Introduction

Subalpine fir[1] is a wide-ranging conifer in boreal and mountain regions of western North America. Although most abundant in the Rocky Mountain region, it is also a major component of high-elevation forests in the Cascade Range of Oregon and Washington and in the Olympic Mountains of Washington.

Recent investigations show that subalpine fir often behaves as a relatively intolerant species and is, therefore, seral on most forested sites in the Cascade Range. It is also an important pioneer species on many severe sites found at higher elevations – on talus, lava flows, and avalanche tracks and at timberline. These features contrast with the shade tolerance and climax status described for subalpine fir in the Rocky Mountains.

This paper describes the successional status of subalpine fir on various sites in the Cascade Range and changes being effected by current epidemic infestations of balsam woolly aphid *(Adelges piceae* (Ratzeburg)). Where appropriate, contrasts are drawn with the behavior of subalpine fir in the Rocky Mountains.

[1]*Common and scientific names of tree species are listed on page 16.*

Identification

Subalpine fir is readily distinguished from associated species in the Cascade Range by its distinctive spirelike form. The ¾- to 1-inch-long dark, blue-green needles and the 2½- to 4-inch-long purplish-gray to black cones also provide positive identification (Alexander 1958). Its inner bark contains numerous tiny resin pockets, lacking in any other indigenous true fir (fig. 1).

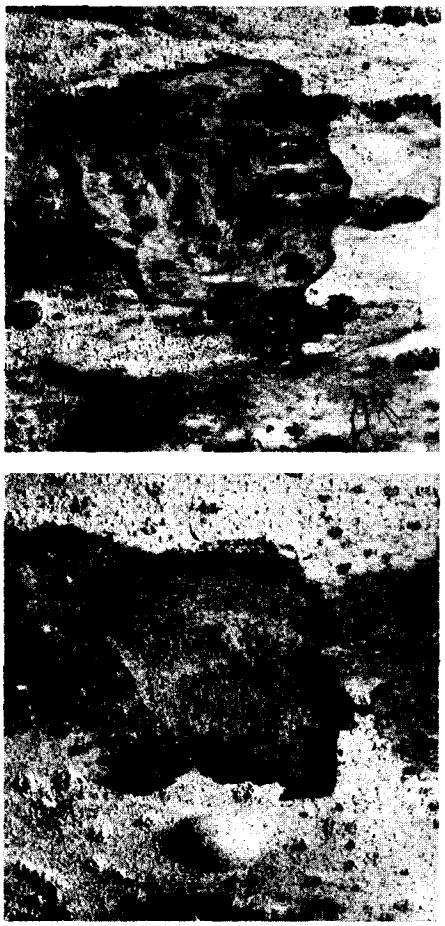


Figure 1.—Tangential cut through bark; A, subalpine fir, showing numerous resin pockets throughout; B, Pacific silver fir, showing lack of resin pockets. (Magnification 1.6X)

Distribution in the Cascade Range

Subalpine fir occurs the length of the Cascade Range in Washington and Oregon but is uncommon south of Crater Lake National Park (fig. 2). Near its southern limits it is increasingly restricted to wet, cool sites along streams or around marshy areas. An earlier report of subalpine fir in California was proved erroneous by Haddock (1961), and the southernmost occurrence now known is at Mount Ashland on the eastern edge of the Siskiyou Mountains.[2]

Subalpine fir is most common at elevations above 4,000 feet, but is often found much lower. On western slopes of the Cascade Range, subalpine fir is common to elevations below 2,000 feet on the West Crater lava beds (fig. 2) and often follows talus and avalanche tracks to elevations of less than 3,000 feet. On eastern slopes of Washington's Cascade Range, subalpine fir drops to lower elevations on cool, moist habitats such as floors of deep valleys and in frost pockets; e.g., at 2,700 feet along Big Meadows Creek in the Chiwawa River drainage; 2,500 feet in Agnes Creek drainage; and 2,000 feet along the Stehekin River, near the upper end of Lake Chelan. In fact, most forests at elevations above 2,500 to 3,000 feet in glaciated valley floors

[2]*Dennis, LaRea June. A taxonomic study of the vascular flora on Ashland Peak, Jackson County, Oregon. 144 pp., illus. 1959. (Unpublished master's thesis on file at Oregon State Univ., Corvallis.)*

Figure 2.—Distribution of subalpine fir in the Cascade Range. Crosshatched area is the Wenatchee Province (Franklin, 1965). Numbers refer to study areas mentioned in this paper: 1, West Crater lava beds; 2, Big Lava Beds; 3, Hood River Meadows; 4, Timberline Road; 5, Santiam Pass; 6, Big Lake; 7, Steamboat Mountain; 8, Pinegrass Ridge; 9, Pasayten River; 10, Chiwawa River; 11, Sunrise Ridge (Mount Rainier); 12, Goat Rocks.

on the east side of the Washington Cascade Range contain subalpine fir and Engelmann spruce as major components.

Sudworth (1908) provides the best summary statement on occurrence of subalpine fir in the Cascade Range: "In cool, moist, and, in part, subalpine situations; commonly on slopes at timberline, and at its lower limits in protected valleys, at heads of streams, and about mountain lakes and meadows."

Associated Tree Species

Species associated with subalpine fir in the Cascade Range are summarized in table 1. Pacific silver fir, mountain hemlock, and lodgepole pine are the major associates in closed forest stands throughout the Cascades except in the Wenatchee Province (Franklin 1965). Major timberline associates are mountain hemlock and whitebark pine. Engelmann spruce is not a constant associate of subalpine fir except in the Wenatchee Province and on exceptionally moist, cool habitats scattered throughout the western and southern Cascade Range.

This group of associates is somewhat different from those typical of interior subalpine fir forests. Throughout the Rocky Mountains Engelmann spruce is subalpine fir's most common companion (Alexander 1958). Several other Rocky Mountain associates – e.g., white spruce, blue spruce, and limber pine – are absent from the Cascades; conversely, Pacific silver fir (always) and mountain hemlock (usually) are not found in the Rocky Mountains. These differences in associated tree species have important implications in successional patterns and composition of climax forest.

Table 1.—Associates of subalpine fir in different provinces of the Cascade Range[1]

Type of forest and species	Province							
	Mount Baker	Mount Rainier	Willamette	Mount Adams	Mount Hood	Three Sisters	Crater Lake	Wenatchee
Closed forest stands:								
Mountain hemlock	M	M	M	M	M	M	M	m
Pacific silver fir	M	M	M	M	M	M	m	m
Lodgepole pine	m	m	m	M	M	M	M	M
Western white pine	m	m	m	m	m	m	m	M
Engelmann spruce		m	m[2]	m[2]	m[2]	m[2]	m[2]	M
Whitebark pine	m	m	m	m	m	m	m	m
Western hemlock	m	m	m	m	m	m	m	m
Douglas-fir	m	m	m	m	m	m	m	m
Alaska-cedar	m	m	m		m	m	m	
Noble fir	m	m	m	m	m	m		
Grand fir				m	m	m	m	m
Shasta red fir							m	
Western larch				m	m			m
Ponderosa pine						m	m	
Timberline stands:								
Mountain hemlock	M	M	M	M	M	M	M	m
Whitebark pine	m	m	m	M	M	M	M	M
Pacific silver fir	m	m	m	m	m	m		
Alaska-cedar	m	m	m					
Subalpine larch								M
Engelmann spruce								m

[1]*Provinces are as defined by Franklin (1965). Symbols indicate: M, major associate; m, minor associate.*
[2]*Except a major associate on localized cool, moist, bottom-land sites.*

Succession on Typical Forest Sites

This section considers the successional status of subalpine fir on typical forest sites; i.e., sites having or capable of developing a closed forest canopy. Two distinctive situations are encountered: (1) subalpine fir as a seral species in most of the Cascade Range, and (2) subalpine fir as a climax species in the Wenatchee Province (fig. 2).

Cascade Range, Excepting Wenatchee Province

Throughout almost the entire Cascade Range, subalpine fir is a seral species on typical forest sites. It invades recently disturbed areas, forming mixed stands with species such as lodgepole pine. But it fails to perpetuate itself in the shade of maturing stands and is gradually replaced by more shade-tolerant associates such as Pacific silver fir and mountain hemlock. The only general exception to this pattern is in the Wenatchee Province of the northeastern Washington Cascades.

The seral status and apparent intolerance of subalpine fir in the Cascade Range has not been previously noted. It is consistently reported as more shade-tolerant than any associates, including Engelmann spruce. Studies have shown subalpine fir forms a stable climax with white or Engelmann spruce; reproduction of subalpine fir is

Table 2.—Number of trees by size classes (diameter) and species on a 15- by 25-meter plot in each of six stands containing subalpine fir; the Cascade Range of northern Oregon and southern Washington, 1961-63

Plot and species	Size class (diameter in inches)						
	< 2		2-4	4-12	12-20	20-28	28-36
	< 3 feet tall	> 3 feet tall					
Big Lake (Willamette National Forest):							
Subalpine fir	661	152	19	3	(1)	1	—
Lodgepole pine: Live	60	12	1	2	1	1	—
Dead	—	—	—	24	3	1	—
Mountain hemlock	8	1	1	—	—	—	—
Hood River Meadows (Mount Hood National Forest):							
Subalpine fir: Live	8	(1)	—	5	4	3	—
Dead	—	—	—	3	1	—	—
Lodgepole pine: Live	—	—	—	—	—	2	—
Dead	—	—	—	—	1	1	—
Pacific silver fir	75	1	—	—	1	—	—
Western white pine	—	—	—	—	—	—	(1)
Grand fir	—	—	—	—	—	—	(1)
Steamboat Mountain (Gifford Pinchot National Forest):							
Subalpine fir: Live	—	—	—	—	6	4	—
Dead	—	—	—	—	5	1	—
Pacific silver fir	22	4	(1)	(1)	—	—	(1)
Mountain hemlock	—	—	—	—	—	1	—
Sunrise Ridge (Mount Rainier National Park):							
Subalpine fir	8	2	1	5	13	—	—
Pacific silver fir	248	14	3	1	—	(1)	(1)
Mountain hemlock	—	(1)	—	—	—	—	—
Timberline Lodge road (Mount Hood National Forest):							
Subalpine fir: Live	—	—	—	1	5	2	—
Dead	—	—	—	2	1	—	—
Pacific silver fir	765	21	1	1	—	(1)	—
Mountain hemlock	15	5	3	3	4	—	—
Santiam Pass (Willamette National Forest):							
Subalpine fir (dead)	—	—	—	4	2	—	—
Lodgepole pine (dead)	—	—	—	2	1	—	—
Pacific silver fir	3,720	15	4	9	1	—	—
Mountain hemlock	8	2	3	19	6	1	—
Western white pine	—	—	—	—	1	—	—

[1] *Size class was represented in an adjacent part of the stand (outside the plot).*

often dominant (Alexander 1958, Daubenmire 1952, LeBarron and Jemison 1953). However, these statements regarding tolerance and successional status of subalpine fir are all based on studies conducted in the Rocky Mountains or boreal Canada. These areas differ from the Cascade Range in (1) major environmental features and (2) total absence of Pacific silver fir and general absence of mountain hemlock. In northern Idaho where mountain hemlock does occur with subalpine fir and Engelmann spruce, both have proved seral to mountain hemlock.[3]

The conclusion that subalpine fir is seral on most forest sites in the Cascade Range is based on examinations of many stands. Six stands in various stages of succession were studied in detail between 1961 and 1963 to illustrate the role of subalpine fir. They are located in the northern Oregon and southern Washington Cascade Range (fig. 2). A 15- by 25-meter plot was located in each stand studied. On each plot, all trees in each size class were recorded, by species, except for seedlings up to 3 feet tall which were tallied on two 1- by 25-meter strips within each larger plot and then projected to a 15- by 25-meter-plot basis.

Resulting size-class distributions were used to determine the successional status of subalpine fir based on the following principles. In mature stands, a climax species will usually exhibit the inverse J-shaped distribution curve, typical of tolerant species, when number of individuals are plotted against size class. Largest numbers of individuals are found in the smallest (seedling) size class; representation decreases rapidly with increasing size class. Seral species, however, lack representation in smaller size classes and exhibit gaps in the distribution curve; e.g., in sapling or pole sizes. Such a void in a stand approaching climax indicates seedlings of this species are unable to survive and grow into larger size classes. Consequently, it would not be represented in the climax forest. Kittredge (1934) used size-class distribution data in a similar fashion to determine successional status of tree species on Star Island, Minnesota.

Size-class distributions in the six stands sampled clearly illustrate the seral status of subalpine fir (table 2). The Big Lake stand (table 2, figs. 3 and 4) represents an early stage of succession. The overstory consists of subalpine fir and lodgepole pine. Many lodgepole pines have died from attacks of mountain pine beetle *(Dendroctonus monticolae* Hopkins) and a lodgepole pine sawfly *(Neodiprion nanulus* Shedl *contortae* Ross). Judged by the large number of seedlings and saplings present, the second generation stand will be predominantly subalpine fir; mountain hemlock has just begun to invade the site.

The Hood River Meadows, Steamboat Mountain, and Sunrise Ridge stands (table 2) provide examples of more advanced successional situations. All three stands have nearly pure subalpine fir overstories. At Hood River Meadows and Steamboat Mountain, older subalpine firs are dying with little or no reproduction. In all three stands, seedlings of Pacific silver fir, the most probable climax species, are abundant. The greater number of Pacific silver fir seedlings in the Sunrise Ridge plot reflects presence of a good seed source adjacent to the subalpine fir stand. A dense herbaceous understory has prevented establishment of abundant reproduction at Steamboat Mountain.

The stand on the Timberline Lodge road (table 2, fig. 5) represents an even more advanced state in suc-

Figure 3.—Lodgepole pine-subalpine fir stand at Big Lake, Willamette National Forest.

Figure 4.—Interior of lodgepole pine-subalpine fir stand at Big Lake, Willamette National Forest. Note abundance of subalpine fir seedlings and saplings.

[3]*Dr. R. Daubenmire, personal communication.*

cession. Subalpine firs in the overstory canopy are dying and smaller size classes are not present. Mountain hemlock constitutes the bulk of basal area in this stand. However, it, too, is poorly represented in younger age classes. The major climax species appears to be Pacific silver fir, which is well represented in younger age classes. Intercession of a stand of mountain hemlock between stands of subalpine fir (or subalpine fir and lodgepole pine) and a climax forest of Pacific silver fir is common, especially where a Pacific silver fir seed source is absent at the beginning of the sere.

The Santiam Pass stand (table 2) represents a near-climax forest of Pacific silver fir and mountain hemlock. Subalpine fir is represented only by dead trees. Mountain hemlock dominates the stand, but relative numbers of seedlings and saplings indicate it, too, will be largely (if not completely) replaced by Pacific silver fir.

Distribution of areas where subalpine fir is abundant in the Cascade Range reinforces the belief that disturbance is necessary for establishment of subalpine fir stands. Except in the northeastern Washington Cascades (Wenatchee Province), subalpine fir is rarely a major component of old-growth stands. Dense stands containing a large component of subalpine fir are generally in areas disturbed within the last 150 years.

Fire appears to have been the most important disturbing agent; all stands listed in table 1 occurred on soils with abundant charcoal in surface horizons. The areas of the Cascade Range where subalpine fir is most abundant, excluding timberline and the Wenatchee Province, are the High Cascades provinces, from the Mount Adams Province south through the Three Sisters Province (Franklin 1965). This pattern of occurrence largely coincides with extensive fires during historic times (fig. 6). Some of the famous spired subalpine fir stands in the vicinity of Paradise Park at Mount Rainier may have also developed following burning (Haines 1962).

Wenatchee Province

The highest elevation forest zone in this province is usually the Subalpine Fir-Engelmann Spruce Zone (Franklin and Trappe 1963). This area is largely free of competitors more tolerant than subalpine fir—mountain hemlock and Pacific silver fir occur only locally. Subalpine fir-Engelmann spruce forests here are much like those of northern Idaho in distribution and composition. Not only do they constitute the zonal climax forests but, as in northern Idaho, "As a topoedaphic climax, peninsular strips of it [spruce-fir forests] extend to

Figure 5.—Interior of subalpine fir-mountain hemlock-Pacific silver fir stand along Timberline Lodge road, Mount Hood National Forest. Reproduction is almost entirely Pacific silver fir. (The stake (arrow) in this and figures 10 and 11 is 1 meter high and is marked off in decimeter segments.)

rather low elevations where they often expand to cover the floors of frost pockets in valleys surrounded by some representative of the Thuja-Tsuga zone" (Daubenmire 1952).

Size-class distributions of species in typical stands from the northeastern Washington Cascades provide conclusive evidence (table 3) that subalpine fir is the major climax species in many spruce-fir stands. In fact, at eastern edges of high east-west-trending ridges (e.g., Wenatchee Mountains, Chelan Mountains, Entiat Mountains), Engelmann spruce is a minor component or even absent from many subalpine fir stands (Franklin and Trappe 1963). Eastern extremities of these ridges are relatively dry, despite their elevation, and Engelmann spruce is either absent or confined to moister habitats.

Figure 6.—Subalpine fir growing on a tract burned over about 1900, near Mount Washington, Willamette National Forest.

Table 3.—Number of trees by size classes (diameter) and species on a 15- by 25-meter plot in each of three stands containing subalpine fir; Wenatchee Province of the Cascade Range, 1961-63[1]

Plot and species	Size class (diameter in inches)						
	< 2		2-4	4-12	12-20	20-28	28-36
	< 3 feet tall	> 3 feet tall					
Pasayten River:							
Subalpine fir	636	48	5	2	1	3	2
Engelmann spruce	16	5	2	—	1	2	4
Lodgepole pine	—	(2)	—	1	—	—	—
Chiwawa River:							
Subalpine fir	116	56	2	2	4	2	(2)
Engelmann spruce	8	2	6	(2)	—	(2)	2
Western white pine	—	—	—	—	—	—	1
Grand fir	(2)	8	—	—	1	1	1
Pinegrass Ridge:							
Subalpine fir	880	141	23	2	6	1	(2)
Engelmann spruce	48	6	1	4	—	2	1
Western hemlock	8	—	—	—	—	1	—
Western redcedar	—	—	—	1	1	—	—
Western white pine	—	—	—	—	—	1	(2)
Lodgepole pine	—	—	—	—	(2)	—	—
Douglas-fir	—	—	—	—	—	—	(2)

[1]*Wenatchee Province is as defined by Franklin (1965).*
[2]*Size class was represented in an adjacent part of the stand (outside the plot).*

Succession on Severe Sites

Subalpine fir is often a pioneer in the development of a forest on severe, generally inhospitable sites. These may be raw, geologically young surfaces, such as lava flows or talus slopes, or climatically severe regions near timberline. The remarkable success of subalpine fir as a pioneer species is accounted for by its ability to become established on sites too severe for less hardy competitors together with its ability to enlarge colonies through layering. On most of these severe sites, the forest will not close over for centuries, and subalpine fir is essentially a climax species.

Lava Flows

On lava flows in southern Washington and northern Oregon, subalpine fir is often the major tree species. For example, it is the most important tree at upper elevations on Big Lava Beds (fig. 7), an extensive flow located between the Wind River valley and Mount Adams in southern Washington. On the West Crater lava flows in the same area, subalpine fir is codominant with Douglas-fir over almost the entire surface, even extending to elevations lower than 2,000 feet. The forest on the West Crater flows is very similar to a Douglas-fir-subalpine fir association described by Roach (1952) on a part of the central Oregon Nash Crater lava flow. Both are open forests growing in a broken crust of block basalt. Greater numbers of seedlings and saplings (table 4 and Roach (1952)) suggest subalpine fir is more aggressive at pioneering the site than is Douglas-fir. Subalpine fir is also a major tree species on some raw lava surfaces southwest of Mount St. Helens, although lodgepole pine is more common on flow surfaces in this area. On the McKenzie Pass lava flows in the central Oregon Cascades, subalpine fir shares pioneer status with mountain hemlock and whitebark pine.

The "forests" growing on these lava flows are comparatively open. Limiting factors in regeneration are related to substrate – not light – and, with limited tree competition, subalpine fir is able to establish and maintain itself. Size-class distributions of tree species in most lava flow stands show little or no evidence of successional change (table 4). Subalpine fir is reproducing in sufficient abundance to at least maintain its proportion of the stand. Accordingly, these stands exemplify situations where subalpine fir is an edaphic climax species.

It must be noted, however, that subalpine fir is not present on all recent lava flows in the Cascade

Table 4.—Number of trees by size classes (diameter) and species on a 15- by 25-meter plot in each of three stands dominated by subalpine fir; Cascade Range lava flow communities, 1961-63

Plot and species	Size class (diameter in inches)						
	< 2		2-4	4-12	12-20	20-28	28-36
	< 3 feet tall	> 3 feet tall					
Big Lava Beds:							
Subalpine fir	32	22	16	24	2	—	—
Western white pine	—	(1)	—	—	—	—	—
West Crater lava flow:							
Subalpine fir	16	10	4	8	14	—	—
Douglas-fir	—	(1)	—	1	—	2	(1)
McKenzie Pass lava flow:							
Subalpine fir	8	2	3	1	—	—	—
Whitebark pine	—	(1)	—	1	1	—	—
Mountain hemlock	—	2	—	1	1	—	—

[1]*Size class was represented in an adjacent part of the stand (outside the plot).*

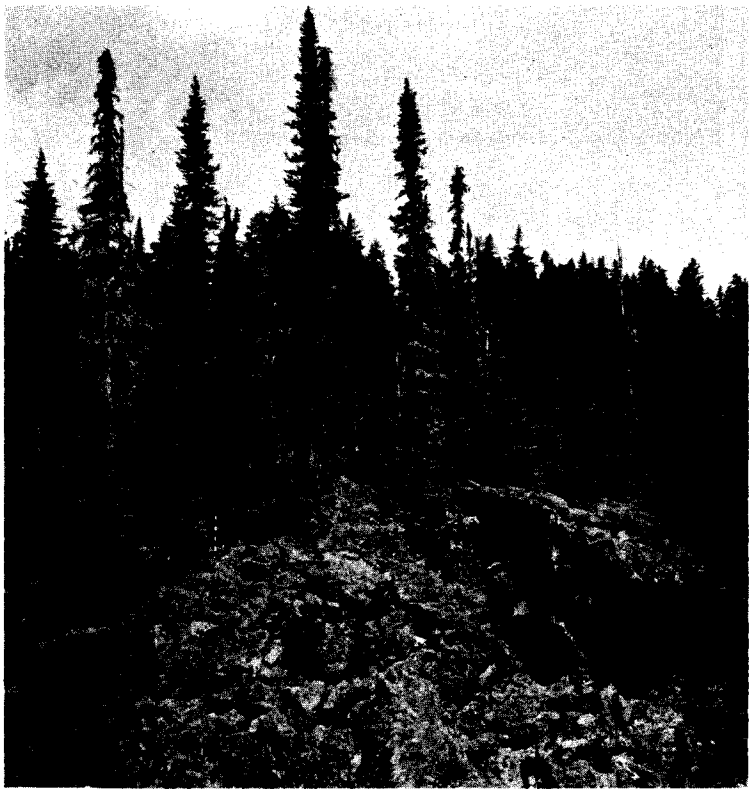
Range. Composition of lava flow communities depends upon many factors, some of the most important being characteristics of the flow surface, elevation, and available seed sources. Roach (1952) noted subalpine fir may be absent from portions of a lava flow well within its geographic range.

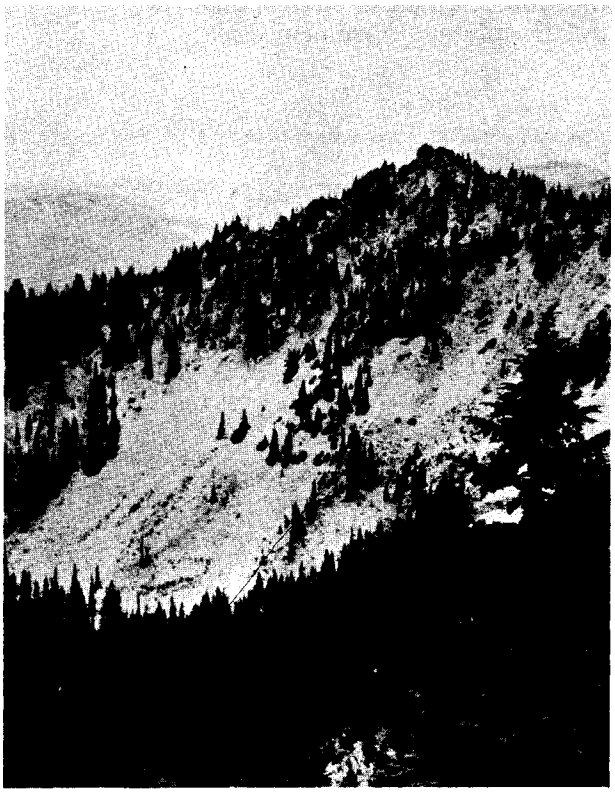
Talus and Avalanche Areas

Subalpine fir is a climax species on high-elevation talus (fig. 8) and on avalanche tracks in the Cascade Range. In the Washington Cascades (including Wenatchee Province), it is often the major tree species and is sometimes the only one present (especially on talus). Frequently the authors have traveled through forests containing little or no subalpine fir, only to come upon intervening talus or slide areas where it is abundant. This phenomenon is especially striking in the Mount Baker and Mount Rainier Provinces (Franklin 1965) where dense old-growth forests of Pacific silver fir, hemlocks, and cedars occupy many acres totally lacking in subalpine fir. Yet, where talus or an avalanche train causes a break in the dense forest, open stands of subalpine fir occur as islands or as peninsular extensions from higher elevations.

Figure 7.—(Left-lower left) Subalpine fir growing on Big Lava Beds in the southern Washington Cascade Range.

Figure 8.—Subalpine fir on an extensive talus near Bumping Lake, Snoqualmie National Forest. Note layering present near bases of many trees.





As on lava flows, subalpine fir is present as a pioneer species. Yet, it forms a topoedaphic climax on these sites because the open stands and exclusion of potential competitors have minimized competition from other trees. On talus the limiting environmental factor is again the substrate, whereas on avalanche tracks it is usually repeated snow slides. Abundant layering of subalpine fir growing on these habitats is a very useful adaptation for their colonization.

Timberline

Subalpine fir is a conspicuous feature of timberline forests in the Cascade Range. This area of subalpine meadows and groups of subalpine fir, mountain hemlock, and whitebark pine (fig. 9) is sometimes called the Hudsonian Zone. It is a tension zone, a dynamic ecotone between tree and treeless vegetation, in which changes are constantly taking place due to allogenic (e.g., long- and short-term climatic variations) as well as autogenic (changes in environment brought about by plants) factors. Successional sequences among tree species are sometimes obscured by allogenic changes in environment and, therefore, discernment of natural patterns in forest succession require extensive, detailed observations. Detailed studies of natural succession among timberline tree species in the wetter portions of the Washington Cascade Range are discussed here. Although timberline forests in the Wenatchee Province are relatively poorly known, openness of the stands and lack of more tolerant arborescent competitors insure subalpine fir a permanent place there.

Subalpine fir occupies a somewhat dichotomous successional position at timberline in the wetter regions of the Washington Cascade Range. It perpetuates itself in open subalpine forest regions and in a certain limited sense can be considered a climax species. But, it does not necessarily retain possession of individual areas which it colonizes. Changes are constantly taking place. There is good evidence that "family" groups of subalpine fir and mountain hemlock have been invading heather or meadow communities for the last 50 years (Brink 1959, Franklin 1966). Brockman (1949) mentions growth and coalescence of subalpine tree groups and resulting replacement of meadow vegetation by forest. Subalpine fir is often the leader in these invasions (Brink 1959, Franklin 1966), although it is sometimes accompanied by mountain hemlock (Van Vechten,[1] Cooper 1942). But what of succession during development and expansion of these tree groups?

A definite sequence in tree species is associated with growth and expansion of subalpine tree groups. It was repeatedly observed during examinations of nearly 100 "family" groups of various sizes (and presumably ages) in the Goat Rocks Wilderness and at Sunrise Ridge and Paradise Park on Mount Rainier, all in western Washington. Initiation of a new group apparently begins with an individual or small group of seedlings. The initiator may be subalpine fir or whitebark pine, the latter often becoming established in small groups (fig. 10) from buried cones or rodent or bird seed caches. Mountain hemlock was not a common pioneer in

[1] *Van Vechten, George Wendell III. The ecology of the timberline and alpine vegetation of the Three Sisters, Oregon. 111 pp., illus. 1960. (Unpublished Ph.D. thesis on file at Oregon State Univ., Corvallis.)*

Figure 9.— Subalpine tree groups near timberline on Sunrise Ridge, Mount Rainier National Park. Groups are predominantly subalpine fir and whitebark pine.

the Mount Rainier area, although it does initiate meadow invasion elsewhere.[5] [6]

As the small patches of seedlings develop, they exert an ever-increasing influence on the microclimate — the blackbody effect causing earlier snowmelt and thereby lengthening the growing season.[7] The group enlarges by layering of subalpine fir as well as establishment of new trees from seed (fig. 11). Mountain hemlock seedlings become established within protection of subalpine fir and whitebark pine. Subalpine fir and whitebark pine fail to reproduce in shaded areas and are gradually eliminated from the center part of the group by mountain hemlock.

The largest, and presumably oldest, stand which could be positively identified as a subalpine forest group was about 100 by 400 feet in size and completely surrounded by meadow vegetation. Here, subalpine fir (mature and reproduction) and occasional whitebark pine were confined to the margins of the group. The center was dominated by large overmature mountain hemlocks, among which were scattered abundant seedlings, saplings, and poles of Pacific silver fir. Mountain hemlock reproduction was sparse and confined to rotten wood. It appears, therefore, that Pacific silver fir will be the major climax species in a family group originally started by seedlings of subalpine fir and whitebark pine.

The development of subalpine tree groups is illustrated schematically in figure 12. Significantly, the successional sequence is the same as that encountered well below timberline following destruction of dense Pacific silver fir-mountain hemlock forests. This developmental pattern also contrasts with the development of subalpine tree groups in comparatively drier regions such as the Teton Range of

[5] *Swedberg, Kenneth Charles. The coniferous ecotone of the east slopes of the northern Oregon Cascades. 118 pp., illus. 1961. (Unpublished Ph.D. thesis on file at Oregon State Univ., Corvallis.)*

[6] *See footnote 4.*

[7] *See footnote 5.*

Figure 11.—Subalpine forest groups in early stages of development. Group in upper picture appears to have been initiated by whitebark pine; group in lower picture by subalpine fir. Some mountain hemlock seedlings have become established within the protection of larger subalpine fir and whitebark pine. Expansion of groups is taking place largely by layering of subalpine fir. In the lower picture, note that whitebark pine saplings are confined to the margin of the group. Sunrise Ridge, Mount Rainier National Park.

Figure 10.—(Below left) Whitebark pine seedlings in subalpine meadow which probably developed from a bird or rodent seed cache. Seedling groups of this type often initiate development of a subalpine forest group. Sunrise Ridge, Mount Rainier National Park.

Wyoming (Griggs 1938) and on cinder flats in the central Oregon Cascade Range.[8] In these areas, "timber atolls" are found in which groups of subalpine fir and other species expand outward by layering and seeding but leave the center of the group hollow or vacant.

"Krummholz" Areas

"Krummholz" refers to individual and small groups of trees growing above timberline. These trees are characteristically contorted and dwarfed due to severe alpine climate (hence "krummholz," a German term meaning crooked or bent wood). Here, environmental influences are much more important in seedling establishment than competition for moisture and light among tree species. Subalpine fir is especially adapted to this environment because of its ability to layer. Other species, notably subalpine larch or whitebark pine, may extend to higher elevations, but a single established subalpine fir is capable of colonizing a greater area than an individual of any other species in the krummholz region.

Seral or climax designations are usually not applied to tree species in krummholz stands, but subalpine fir is definitely a pioneer in this environment. Archer (1964) has described a successional sequence in krummholz stands in coastal British Columbia in which subalpine fir succeeds Alaska-cedar and is in turn replaced by mountain hemlock.

[8] *See footnote 5.*

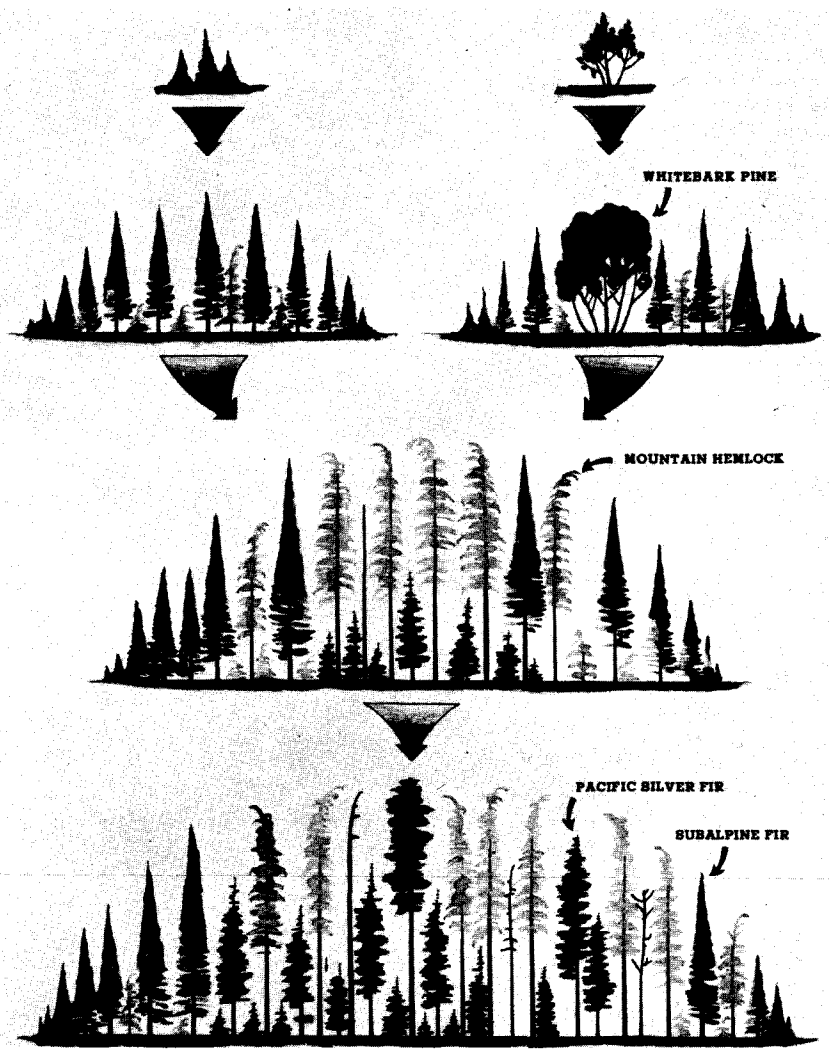


Figure 12.— Schematic diagram showing the development of subalpine forest groups on western slopes of the Washington Cascade Range.

Pests Affecting Subalpine Fir

The insect and disease situation with subalpine fir is generally poorly known, though the species apparently has few enemies. Some primary root diseases, such as *Armillaria mellea* Vahl ex Fr. and *Fomes annosus* (Fries) Karst, are apparent and bark beetles such as *Pseudohylesinus grandis* Swaine and *Dryocoetes confusus* Swaine have been known to attack a few trees, but the total impact of these pests has not appeared significant. The important enemy of subalpine fir in the Pacific Northwest is an introduced pest from Europe – the balsam woolly aphid *(Adelges (= Chermes) piceae* (Ratzeburg)).

Of native true firs, subalpine fir is the most sensitive to balsam woolly aphid (Mitchell 1966), and epidemic infestations of the woolly aphid have been responsible for dramatic changes in the ecology of subalpine fir over a wide area. Since discovery of the aphid in 1954 (Johnson and Wright 1957), the pest has killed subalpine fir along the Cascade Range from Mount Rainier in central Washington to Crater Lake in southern Oregon. The southward spread of the aphid in the Crater Lake area is continuing, although it is nearing the southern limit of subalpine fir. In the north, around Mount Rainier, the status of the aphid is unknown. One spot infestation of undetermined size has been found north of Mount Rainier, in the Middle Fork drainage of the Snoqualmie River.

Mortality due to the balsam woolly aphid is sometimes quite severe. Subalpine fir growing in moist stream bottoms and around lower mountain meadows (fig. 13) is extremely sensitive to the aphid. Stands growing on and around

lava beds have also suffered severe damage. Over 80-percent mortality was observed in a mature stand growing on the West Crater lava flow in the Wind River drainage of southwest Washington. Significant mortality has also been observed in other lava beds, particularly at lower elevations.

Conceivably, aphid outbreaks could eliminate subalpine fir from localized areas. In closed, mixed stands, the aphid will hasten replacement of subalpine fir by more tolerant species. Greatest impact of the aphid appears to be on the pioneering ability of subalpine fir—those instances where the fir invades lava beds, talus slopes, old beaver marshes, etc. Adversities of the physical environment—already considerable in these situations—are greatly magnified by the aphid. Also, the aphid's habit of settling on terminal buds inhibits new growth and reduces the possibility of seed production, further reducing effectiveness of subalpine fir in colonizing nonforested land and maintaining its tenuous hold in some areas.

Fortunately, mortality is seldom complete in an infested area. Suppressed trees and poor-site trees are far less sensitive to aphid infestations than was once believed. Even in areas where mortality is heavy, a few large trees nearly always escape attack, because of chance, local environment, or possibly genetic characteristics. But the most significant characteristic of infestation patterns is that attacks are most abundant and most serious at lower elevations. Subalpine fir above 5,500 to 6,000 feet is rarely attacked, and a wide zone is left between timberline and the infestation area. Here, it appears, succession will proceed normally, without interference from the balsam woolly aphid.

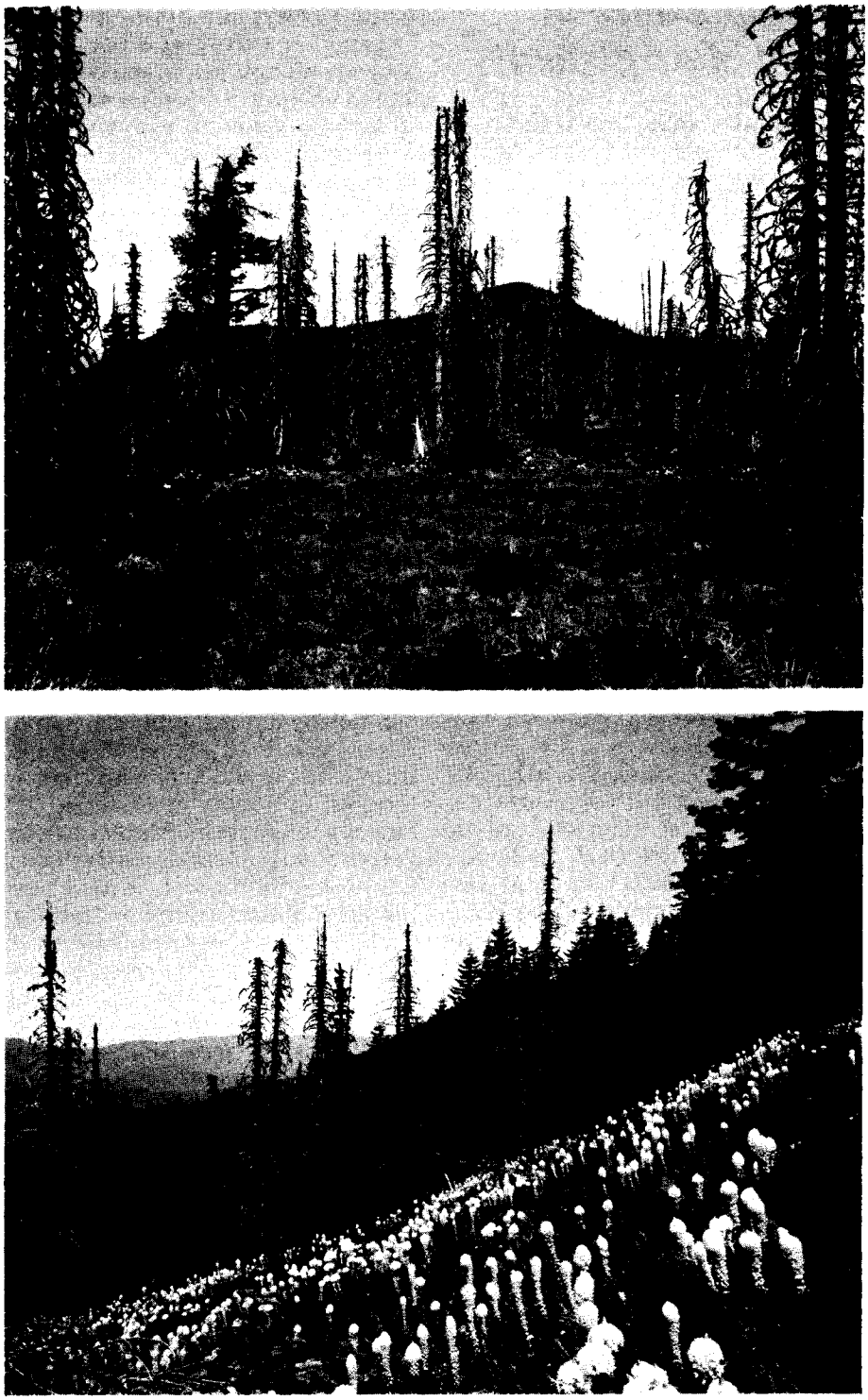


Figure 13.—Destruction of subalpine fir by balsam woolly aphid is complete in many stands surrounding mountain meadows in the western Cascades of Oregon. Lookout Mountain, Willamette National Forest.

Significance in Land Management

Ecologically, subalpine fir is a very important species in high-elevation forests. As a forest pioneer on lava flows, avalanches, and other severe sites in the high Cascades, it is probably unequaled. By providing cover on these and fire-devastated tracts, subalpine fir can be a distinct asset in watershed protection and landscape rehabilitation.

In commercial management of subalpine fir forests, foresters must consider the tree's successional status as well as the probable impact of the balsam woolly aphid. In the Wenatchee Province, subalpine fir is both abundant and free of aphid infestation. In this area, subalpine fir will be favored by shelterwood or selection cutting since it is the most tolerant species normally present, and clearcutting will tend to favor associated, less tolerant species. Silvicultural knowledge developed in Rocky Mountain subalpine fir stands (Alexander 1958, Daubenmire 1952, LeBarron and Jemison 1953) can be drawn upon with reasonable safety until detailed studies have been conducted in the Wenatchee Province.

Elsewhere in the Cascade Range, subalpine fir has little commercial value, is generally infested by balsam woolly aphid, and behaves as an intolerant species. It is sometimes logged along with other high-elevation species, but low stumpage values render timber sales aimed specifically at subalpine fir impractical. In many cases, such stands are best left alone — salvable timber values are not commensurate with losses of other multiple-use values. However, in stands where timber harvesting is planned, it must be recognized that shelterwood or selective cutting will favor regeneration of species other than subalpine fir, especially if subalpine fir seed source is eliminated. The closed stands would have little or no advance regeneration present.

Esthetically, subalpine fir is unequaled as a dramatic backdrop. More than any other species, subalpine fir symbolizes high-elevation beauty, a sense of eternity, and wilderness. Most outdoor enthusiasts in the West could scarcely imagine a mountain meadow without subalpine fir. In high-use recreation areas, such as National Parks, this factor deserves much consideration. Alpine meadows may need some management to keep the wilderness image that the public has been conditioned to expect.

It is not yet clear what the full effects of balsam woolly aphid will be on subalpine fir and, as a consequence, the natural ecology and management of the Cascade Range. The outbreak has not yet run its course; it still appears to be spreading in many areas. Nevertheless, present indications are that stands on the east side of the Cascades will not be damaged by the aphid. Elsewhere, high-elevation stands, from 5,500 or 6,000 feet to timberline, will probably also escape significant infestation. Many low-elevation stands are apparently doomed, destruction by the aphid having been almost complete. Ecologically, the widespread death of subalpine firs in pioneer situations — around meadows, avalanche areas, and lava beds — is particularly serious because there often appears to be no other tree species capable of taking its place. Loss of subalpine fir from commercial forest stands is at least economically less serious since many other species of higher or equivalent value are adapted to these sites.

Summary

Subalpine fir has a far different ecological role in most parts of the Cascade Range than it does in Rocky Mountain spruce-fir forests. Subalpine fir is seral on sites which will support closed forest stands; it regenerates following disturbance and is gradually eliminated by more tolerant associates such as mountain hemlock and Pacific silver fir. On some other sites, such as recent lava flows and talus, subalpine fir pioneers and is maintained as a topoedaphic or edaphic climax species. In open subalpine forests near timberline (forest groups scattered through subalpine meadows), it often pioneers but is sometimes replaced by mountain hemlock and Pacific silver fir if forest succession is allowed to continue. The ability of subalpine fir to enlarge original colonies by layering partially accounts for its success as a pioneer species on some of these difficult sites. In the northeastern part of the Cascade Range (Wenatchee Province), more tolerant associates of subalpine fir are generally lacking. There it is a climax species, occupying the same ecological niche as in interior mountain ranges.

Balsam woolly aphid is causing significant mortality in many subalpine fir stands in Oregon and southern Washington, virtually eliminating it from some areas. This destruction, coupled with the seral role of subalpine fir on most forest sites, is producing a drastic downward trend in importance of subalpine fir in areas of aphid infestation.

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Common and Scientific Names of Tree Species Mentioned in the Text

Abies amabilis (Dougl.) Forbes	Pacific silver fir
Abies grandis (Dougl.) Lindl.	grand fir
Abies lasiocarpa (Hook.) Nutt.	subalpine fir
Abies magnifica var. **shastensis** Lemm.	Shasta red fir
Abies procera Rehd.	noble fir
Chamaecyparis nootkatensis (D. Don) Spach	Alaska-cedar
Larix lyallii Parl.	subalpine larch
Larix occidentalis Nutt.	western larch
Picea engelmannii Parry	Engelmann spruce
Picea glauca (Moench) Voss	white spruce
Picea pungens Engelm.	blue spruce
Pinus albicaulis Engelm.	whitebark pine
Pinus contorta Dougl.	lodgepole pine
Pinus flexilis James	limber pine
Pinus monticola Dougl.	western white pine
Pinus ponderosa Laws.	ponderosa pine
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir
Tsuga heterophylla (Raf.) Sarg.	western hemlock
Tsuga mertensiana (Bong.) Carr.	mountain hemlock