalpine zone of the High Cascades may be different, though, due to a long summer drought and to the highly porous nature of the substrate. In both the Alps and the High Cascades, however, the winter climate can apparently become critical to the tree's water balance. Water potentials of trees on Bachelor Butte were measured during the summer drought.

METHODS

The eleven sample trees on Bachelor Butte's north flank (Table III) were again used to study the effect of annual variation of temperature and precipitation on the vegetative growth of the whitebark pines. Twenty-four seed branchlets were removed from the eleven trees at the end of the 1979 growing season (early September). For each seed branchlet, a nearby pollen branchlet was also removed. Each year's needles were then removed and their lengths measured for the last seven years (1973-79). Annual branchlet growth was also measured and the presence of cone scars on seed branchlets was noted.

Climatic data since 1972 were obtained from the Santiam Pass weather station. A stepwise multiple regression analysis was performed for each of the following dependent variables: needle and branchlet length for both pollen and seed branchlets for each year, and presence or absence of cones during a particular year. Fourteen independent variables were used: elevation of the tree, snow depth on Dutchman Flat 1 June of that year, and mean monthly temperature and precipitation for June, July, and August of both the year during which the vegetative growth was produced and the year previous to that. Combinations of June-July, July-August, and June-July-August values were
also used for temperature and precipitation for each year and the previous year. Equations including all independent variables which were significant at the 0.05 level were generated.

To test the hypothesis that needle length and longevity differ on opposite sides of the tree, 35 trees were sampled during summer 1978 in four different areas of the High Cascades, and on two nearby mountain peaks in central Oregon. Twenty-nine of the trees sampled were on Bachelor Butte at elevations between 2300 and 2510 m. The remainder, from Mount Hood to Crater Lake National Park, were at similar elevations.

Four branchlets were taken from each tree, two from what appeared to be the windward side, and two from the leeward side. Only pollen branchlets were sampled, as seed branchlets occur high in the crown where windward and leeward sides of the tree are difficult to distinguish, and differences in microenvironment between sides are less likely to exist.

For each of the 140 branchlets, the age of the oldest needles was determined. For each area with more than one sample tree, a t-test of paired samples (0.05 level) was used to see if there were, in fact, significant differences in needle longevity between windward and leeward branchlets.

For each tree and each year, the mean needle length on the two windward and the two leeward branchlets was calculated for all years for which all four branchlets had needles. The difference between these means was analyzed to determine if needle length differed significantly between the two sides of the tree. Significance at the 0.05 level was determined by a paired-t test.

Crown asymmetry was examined in forty groves at different elevations and aspects. Twenty-five of the groves were those described in Chapter III. The other fifteen were located as necessary to sample all parts of the butte. All trees exhibited at least some deformation. A Brunton compass was used to determine the direction toward which the crown was swept. Four trees per grove were measured, and their mean was calculated. The forty vectors were plotted on a map of the
mountain to determine what pattern was associated with them.

Increment cores through the entire trunk at a height of one meter were obtained from some of the younger trees to determine the compression ratio. The compression ratio is equal to the distance to the pith on the side of the tree away from the force presumably causing its asymmetry, divided by the distance to the pith on the side toward that force.

For the 25 groves studied in Chapter III, crown deformation was quantified using indices which were developed for use with other tree species. The extent of tree crown asymmetry was given a numerical value between one and six for the Weischet-Barsch system or from zero to seven for the Griggs-Putnam system (Table VII). These values were then compared to see if the indices might also be applicable to white-bark pine.

A pressure chamber (Scholander et al., 1965) was used to determine whether water potential differed significantly on windward and leeward sides of trees at two different times of day. Measurements were made in early August 1978 on branchlets in the upper crown of ten trees in two groves in the lower Timberline Zone (just west of Pine Marten Knob) and on ten trees in two groves on the highest vegetated ridge just east of the cirque. Both pre-dawn and mid-day water potentials were measured. Samples were taken on only the leeward side before dawn, and on both sides of the tree at mid-day.

**RESULTS AND DISCUSSION: CLIMATIC INFLUENCES**

**TEMPERATURE AND PRECIPITATION EFFECTS ON ANNUAL VARIATION OF GROWTH**

Needle lengths of both pollen and seed branchlets seem fairly responsive to annual changes in climate (Table VIII) as indicated by the $R^2$ values of 0.61 and 0.65. Annual branchlet growth appears much less sensitive to climate than does needle length, with $R^2$ values for pollen and seed branchlet growth being 0.18 and 0.22, respectively. The production of cones is also less related to climatic factors than is needle length ($R^2$=0.38).
TABLE VII. THE TWO INDICES USED IN DETERMINING THE DEGREE OF TREE CROWN DEFORMATION (ADAPTED FROM HEWSON ET AL., 1979).

<table>
<thead>
<tr>
<th>WEISCHET-BARSCH INDEX</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 = bending of outer small twigs to leeward</td>
</tr>
<tr>
<td>2 = clearly expressed asymmetrical tree top with stronger twigs bent to leeward</td>
</tr>
<tr>
<td>3 = strongly asymmetrical tree top, although branches and twigs are still present on the windward side</td>
</tr>
<tr>
<td>4 = flag form, with branches absent on the windward side</td>
</tr>
<tr>
<td>5 = wind hedge form; the plant body rises toward the lee, the growth being dense and interlaced</td>
</tr>
<tr>
<td>6 = carpet form, with the main stem appressed to the ground</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>GRIGGS-PUTNAM INDEX</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 = no effect: careful examination of the needles, twigs, and branches reveals no apparent influence of wind on the tree</td>
</tr>
<tr>
<td>1 = brushing: small branches and twigs appear bent away from the prevailing wind direction, and tree crown may be slightly asymmetric</td>
</tr>
<tr>
<td>2 = light flagging: small branches as well as the ends of larger branches are bent by the wind, the tree having a noticeably asymmetric crown</td>
</tr>
<tr>
<td>3 = moderate flagging: large branches are bent toward the leeward side of the tree, resulting in a nearly one-sided crown</td>
</tr>
<tr>
<td>4 = strong flagging: all branches swept to the leeward side, and trunk is branchless on windward side, the tree resembling a banner</td>
</tr>
<tr>
<td>5 = partial throwing: trunk as well as branches are bent to the lee, the trunk rising vertically from the ground, with bending increasing toward its top</td>
</tr>
<tr>
<td>6 = complete throwing: tree grows nearly parallel to the ground, along the path of the prevailing wind</td>
</tr>
<tr>
<td>7 = carpeting: tree takes the form of a shrub (krummholz), with upright leaders killed, and lateral growth predominating</td>
</tr>
</tbody>
</table>
### TABLE VIII. THE RELATIONSHIP OF NEEDLE LENGTH, BRANCHLET LENGTH, AND CONE PRODUCTION TO ELEVATION, SPRING SNOW DEPTH AT DUTCHMAN FLAT, AND CURRENT AND PREVIOUS YEAR CLIMATE AT SANTIAM PASS FOR 1973-79 FOR 11 SAMPLE TREES (SEE TABLE III). VARIABLES LISTED ARE THOSE SIGNIFICANT AT THE 0.05 LEVEL IN A REGRESSION EQUATION.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>n</th>
<th>( R^2 )</th>
<th>Contributing Independent Variables</th>
<th>T-value of Each Contributing Indp’t Variable</th>
<th>Simple Correlation Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Needle length on pollen branchlets</td>
<td>142</td>
<td>0.61</td>
<td>elevation</td>
<td>-11.35</td>
<td>-0.584</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>current Jul-Aug temp</td>
<td>3.29</td>
<td>0.299</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>previous Jun-Jul temp</td>
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<tr>
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<td></td>
<td></td>
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<tr>
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<td>-0.417</td>
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<td></td>
<td></td>
<td></td>
<td>Jun snow depth</td>
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<td>0.150</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>previous Jun precip</td>
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<td>-0.373</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>previous Aug precip</td>
<td>-4.25</td>
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<td></td>
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<td></td>
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<td>0.148</td>
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<td>Seed branchlet length</td>
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<td></td>
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<tr>
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<td>-8.31</td>
<td>-0.495</td>
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1 The significance level for simple correlation coefficients at the 0.05 level is 0.165 (140 degrees of freedom)
For all the dependent variables except seed branchlet length, growth decreases with increasing elevation, confirming my previous assertion that branchlet growth, needle growth, and cone production are greatest at the peak's base, and least on the highest vegetated ridges.

Simple correlation coefficients and regression equations (Table VIII) indicate that seed branchlets and needles of both pollen and seed branchlets respond to the current year's environment as well as to that of the previous year. Pollen branchlet growth seems to be most influenced by elevation and the depth of snow at the summer's beginning. Cone production appears to be most affected by temperatures of the previous summer.

The length of needles on pollen branchlets is mostly associated with temperatures of both the year during which the needles are elongating and the previous year (Table VIII). Higher mean monthly temperatures in July and August of both years are associated with greater branchlet elongation. High temperatures in June and July of the previous year, however, are related to a decrease in shoot growth the following year.

The length of needles on seed branchlets responds mostly to variation in precipitation. Deeper snow in early June and higher mean monthly precipitation in both June and August of the previous year all are associated with decreased needle length. Needle length on seed branchlets increases as the mean summer temperature (June through August) of the current year does.

The fact that elevation and June snow depth are related to only 18% of the variability in pollen branchlet length indicates that factors other than climatic ones probably are important. Since growth is very little each year, there may be little possibility for annual variation and the effect of any measurement errors would be large.

The depth of snow in June, the mean temperature the previous June, and the August precipitation of the year of elongation are all associated with increased seed branchlet growth, with previous June temperature contributing most.
The simple correlation coefficient for needle length on pollen versus seed branchlets is 0.65. This indicated that about 42% of the variability in one branchlet type's needle length can be predicted by knowing the variability in the length of the other type's needles. Branchlet lengths for the two types have a coefficient of only 0.25, showing that their elongations are little related to each other.

Several environmental factors have been implicated in the decrease of tree growth at high elevations. The principal factor preventing tree growth from occurring above timberline seems to be temperature (Fonda, 1976; Kramer and Kozlowski, 1979; Mork, 1968; Tranquillini, 1979). As temperature decreases at higher elevation, trees can no longer obtain enough warmth to complete their annual growth.

Zimmermann and Brown (1974) suggested that needle length depends on the climate of the year during which they are elongating, with temperature being the limiting factor. Bednarz (1976) also states that sunny weather, with presumably higher daily mean temperatures, increases growth and cloudy, rainy weather decreases it. On Bachelor Butte, current summer temperature seems to be important in the growth of whitebark pine needles (Table VIII).

Most authors agree that a decrease in soil moisture during elongation results in inhibition of the current year's needle growth (Cannell et al., 1976; Garrett and Zahner, 1973; Hansen, 1969; Kramer and Kozlowski, 1979). On Bachelor Butte, however, the growth of needles on pollen branchlets does not appear to be influenced by moisture, and that of needles on seed branchlets only slightly. The latter are more affected by precipitation of the previous year (Table VIII). Kramer and Kozlowski (1979) suggest that a decrease in available water during the season of elongation results in less enlargement of nodes and does not affect the number of nodes being produced. Białobok (1971), on the other hand, found that high precipitation during the growth period actually restricted growth. Presumably, this was caused by below average temperatures typically associated with periods of precipitation, which may be especially critical in a timberline habitat.
Annual branchlet and needle growth consists primarily of the elongation of nodes initiated the year before which have remained dormant in the winter bud. It follows that the environment of the year previous to elongation should play an important role in determining the extent to which the branchlet might develop the following summer. Most authors agree with this suggestion (Garrett and Zahner, 1973; Heide, 1974; Kramer and Kozlowski, 1979; Zimmermann and Brown, 1974). Temperature of the year of expansion influences the rate and duration of branchlet elongation (Kramer and Kozlowski, 1979). The growth of seed branchlets of whitebark pine on Bachelor Butte seems somewhat affected by temperatures of the previous year (Table VIII). Neither pollen nor seed branchlets, however, appear to be affected by temperatures of the current year.

Cone production is also influenced by environmental conditions during their development. Shimanyuk (1963) found that cold, wet weather during the inception and development of reproductive primordia is detrimental. In his studies on Pinus sibirica in the U.S.S.R., he also established that low temperatures in late May and June can destroy the cones that were initiated the previous summer. Rain during the flowering period (early August on Bachelor Butte) also had a negative effect on cone maturation of Pinus sibirica the following year, as it hindered successful pollination. For Pinus albicaulis, however, cone maturation was hindered by high temperature late in the year of pollination (Table VIII).

WIND EFFECTS

Crown Asymmetry: Most of the whitebark pines growing on Bachelor Butte have somewhat asymmetrical crowns. Many authors have found that tree shape indicates seasonal and annual wind patterns of the site where the plants grow (Holroyd, 1970; Runge, 1955; Runge, 1959; Weischet, 1951; Yoshimura, 1971; and others). The study of wind-deformed trees can lend insight into long-term wind patterns and thus be of great practical value. Such trees can be used for reconnaissance studies (e.g. wind-power plant siting) if the winds are consistent.
throughout the year. Crown asymmetry is also of physiological interest.

The whitebark pines of Bachelor Butte exhibit three general types of crown deformation. In the first type, most common at lower elevations, many of the larger branches are oriented in a single direction, though branches are plentiful on all sides of the trunk. The second type of deformation, trimming, occurs primarily in the tops of older trees in the lower Timberline Zone, and also on many of the dwarfed trees atop the high ridge east of the cirque (Figure 15). In this type, a dense mass of short pollen branchlets develops at the top of the crown. The trimming is generally very even, the crown surface occasionally resembling a tabletop. In some cases, the branchlets may be so dense and compact that one can lie atop them as if on a bed. This type of deformation occurs only on trees whose crowns are exposed for most of the winter. The third type of deformation results in the development of a crown which resembles a banner, with all the branches growing to one side of a nearly vertical trunk (Figure 16). This type occurs occasionally in the upper part of the Timberline Zone on all aspects, but is found primarily just east of the high ridge east of the cirque, where snow drifting is greatest, and the trees are annually buried (Figure 15). Combinations of any two or all three types of asymmetry can also be found.

The two types of branchlets within any particular crown are affected differently. Pollen branchlets are most easily deformed, whereas the stouter seed branchlets appear much more resistant to damage. In some cases, the pollen branchlets will be severely trimmed, yet rising above the dense mat of pollen branchlets will be seed branchlets which then trail off to one side of the crown (Figure 15).

Broken and split branches may also indicate the severity of wind. In the upper part of the Timberline Zone, the frequency of breaks and splits is highest in the groves on the southwest aspect. On all other aspects, however, such damage is very infrequent. These observations indicate that the strongest forces of the prevailing southwest winter winds act on the trees on the mountain's southwest side.

In the lower part of the Timberline Zone, many broken and/or
Figure 15. Morphological differences of pines and distribution of other vegetation on the highest vegetated ridge (2500 m) on the northeast flank of Bachelor Butte. Dotted line represents the level of typical winter snow cover. Arrows indicate the direction of the prevailing winter wind.
Figure 16. Close-up of crown deformation of whitebark pine resulting in banner-like growth form (2500 m elevation) as illustrated in Figure 15.
split limbs also occur. Here, damage is more likely due to the massive accumulations of rime and snow which develop in the dense crowns of older trees. The force exerted by so much weight on the branches is apparently too great for the limb to bear. Such is not the case in the higher, younger groves where trees have smaller, more diffuse crowns which permit less rime and snow to accumulate.

In the upper part of the Timberline Zone, the windiness of a particular site may also be shown by the pattern of trunk bending. On the southwest aspect, trunks lie pointing in many different directions in some groves. Here, a prevailing wind direction fluctuation of only a few degrees can influence the direction in which trunks are bent or broken, since winds hit here with greatest force. Most of the trunks in this part of the Timberline Zone, especially on other aspects, are thin and flexible enough to withstand the onslaught of wind and snow during winter. The majority of the trees here remain buried under snow until late spring.

The flagging direction of trees on Bachelor Butte occurs in a definite pattern (Figure 17). Trees at the base of the butte's south flank are flagged almost directly from the southwest, apparently being directly affected by the prevailing winter winds. Higher on the butte, however, direction of flagging varies with aspect. The most radical difference occurs in the southwest octant, where groves only a few hundred meters apart differ in flagging direction by almost 90 degrees. Continuing around the mountain from the west side, flagging directions take on more of an eastern component until, on the east flank, they are almost due east. These results clearly indicate the effect of prevailing southwesterly winter winds which go two different directions, with part of the air being forced north and east around the butte, and the remainder being forced south and east. Some air is probably forced up over the summit, as well (Figure 18), as krummholz whitebark pines near the peak's top are also flagged mostly from the southwest.

To quantify the degree of tree crown deformation on Bachelor Butte, I used the two systems of indices (Table VII). In the Weischet-
Figure 17. Tree flagging direction in 40 groves on Bachelor Butte. Each point signifies the location of the sample grove, and each line indicates the direction toward which most branches are swept. Numbers in parentheses indicate more than one grove in the same location. In the grove on the southwest face indicated by a question mark, the direction of flagging was highly inconsistent.
Figure 18. Prevailing wind pattern on Bachelor Butte, as indicated by flagged trees.
Barsch system, groves in the upper part of the Timberline Zone had a mean value of 3.3 (range from 3-4). Trees in the lower part of the same zone had the same mean value (3.3) and ranged from 3-5. Likewise, for the Griggs-Putnam index, high groves had an average value of 3.92, and lower groves 4.00. These nearly identical values for trees growing under presumably different wind regimes indicate that these indices do not effectively distinguish the variety of deformation exhibited by whitebark pines. Both indices seem to work best with trees that, under severe environmental conditions, develop a banner-like growth form. Based on my observations, Pinus albicaulis does not react to climatic stress as do other conifers. Instead, even under the most rigorous conditions like those atop the high ridge east of the cirque, the trees retain branches on both sides of the trunk. Only those trees which are buried in snow throughout most the winter ever develop a true banner form. Pines were also deformed differently than other coniferous genera at timberline in the Rocky Mountains (Daubenmire, 1943).

In conifers, reaction wood (compression wood) forms preferentially on the lower sides of inclined stems. In the Timberline Zone on Bachelor Butte, it develops on the side of the trunk away from the prevailing winter winds. Compression ratios of trees sampled in seven different groves were slightly higher (mean=1.5, range=1.3-1.7) for four trees in high groves than for those in lower, older groves, where the ratio for all three sampled trees was 1.2. Some researchers suggest that the compression ratio reflects the windiness of particular sites, since it indicates the forces acting on the tree (Hewson et al., 1979).

The greater amount of xylem growth on the one side of the trunk may result, in part, because the presence of the branches mostly to one side of the trunk creates a force that causes compression wood to be put down on that side of the tree. Another hypothesis is that most of the branches are concentrated on one side of the tree, and the photosynthate which they produce is used to form wood primarily on that side. Tranquillini (1979) concurs, stating that trees at and above
timberline form reaction wood in response to mechanical pressure from
wind or snow, or simply because of one-sided crown development.

Possible Causes of Crown Asymmetry: There are several possible mecha-
nisms for the development of asymmetrical crowns. First, buds on the
windward side of the tree might be killed in winter due to desiccation
and ice-abrasion (Holroyd, 1970; Holtmeier, 1971). The following
spring, then, little growth would occur on the windward side of the
tree, but normal growth on the leeward side would eventually create a
misshapen crown. Those trees which became buried in snow throughout
the winter would show fewer effects of desiccation and abrasion than
do trees which remain exposed all winter. Second, due to ice accumu-
lation during winter, branches on the windward side might be broken off,
creating a lopsided top (Holroyd, 1970; Lawrence, 1939; Yoshino, 1968).
Third, a constant unidirectional wind during the growing season might
be influential in causing flagging (Holroyd, 1970; Lawrence, 1939).

According to Reitz (1978), wind plays only a subordinate rôle in
crown deformation, since it acts primarily as a vector for the trans-
port of "contaminants" (salt spray along the coast, or snow and rime at
higher or more continental sites). In his studies in Schleswig-
Holstein in northwestern Germany, Reitz concluded that crown deforma-
tion is impossible unless the air contain some contaminant.

Major crown deformation due to conditions during the growing
season can be discounted on Bachelor Butte because of the seasonal
difference in wind patterns there. Summer winds are light, mostly
coming from the north and east. Flagging directions of the groves on
the peak indicate, however, predominating southwest winds, the
direction from which most winter storms come.

Trees which have a banner crown typically remain under the snow
for six months or more of the year. Such trees are usually fewer than
100 years old, so their slender, flexible trunks become prostrate
under the weight of snow and rime during the first storms of winter.
The trees' branches are swept to the leeward during those storms, and
all winter the branches are held in that position under the snow. In
spring, during snowmelt, the arched trunk of each buried tree is slowly uncovered, the branches still held downward by the snowpack. Even after the tree becomes erect, such branches never do return to the windward side of the trunk. The crown deformation here seems to be a result of the force which is exerted upon the branches for an extended period from wind, rime accumulation, and that exerted on the branches by the trunk after it becomes snow free, but branches are still frozen in the snowpack. Trees which remain above the snow may experience similar forces from rime or wind, but the pressure is not continuous.

The cause of the severe trimming on the windward sides of some tree crowns is probably desiccation. These areas of dense, clipped branchlets in the upper crowns are most exposed to winds during the winter. Although they may periodically be protected from the wind by a covering of snow or rime, they are frequently directly exposed to the strongest winds. These winds may cause excessive evaporation from the tissues of the branchlets, thus apparently reducing their potential for growth the following season. The height of the trimmed area depends upon the elevation and site microtopography. In the lower Timberline Zone, trimming may occur as high as 5 m in some trees, whereas on the high ridge east of the cirque, where wind is undoubt- edly much stronger, trimming occurs below about 1.5 m. Wind velocity at the trimline at different elevations is presumably similar. At lower elevations, the trees can grow taller, since wind speeds do not reach the branchlets' tolerance limit for several meters. However, at the highest elevations, especially on sharp ridges, wind speeds attain branchlet tolerance limit at only a short distance from the ground.

Trees which consist mostly of large branches swept in one direction generally acquire great loads of snow during the winter, but are never completely buried. When younger, such trees probably lost most of their large, windward branches which faced into the wind, due to breakage. The only branches which survived were those which faced away from the wind. Eventually, nearly all of the seed branchlets become more or less parallel to one another. Pollen branchlets may
still occur on the windward side, but they are very dense and stunted because of the desiccation discussed earlier.

**Needle Length and Longevity:** In fewer than half of the trees sampled (15 of the 35) is there a significant difference in needle length between the windward and leeward sides (Table IX). This indicates that needle length on different sides of a whitebark pine tree in the Oregon Cascades cannot satisfactorily be used to predict much about the wind of that area. This presupposes that the tree crown's shape is indeed due to wind conditions. Should the crown deformation be due to environmental conditions other than, or in addition to, wind, then the initial selection of branchlets from the apparently windward and leeward sides would be inappropriate.

The number of years which needles remained on the branchlet varied, with some needles lasting as long as eleven years, while other branchlets had no needles older than four years. For all areas sampled, the mean number of years for which needles are retained on the windward branches was 6.6. On the leeward branches, the mean was 7.0 years. Statistical analysis showed that only in area A, the extremely exposed ridge on the northeast flank of Bachelor Butte, were the leeward side's needles retained significantly longer than on the windward side (Table IX).

Constant wind during the growing season can cause significant growth reduction in plants (Heiligmann and Schneider, 1974), the decrease on the windward side of the plant being due to the cooling, rather than the drying, effect of the wind (Smith, 1972; Warren-Wilson, 1959). The lack of differences here suggest that the growing season is not effective in this way. If the main effect of the wind on the trees in subalpine areas is during the winter, it is somewhat more understandable that the suggested differences in needle length and longevity were not detected. This is particularly apparent in the Bachelor Butte study area, where strong winds persist only in winter. In regions where winters are not as severe, or where winds remain strong from a single direction during the growing season, needle length and longevity
TABLE IX. NEEDLE LONGEVITY AND DIFFERENCES IN NEEDLE LENGTH BETWEEN WINDWARD AND LEEWARD BRANCHES FOR PINUS ALBICAULIS IN OREGON.

<table>
<thead>
<tr>
<th>Sample Area</th>
<th>Number of Trees (n=35)</th>
<th>Needle Area Mean (ys)</th>
<th>Needle Longevity Mean Difference (Leeward - Windward) (ys)</th>
<th>Significant Difference?</th>
<th>Needle Length Mean Difference (Leeward - Windward) (cm)</th>
<th>Number of Trees with Significant Difference</th>
<th>Percent of Trees with Significant Difference</th>
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<td>0</td>
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1 Description in Table X
TABLE X. AREAS SAMPLED FOR STUDY OF WINDWARD/LEEWARD DIFFERENCES IN NEEDLE LENGTH AND LONGEVITY ON POLLEN BRANCHED ON DIFFERENT SIDES OF WHITEBARK PINE

A - high ridge on the northeast flank of Bachelor Butte (elevation 2520 m, aspect 60°)
B - high ridge on the south flank of Bachelor Butte (2500 m, 200°)
C - ridge on the north flank of Bachelor Butte (2370 m, 0°)
D - ridge on east flank of Bachelor Butte (2410 m, 90°)
E - ridge on west side of Bachelor Butte (2400 m, 260°)
F - older grove of large trees on north flank of Bachelor Butte (2340 m, 0°)
G - summit of Black Butte, 20 km north of Sisters, Oregon (1963 m)
H - northwestern edge of rim of Crater Lake (2320 m)
I - directly north (upslope) of Timberline Lodge on Mount Hood (2030 m)
J - summit of Paulina Peak, 30 km southeast of Bend, Oregon (2460 m)
K - Tam McArthur Rim, a high bluff just east of Broken Top peak in the High Cascades (2370 m)
seem more likely to be related to the amount of wind encountered by different sides of the tree.

Water Relations: As long as plants absorb as much water as they lose, their internal water relations remain favourable. However, when water loss exceeds replacement in the plant tissues, the water potential decreases. In extreme cases, desiccation of certain tissues can result and death follows.

Smith (1972) found that wind induced water stress in plants of the páramo in Venezuela. An increase in windspeed results in a higher rate of transpiration due to the decrease in boundary layer resistance to diffusion (Heiligmann and Schneider, 1974; Grace, 1977). Perhaps the windward and leeward sides of whitebark pines in the Timberline Zone on Bachelor Butte might have differing degrees of water stress during the period of summer drought.

The pre-dawn range of xylem pressure potential of -8.0 to -12.5 bars was similar for branchlets of trees in both the upper and lower parts of the Timberline Zone. The mean potential was -10.5 bars in the lower Timberline Zone and -9.7 bars in the upper Timberline Zone. At mid-day, the range was slightly lower for trees in the upper Timberline Zone (-11.5 to 17.0 bars on the windward side and -13.0 to -18.0 on the leeward side) than in the lower part of the zone, where it was -14.0 to -18.0 on the windward side and -14.5 to -21.0 bars on the leeward side.

Mean mid-day xylem pressure potential on trees in the lower Timberline Zone was -15.3 bars (s.d.=1.44) on the windward side and -16.5 bars (s.d.=1.83) on the leeward. In the upper part of the zone, it was -12.8 bars and -14.6 bars on the windward and leeward sides, respectively. A paired-\(t\) test for the difference between windward and leeward water stress for the four sampled groves showed a significant difference at the 0.05 level for all four. At mid-day, leeward xylem pressure potential ranged from 0.5 bars higher to 3.5 bars lower than windward (mean=1.48, s.d.=0.95). In all four groves, the leeward side had a more severe xylem pressure potential.
Puritch (1973) found that in potted seedlings of *Abies lasiocarpa* (a subalpine conifer species which grows only as understory krummholz on Bachelor Butte), photosynthesis had already begun to decrease with -10 bars xylem pressure potential. Similar results were obtained for *Pinus cembra* (a close relative of *Pinus albicaulis*), based on results of a study using soil water potential (Havranek and Benecke, 1978). Thus, even in the pre-dawn measurements for whitebark pine, water deficiency may already be significant enough to reduce the potential for growth in these pines.

The results of this study appear at first to be the reverse of what one might expect. During the experiment, there was a persistent breeze from the west, on the same side of the tree as the windward branches. In spite of that, the leeward branchlets showed lower xylem pressure potential. This paradox might be explained by the fact that the needles on the leeward, or east, side of the tree received heavy insolation the entire morning. As a result, they may have transpired to a much greater extent than those needles on the west or windward side. Moreover, the leeward side of the tree typically experiences somewhat warmer temperatures than the windward side because evaporative cooling is reduced in the former (Smith, 1972).

In the subalpine zone at Bachelor Butte, the winter environment probably plays a much greater rôle in plants' internal water relations. If the soil is frozen, water lost from the plant cannot be rapidly replaced. Winter-exposed needles exhibit severe water stress due primarily to increased losses through transpiration due to increased windspeed (Lindsay, 1971). Also, the high levels of radiation on clear days in late spring, while the soil may still be frozen, result in great losses of water from plant tissues (Larcher, 1974). Although few signs of desiccated needles were apparent on Bachelor Butte after winter 1979, such damage was common on the most exposed trees growing near Tam McArthur Rim just 15 km to the north-northeast of Bachelor Butte. There, needles on the windward side had reddish-brown tips when observed in late July 1979, apparently indicative of the drying effect of the previous winter's winds.
Tree Distribution: On Bachelor Butte, most whitebark pines occur in lines atop ridges radiating from the summit. These lines become longer and narrower with increasing elevation. In one sense, the trees growing there are at a disadvantage because their position exposes them more to the winter winds. However, they also benefit in two ways from their location. First, the persistent winter winds reduce snow accumulation, the trees benefit from an early snowmelt in spring, and they can recommence growth while snow still lies deep in nearby depressions. Second, their position atop the ridges permits them to escape the damage from snowcreep and avalanches, both common phenomena in the steep, snowy depressions between the higher ridges.

In the Medicine Bow Mountains of Wyoming, the tree groves occur in elongated strips (Billings, 1969). This distribution is attributed to the accumulation of snowdrifts between the groves during the winter. The following spring, snow melted too late in these areas to allow trees to become established. On Bachelor Butte, this phenomenon occurs in the area around Pine Marten Knob. There, on both the north and south flanks of the knob, elongated tree groves are elevated only slightly above the adjacent depressions. This area was presumably more or less level at one time, and the groves became established as described by Billings. During centuries of erosion of the non-vegetated areas between the strips of trees, those areas eventually became somewhat lower, so the groves now occur on slightly domed ridges. These groves occur in lines perpendicular to the prevailing winter wind direction. Elsewhere in the High Cascades, groves may occur parallel to the prevailing winter winds. On Tam McArthur Rim, scores of lines of trees, some more than 100 m long, parallel each other and the southwesterly winter winds. Most of these tree lines start from a single tree in the lee of a boulder. Apparently, other trees eventually begin growing in the lee of the first tree, until a long line develops.

On Bachelor Butte, trees grow in the protection of a large boulder only near the highest vegetated ridge on the northeast flank. Elsewhere on Bachelor Butte, the whitebark pines are more or less
exposed to the full force of the wind. However, in the severely wind-trimmed groves on Tam McArthur Rim, nearly all of the trees grow in the "protection" of boulders.

At other sites in the High Cascades (Tumalo Mountain, 6 km north-east of Bachelor Butte; Mount Hood; Black Butte; Paulina Peak; and Crater Lake National Park), most whitebark pines occur in island-like groves which are scattered across relatively even terrain. Of the sites observed, only on Mount Hood do whitebark pine groves occur on ridgetops as they do on Bachelor Butte.

RESULTS AND DISCUSSION: BIOTIC INFLUENCES

DISEASE

Needles on branches which remain under the snow for extended periods of time may become infected with snow-blight fungus (*Phacidium abietis*). Björkman (1948) studied a closely related species of fungus (*Phacidium infestans*) which causes similar damage to conifers in northern Europe. The fungus probably attacks the needles via the stomata, with infection occurring in autumn, and mycelial growth continuing while the branch is under the snow. When snow melts, the needles are covered with the gray-black mycelium of the fungus, and death of the branch usually follows shortly thereafter.

On occasional younger pine trunks, the smooth bark is broken by blisters caused by the fungus *Cronartium ribicola*. This disease, the white pine blister rust common mostly at lower elevations elsewhere on the American continent, has apparently only recently begun attacking whitebark pine on Bachelor Butte. The damage is very light, apparently with few branches and no entire trees having died from the infection. However, during summer 1979 numerous blisters produced ripe spores which may contribute to an increase in damage done by this disease. The fungus' alternate host, *Ribes cereum*, is common at lower elevations south and east of Bachelor Butte, and occurs rarely to 2300 m on the north side of the peak.
ANIMALS

The damage done to whitebark pines by vertebrates is difficult to assess. On one hand, the animals (mostly birds and rodents) consume numerous seeds, and in harvesting the seeds, occasionally damage the tree itself. Yet, because of the seed harvest, and the fact that some stored seeds subsequently germinate, these same animals disseminate the seeds. The whitebark pine's indehiscent cones and heavy, wingless seeds would not be dispersed very far, were it not for these animal vectors.

Already in mid-summer 1979, Clark's nutcrackers began testing the seeds in the ripening cones. The birds would alight at the tip of a seed branchlet, position themselves sturdily astride it, and begin making powerful jabs at the still unripe cones. Early in the harvest, they consumed most of the unripe seeds on the spot, and left the yet unhardened seedcoats still attached to the cone scales. By late August, however, when the seeds were mature, the nutcrackers extracted them whole. The birds typically removed cone-scale tips only on one side of the cone, then removed all the cone's seeds via that single opening, leaving a completely hollow cone.

When whole seeds were being extracted, the birds began caching them. They filled their gullets (a specially modified sub-lingual pouch) with seeds, then flew some distance from the tree to deposit them in small groups in holes several centimeters deep which they dug with their bills. Most caches were near rocks or tree roots, especially on ridge tops and in other high, open areas.

Many authors in both America and Europe have noted this type of zoöchorous dissemination accomplished primarily by nutcrackers (Białobok, 1971; Furrer, 1955; Holtmeier, 1967; Shaw, 1914; Tombback, 1977; Tranquillini, 1979). Where all the native Swiss stone pines (Pinus cembra) had been removed centuries ago in central Europe, the natural reforestation of high alpine slopes is now being effected solely by nutcrackers (Furrer, 1955). The treeline there is ascending as the birds cache the seeds higher and higher on the slopes.
Nutcrackers may also contribute to a mixing of germplasms over a locally extensive area. In summer 1978, pines on Bachelor Butte produced scarcely any cones, yet in late August of that year, nutcrackers were frequently seen caching pine seeds there. Such seeds were apparently harvested on other peaks where the pines had abundant cones that year, and then flown to Bachelor Butte for caching. The nearest source of seeds would be Tumalo Mountain, 6 km away. By introducing seeds of different provenances into a new area, a wider range of pine genotypes may develop, which could evolutionarily aid the pine in adapting to its harsh environment.

Compared to the nutcrackers, rodents harvested few seeds. Their effect on the pines was significant, however, because of the manner in which they gathered seeds. Chickarees (Tamiasciurus douglasii) were the most frequently observed rodent in the Timberline Zone of Bachelor Butte, although some golden-mantled squirrels (Spermophilus lateralis) also harvested seeds. The rodents never remained long in the tops of trees; they would scurry to the tip of a branchlet bearing cones, quickly chew off the entire end of the branchlet, and then hide again. The branchlet, with its accompanying cone(s) fell to the ground, where it was later retrieved by the chickaree and partially buried, cones pointing down, in the litter within the grove of trees. Apparently, the rodents return to these caches beneath the snow during the winter. The animals eat all the scale tips off the cone, then consume the seeds, leaving the central portion, which then resembles a morel.

Most of the damage incurred results from chickarees removing entire seed branchlet tips. In some trees, nearly half of the cone-bearing branchlets were removed in 1979 alone. Since I saw no evidence that such branchlets ever grow out again, the tree's potential cone production can be drastically reduced if repeatedly visited by hungry chickarees. However, the Timberline Zone does not support many of the animals, so damage is relatively light.
LITERATURE CITED


Mork, E. 1968. Økologiske undersøkelser i fjellskogen i Hirkjølen forsøksområde. [Ecological investigations in the mountain forest at Hirkjølen Experimental Area.] Meddelelser fra det norske skogforsøksvesen. [Reports of the Norwegian Forest Research Institute.] 25:467-596.


APPENDIX A

VASCULAR PLANTS OF THE TIMBERLINE AND ALPINE ZONES OF BACHELOR BUTTE, OREGON

Zone:  
T = plants found only in the Timberline Zone  
A = plants found only in the Alpine Zone  
TA = plants found in both the Timberline and Alpine Zones

Abundance:  Plants are rated according to the frequency with which they occurred in or near the 25 sampled groves of the Timberline Zone and/or in areas of the Alpine Zone where plant community composition was examined

R = rare (found in less than 5% of the sampled areas)  
O = occasional (found in 5-25% of the sampled areas)  
F = frequent (found in 25-75% of the sampled areas)  
A = abundant (found in more than 75% of the sampled areas)

Pine Associates:  Those plants found growing in whitebark pine groves within the Timberline Zone are indicated by a plus sign (+) and those found growing nearby (e.g. in adjacent vegetated depressions) with a minus sign (-)

<table>
<thead>
<tr>
<th>Zone</th>
<th>Abundance</th>
<th>Pine Assoc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>T F</td>
<td>+</td>
<td>Anemone drummondii Wats.</td>
</tr>
<tr>
<td>T O</td>
<td>+</td>
<td>Antennaria alpina (L.) Gaertn. var. media (Greene) Jeps.</td>
</tr>
<tr>
<td>TA O</td>
<td>-</td>
<td>Arabis platysperma Gray</td>
</tr>
<tr>
<td>T R</td>
<td>-</td>
<td>Arctostaphylos nevadensis Gray</td>
</tr>
<tr>
<td>T R</td>
<td>+</td>
<td>Arnica diversifolia Greene</td>
</tr>
<tr>
<td>T O</td>
<td>-</td>
<td>Aster alpigenus (T. &amp; G.) Gray</td>
</tr>
<tr>
<td>TA F</td>
<td>-</td>
<td>Calyptridium umbellatum (Torr.) Greene</td>
</tr>
<tr>
<td>TA O</td>
<td>+</td>
<td>Cardamine bellidifolia L. var. pachyphylla Cov. &amp; Leib.</td>
</tr>
<tr>
<td>T O</td>
<td>+</td>
<td>Castilleja applegatei Fern. var. applegatei</td>
</tr>
<tr>
<td>A O</td>
<td></td>
<td>Cryptogramma crispa (L.) R. Br. var. acrostichoides (R. Br.) Clarke</td>
</tr>
<tr>
<td>A F</td>
<td></td>
<td>Draba aureola Wats.</td>
</tr>
<tr>
<td>T R</td>
<td>+</td>
<td>Epilobium alpinum L.</td>
</tr>
</tbody>
</table>

1 List does not include grasses and Carex spp. (both for which several species were noted, but not identified)
<table>
<thead>
<tr>
<th>Zone</th>
<th>Abundance</th>
<th>Pine Assoc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>O</td>
<td><em>Erigeron compositus</em> Pursh</td>
</tr>
<tr>
<td>T</td>
<td>A</td>
<td><em>Eriogonum maritum</em> T. &amp; G.</td>
</tr>
<tr>
<td>A</td>
<td>F</td>
<td><em>Eriogonum pyrolifolium</em> Hook.</td>
</tr>
<tr>
<td>T</td>
<td>O</td>
<td>+ <em>Hieracium gracile</em> Hook.</td>
</tr>
<tr>
<td>A</td>
<td>F</td>
<td>+ <em>Hulsea nana</em> Gray</td>
</tr>
<tr>
<td>T</td>
<td>O</td>
<td>+ <em>Juniperus communis</em> L. var. montana Ait.</td>
</tr>
<tr>
<td>T</td>
<td>R</td>
<td>+ <em>Lomatium sp.</em></td>
</tr>
<tr>
<td>T</td>
<td>F</td>
<td>- <em>Luetkea pectinata</em> (Pursh) Kuntze</td>
</tr>
<tr>
<td>T</td>
<td>A</td>
<td>+ <em>Luzula hitchcockii</em> Hamet-Ahti</td>
</tr>
<tr>
<td>T</td>
<td>O</td>
<td>- <em>Nothocalais alpestris</em> (Gray) Chambers</td>
</tr>
<tr>
<td>A</td>
<td>O</td>
<td><em>Oxyria digyna</em> (L.) Hill</td>
</tr>
<tr>
<td>TA</td>
<td>A</td>
<td>+ <em>Penstemon davidsonii</em> Greene var. davidsonii</td>
</tr>
<tr>
<td>T</td>
<td>O</td>
<td>- <em>Penstemon procerus</em> Dougl.</td>
</tr>
<tr>
<td>T</td>
<td>R</td>
<td>- <em>Phyllocladus empetriformis</em> (Sw.) D. Don</td>
</tr>
<tr>
<td>A</td>
<td>O</td>
<td><em>Polemonium pulcherrimum</em> Hook. var. pulcherrimum</td>
</tr>
<tr>
<td>T</td>
<td>O</td>
<td>- <em>Polygonum newberryi</em> Small var. newberryi</td>
</tr>
<tr>
<td>T</td>
<td>O</td>
<td>- <em>Raillardella argentea</em> Gray</td>
</tr>
<tr>
<td>T</td>
<td>O</td>
<td>+ <em>Ranunculus eschscholtzii</em> Schlecht.</td>
</tr>
<tr>
<td>T</td>
<td>R</td>
<td>+ <em>Ribes cereum</em> Dougl.</td>
</tr>
<tr>
<td>TA</td>
<td>A</td>
<td>- <em>Saxifraga tolmiei</em> T. &amp; G. var. tolmiei</td>
</tr>
<tr>
<td>TA</td>
<td>O</td>
<td>+ <em>Sibbaldia procumbens</em> L.</td>
</tr>
<tr>
<td>T</td>
<td>R</td>
<td>+ <em>Sorbus sitchensis</em> Roemer</td>
</tr>
<tr>
<td>T</td>
<td>A</td>
<td>+ <em>Vaccinium scoparium</em> Leiberg</td>
</tr>
</tbody>
</table>

**Trees**

| T    | F         | + *Abies lasiocarpa* (Hook.) Nutt. |
| TA   | A         | + *Pinus albicaulis* Engelm. |
| T    | R         | - *Pinus contorta* Dougl. |
| T    | F         | + *Tsuga mertensiana* (Bong.) Carr. |
APPENDIX B

BIRDS OBSERVED IN THE TIMBERLINE AND ALPINE ZONES OF BACHELOR BUTTE, OREGON

turkey vulture (Cathartes aura)
red-tailed hawk (Buteo jamaicensis)
golden eagle (Aquila chrysaetos)
bald eagle (Haliaeetus leucocephalus)
prairie falcon (Falco mexicanus)
ruffed grouse (Bonasa umbellus)
common nighthawk (Chordeiles minor)
calliope hummingbird (Stellula calliope)
rufous hummingbird (Selasphorus rufus)
red-shafted flicker (Colaptes cafer)
Steller's jay (Cyanocitta stelleri)
grey jay (Perisoreus canadensis)
Clark's nutcracker (Nucifraga columbiana)
common raven (Corvus corax)
common crow (Corvus brachyrynchos)
black-capped chickadee (Parus atricapillus)
mountain chickadee (Parus gambeli)
white-breasted nuthatch (Sitta carolinensis)
red-breasted nuthatch (Sitta canadensis)
brown creeper (Certhia familiaris)
robin (Turdus migratorius)
mountain bluebird (Sialia currucoides)
golden-crowned kinglet (Regulus satrapa)
ruby-crowned kinglet (Regulus calendula)
water pipit (Anthus spinoletta)
Audubon's warbler (Dendroica auduboni)
western tanager (Piranga ludoviciana)
purple finch (Carpodacus purpureus)
Cassin's finch (Carpodacus cassini)
grey-crowned rosy finch (Leucosticte tephrocotis)
pine siskin (Spinus pinus)
Oregon junco (Junco oreganus)
APPENDIX C

MAMMALS OBSERVED IN THE TIMBERLINE AND ALPINE ZONES OF BACHELOR BUTTE, OREGON

marten (Martes americana)
short-tail weasel (Mustela erminea)
mountain lion (Felis concolor)
bobcat (Lynx rufus)
yellowbelly marmot (Marmota flaviventris)
chickaree (Tamiasciurus douglasii)
golden-mantled squirrel (Spermophilus lateralis)
least chipmunk (Eutamias minimus)
pika (Ochotona princeps)
mule deer (Odocoileus hemionus)