Tsuga mertensiana (Bong.) Carr. Mountain Hemlock

Pinaceae Pine family

Joseph E. Means

Mountain hemlock *(Tsuga mertensiana)* is usually found on cold, snowy subalpine sites where it grows slowly, sometimes attaining more than 800 years in age. Arborescent individuals that have narrowly conical crowns until old age (300 to 400 years) and shrubby krummholz on cold, windy sites near timberline add beauty to mountain landscapes. Taylor and Taylor *(76)* thoroughly describe its form. Uses of its moderately strong, light-colored wood include small-dimension lumber and pulp.

Habitat

Native Range

Mountain hemlock (fig. 1) grows from Sequoia National Park in California (lat. 36° 38′ N.) *(62)* to Cook Inlet in Alaska (lat. 61° 25′ N.) *(83)*. It grows along the crest of the Sierra Nevada in California *(31)*; the Cascade Range in Oregon; the Cascade Range and Olympic Mountains in Washington; the northern Rocky Mountains in Idaho and western Montana; the Insular, Coast, and Columbia Mountains in British Columbia; and in southeast and south-central Alaska.

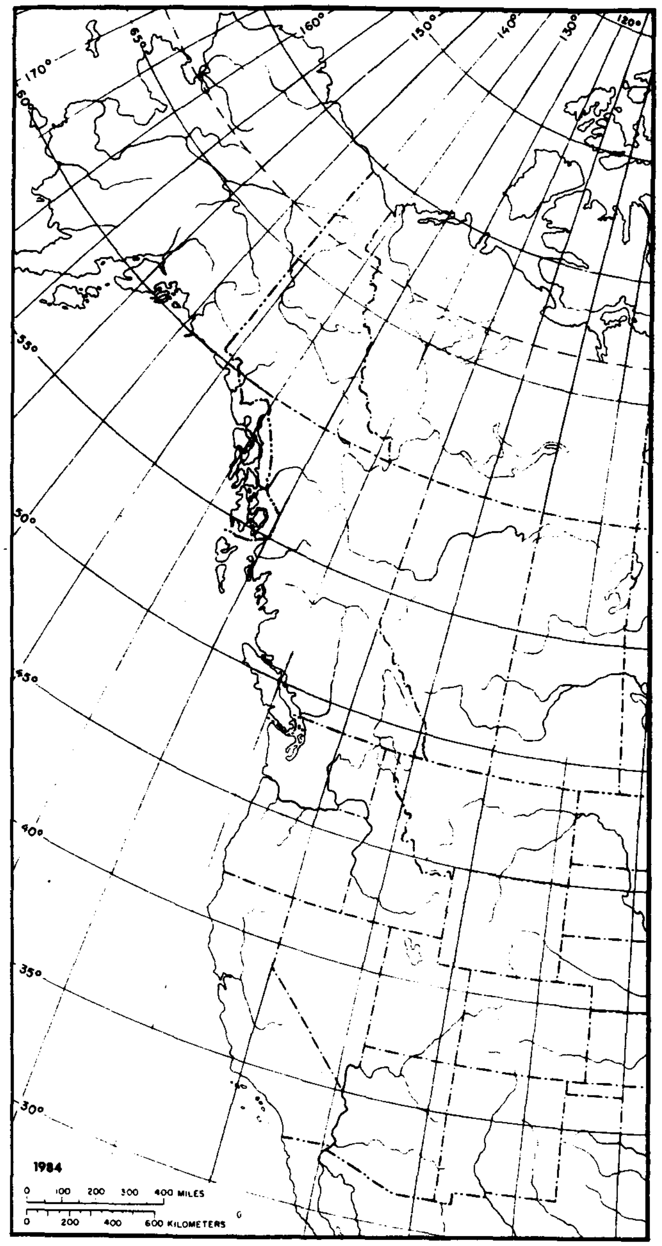

Figure 1—*The native range of mountain hemlock.*

Climate

Areas occupied by mountain hemlock (fig. 2) generally have a cool to cold maritime climate that includes mild to cold winters, a short, warm to cool growing season and moderate to high precipitation (table 1). Annual and summer precipitation and the proportion of precipitation as snow show notable latitudinal climatic trends in the range of mountain hemlock (table 1). Latitudinal trends in mean temperatures are not evident.

The high snowfall results in snowpacks with maximum depths that range from 245 cm (96 in) in Idaho to 380 cm (150 in) in British Columbia *(9)*. A snowpack may cover the ground for long periods (7 to 10 months in southwestern British Columbia) *(9)*. The relatively short growing season (frost-free period) ranges from 95 to 148 days in southwestern British Columbia *(9,45)* and from 49 to 63 days in the central Sierra Nevada *(64)*.

Climatic extremes include a temperature range of –29° to 38° C (–20° to 100° F) *(11)*, annual snowfall in excess of 2200 cm (866 in) *(66)*, snowpack up to 750 cm (295 in) *(20)*, and persistence of the snowpack

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until August or September (9,66). Because there are few weather stations in the range of mountain hemlock, reported extremes are probably often exceeded.

Mountain hemlock grows in an altitudinal band 300 to 1000 m (1,000 to 3,300 ft) wide that increases in altitude from north to south:

	Altitude	
	m	*ft*
Alaska (83)	0 to 1067	0 to 3,500
Northern British Columbia (46)	300 to 900	1,000 to 3,000
Southern British Columbia (46)	900 to 1800	3,000 to 5,900
Northern Washington (20)	1300 to 1700	4,200 to 5,600
Rocky Mountains (12,33,63)	1550 to 2100	5,100 to 6,900
Southern Oregon (42)	1600 to 2300	5,200 to 7,500
Northern Sierra Nevada (64)	2400 to 3050	7,900 to 10,000
Southern Sierra Nevada (62)	2750 to 3050	9,050 to 10,000

The presence of mountain hemlock in the Rocky Mountains is closely correlated with the eastward penetration of moist maritime air masses (33). On the east side of the Coast Mountains in British Columbia, mountain hemlock is limited to relatively moist sites where snow accumulates early in the fall (46). Krajina (46) proposes that mountain hemlock does not grow on sites with later, thinner snowpacks because it cannot tolerate the frozen soils there.

Figure 2—*Winter landscape in the subalpine mountain hemlock zone, high Cascades of Oregon. In the middle distance is a stand representative of the continuous forest subzone; above this and to the right is an example of the parkland subzone.*

Table 1—Climatological data from 14 weather stations within the range of mountain hemlock

Location and number of stations	Temperature			Precipitation		
	Annual	January	July	Annual	June to August	Portion[1] as snowfall
		°C		*mm*	*mm*	*pct*
Alaska,[2] 3	4	−7	13	1681	346	14
British Columbia, 4	3	−3	11	3021	361	29
Washington, 2	4	−3	12	2728	270	51
Northern Idaho, 1	3	−7	15	971	124	65
Oregon, 1	4	−4	13	1643	99	81
California, 3	3	−4	13	1048	51	88
		°F		*in*	*in*	*pct*
Alaska[2] (80)	39	20	56	62	13	14
British Columbia (9,45)	38	26	52	104	14	29
Washington (20)	39	27	53	107	11	51
Northern Idaho (79)	37	19	59	38	5	65
Oregon (20)	39	25	56	65	4	81
California (64,77)	38	24	56	39	2	88

[1]Estimated from snowfall by assuming 10 cm (4 in) of snow is equivalent to 1 cm (0.4 in) of rain, for all locations but those in British Columbia.
[2]Stations in Alaska are near sea level. Mountain hemlock grows at higher elevations where

Throughout most of the range of mountain hemlock local climate differentiates two types of subalpine mountain hemlock forest. A **parkland subzone** of single trees and small tree clumps (average canopy cover less than 25 percent) extends from treeline or near treeline to the lower **forest subzone** of relatively continuous forest cover (canopy cover more than 25 percent) (2,9,21,82). Most climatic data (table 1) are from the forest subzone. Detailed microclimatic data (9) and data extrapolated upslope from the weather stations (45) in southwestern British Columbia indicate that the parkland subzone has shorter frost-free and snow-free periods and that maximum snowpack, range of summer temperatures, and actual evapotranspiration are greater than in the forest subzone. Mountain hemlock also grows above treeline in the alpine environment as prostrate krummholz (elfinwood) throughout most of its range (10,20,35).

If climate warms as hypothesized for western North America (24), existing mountain hemlock forests will probably increase in productivity; upper and lower boundaries of the mountain hemlock zone, within which new mountain hemlock forests become established after disturbance, will increase in elevation; and the zone will decrease in area. Near Mount Baker, Washington, ring width of mountain hemlock increases with increasing monthly temperatures in the preceding 12 months, decreasing winter precipitation *(37)*, and decreasing spring snow depth, down to about 1 m (3.3 ft) *(27)*. This implies productivity should increase with predicted temperature increases. Graumlich and others *(28)* estimated that productivity increased 60 percent in the last century in four high-elevation stands in Washington, three of which contained 48 to 96 percent mountain hemlock. They related this increase most strongly to the increase in growing-season temperature during this period (about 1.5° C or 2.7° F). Thus, further increases in temperature may cause further increases in productivity.

Based on the current elevational distribution of major forest zones in the Oregon Cascades and a mean temperature lapse rate of 4.4° C/100 m (2.4° F/1,000 ft), Franklin and others *(24)* have hypothesized the effects of two warmer climates. If mean annual temperature increases 2.5° C (4.5° F), the mountain hemlock zone in Oregon may be shifted upwards 570 m (1,900 ft) and decrease in area from 9 to 2 percent; an increase of 5.0° C (9° F) may move it upwards 1140 m (3,700 ft)—above all but the tallest peaks—so it is effectively eliminated.

Soils and Topography

Over its range, mountain hemlock grows on soils derived from a wide variety of parent materials, including those of volcanic, sedimentary, metamorphic, and glacial origin. It is, however, relatively rare and stunted on soils derived from calcareous parent materials in the Selkirk Mountains of British Columbia *(11)*. Mountain hemlock was not found on calcareous parent materials in the Rocky Mountains of the United States, but edaphic factors influencing its distribution in that area are not clear *(12,63)*.

Mountain hemlock is reported on organic soils (Histosols) in the northern portion of its range *(9,82)* more often than in the southern portion *(62,64)*. In Alaska it is found down to sea level on noncommercial forest land on organic soils bordering muskegs where it may be a major stand component *(35)*. A stunted or prostrate form is often found on these muskegs. It also grows below its usual altitudinal range in British Columbia on poorly drained sites where other species offer little competition *(11)*.

Best development of mountain hemlock is on loose, coarse-textured, well-drained soils with adequate moisture *(9,11,62)*, and in British Columbia *(9)*, on thick and very acidic organic matter and decayed wood. Adequate soil moisture appears to be especially important in California *(11,62)* and Montana *(33)*—portions of its range where summer drought is most pronounced. Mature soils typically found under mountain hemlock stands in Alaska, British Columbia, and Washington are Cryaquods and Cryorthods of the order Spodosols. These soils typically have a 13- to 28-cm (5- to 11-in) forest floor with a root mor or mycelial root mor humus layer in British Columbia *(9)*, and a 5- to 10-cm (2- to 4-in) forest floor with a mor or duff mull humus layer in the Washington Cascades *(20)*. In the central and southern Oregon Cascades and in northeastern Washington and northern Idaho, mature soils are generally weakly developed Haplorthods with densely matted felty mor humus layers 2 to 5 cm (1 to 2 in) thick *(12,20,90)*. Mountain hemlock also commonly grows on immature soils (Entisols and Inceptisols). For example, it grows on Andepts (soils derived from volcanic ash) in the Cascade Range in Oregon *(38,42)*. Forest floors and mineral soil surfaces of pumice and ash soils supporting mountain hemlock in Oregon show moderate resistance to wetting when dry *(42)*.

Stands dominated by mountain hemlock typically have very acidic forest floors (pH 3.4 to 5.0, rarely 6.0) and mineral soils (pH 4.2 to 6.2) with low base saturation (9 to 18, rarely 37 percent) in British Columbia *(9)*, Washington, Oregon *(77,90)*, and northern Idaho *(12)*. Mountain hemlock accumulates aluminum in its foliage and fine roots, so it may increase the acidity and speed up podzolization of these soils *(85)*. Total nitrogen in the forest floor (0.4 to 1.13 percent) and mineral soil (0.05 to 0.4 percent) in British Columbia *(9)*, Washington, and Oregon *(51,77,90)* are comparable to those of other coniferous forests in the region. Levels of available nitrogen in an old-growth stand in Oregon, as indexed by 7-day anaerobic 40° C (104° F) incubations, are extremely low in the mineral soil (1.7 to -2.3 µg N/g) and 100 times higher but still low in the forest floor (45 to 225 µg N/g) relative to levels for lower elevation stands in Oregon and Washington *(51)*. A study of forests on an altitudinal gradient in western Oregon indicates that, as for available nitrogen, a high proportion of soil calcium (98 percent), organic matter (50 percent), and total nitrogen (34 percent) is in the forest floor relative to most lower elevation forest types *(77)*. Because of this, nutrients in the forest floor are very important to the productivity of these forests. These edaphic differences are caused by slower (measured) decomposition rates caused in large part by lower temperatures and, on some sites, by the youth and infertility of the volcanic ash parent material.

Mountain hemlock will grow on most landforms, but individuals typically develop best in mixed stands of the forest subzone on sheltered slopes or in draws. From southern British Columbia south, the tree grows better on northerly exposures *(11)*. The preference for relatively moist, cool sites evidently becomes a necessity as the climate becomes more continental in western Montana *(33)* and more mediterranean in the central Sierra Nevada *(62)* at these extremes of its range. In these locations, mountain hemlock typically grows in isolated populations in north-facing glens and cirque basins where snow collects and may remain well into summer.

Limited data on stomatal behavior from Carson Pass, CA, indicate that mountain hemlock is adapted to sites with long-lasting snowpacks. In the spring, mountain hemlocks emerging through 2 to 4 m (7 to 13 ft) of snow were transpiring and, presumably, photosynthesizing *(73)*, whereas nearby whitebark pines *(Pinus albicaulis)* did not transpire until the soil beneath them was free of snow. Water uptake by seedlings in a greenhouse decreases to near zero at soil water potential of about –2 MPa (versus about –3 MPa for Douglas-fir) because of greater uptake resistance *(5)*. Such decreases suggest that mountain hemlock is less well adapted to droughty sites or sites with high evaporative demand.

Associated Forest Cover

The mountain hemlock zone includes the upper Canadian and most of the Hudsonian Life Zones *(11)* and includes all of the forest cover type Mountain Hemlock (Society of American Foresters, Type 205) *(16)*. Mountain hemlock is a major component of Coastal True Fir–Hemlock (Type 226), California Mixed Subalpine (Type 256) and (in the Cascade Range) Whitebark Pine (Type 208). Mountain hemlock is a minor associate in 12 other coniferous types: Engelmann Spruce–Subalpine Fir (Type 206), Red Fir (Type 207), Interior Douglas-Fir (Type 210), Western Larch (Type 212), Western White Pine (Type 215), Lodgepole Pine (Type 218), Sitka Spruce (Type 223), Western Hemlock (Type 224), Western Hemlock–Sitka Spruce (Type 225), Western Redcedar–Western Hemlock (Type 227), Western Redcedar (Type 228), and Port-Orford-Cedar (Type 231).

Mountain hemlock usually grows in mixture with other trees, and it has many associates, as is evident from the large number of forest types in which it is found. Though pure stands are less common than mixed stands, there are extensive pure stands of mountain hemlock in Alaska *(11)* and in the central high Cascades of Oregon *(20)*.

One of the most widespread mountain hemlock communities is the mountain hemlock–Pacific silver fir/big huckleberry *(Tsuga mertensiana–Abies amabilis/Vaccinium membranaceum)* type found in British Columbia *(9)* and the Oregon and Washington Cascades *(1,20)*. In British Columbia, the understory is dominated by deciduous ericaceous shrubs: Cascades azalea *(Rhododendron albiflorum)*, Alaska huckleberry *(Vaccinium alaskaense)*, rustyleaf menziesia *(Menziesia ferruginea)*, ovalleaf huckleberry *(Vaccinium ovalifolium)*, and big huckleberry. Also included are strawberryleaf blackberry *(Rubus pedatus)* and several mosses. Silver fir and Alaska-cedar *(Chamaecyparis nootkatensis)* are common tree associates in this community in coastal areas, and subalpine fir *(Abies lasiocarpa)* and Engelmann spruce *(Picea engelmannii)* are common associates in inland areas *(9)*.

In the Rocky Mountains, the mountain hemlock/beargrass *(Xerophyllum tenax)* habitat type is generally found on south slopes and is characterized by a high cover of beargrass with big huckleberry and grouse whortleberry *(Vaccinium scoparium)* as common associates *(12,63)*. Subalpine fir and lodgepole pine *(Pinus contorta)* are common arborescent associates. A similar Pacific silver fir–mountain hemlock/beargrass association is found in Oregon *(20)*.

The extensive pure or nearly pure mountain hemlock forests in the high Cascades of Oregon are primarily in the mountain hemlock/grouse whortleberry community *(38,42,48,72)*. Except for grouse whortleberry, understory plant cover is generally low, long-stoloned sedge *(Carex pensylvanica)* being the most commonly mentioned associate.

Mountain hemlock forests in Crater Lake National Park were classified with 89 percent accuracy using Landsat imagery *(86)*, which offers hope for broad-scale mapping of this forest type.

Life History

Reproduction and Early Growth

Flowering and Fruiting—Mountain hemlock is monoecious. Pollen release occurs in June in the Cascade Range in Oregon *(11)*, from mid-June to mid-July in British Columbia *(14,61)*, and from mid-May to late June in Alaska. In a British Columbia study, mountain hemlock and subalpine fir were the last of 10 species to release pollen *(14)*. Daytime temperature appeared to be the most important variable regulating release of pollen, with more release (and by inference more pollination) on warm, dry days. Both protogyny *(53)* and synchrony between pollen release and female cone receptivity on individual trees have been observed in British Columbia. Fertilization occurs from about late July to early August in British Columbia *(61)*. Reproductive buds can easily be identified in the late summer and fall *(15)*.

Many female strobili indicate the potential for a large cone crop next year. Mature cones are oblong, purple or brownish purple, and are generally longer than the other species of *Tsuga* (2 to 9 cm or 0.75 to 3.5 in) *(53)*. Owens and Molder *(60)* have thoroughly described the reproductive cycle of mountain hemlock.

Seed Production and Dissemination—Three years of data from British Columbia indicate that high temperatures in July the year before cone production favor cone-bud initiation *(14)*. Cones ripen and open from late September to November *(11,61)*. Wild mountain hemlock as young as 20 years may bear cones *(11,65)*. A study of cone-bud initiation indicates it may be possible to induce cone production at younger ages *(58)*. Mature trees 175 to 250 years old produce medium to very heavy cone crops at about 3-year intervals in Oregon and Washington but crops may be complete failures in other years *(22)*. Mountain hemlock seeds are dispersed primarily by wind. During a bumper mountain hemlock seed year in Oregon, seedfall at the clearcut-forest boundary was very high (215,000 to 4,144,000/ha or 87,000 to 1,677,000/acre) and was greatest at the south edge and least at the north edge of a gently sloping 12.5-ha (31-acre) clearcut *(21)*. Seedfall was correlated with stand basal area in this study, as basal areas at the north and south edges were 34 and 94 m^2/ha (149 and 410 ft^2/acre), respectively. Seedfall was much less 114 m (375 ft) from the edge of the clearcut but was still quite heavy (40,000 to 230,000/ha or 16,000 to 93,000/acre). Sound seed in this study varied from 36 to 76 percent over 2 years. Germination of mountain hemlock seed ranges from 47 to 75 percent *(66)*.

Seedling Development—Mountain hemlock is easily transplanted and propagated by seed and cuttings *(76)*. Heavy seeds germinate more rapidly *(44)*. Germination, which is epigeal, occurs on snow, mineral soil, or organic soil if sufficient moisture is available. Young seedlings grow best in partial shade *(11)*, and early development is often slow. Increasing light intensity and day-length increase seedling height but delay or prevent terminal-bud formation under shelter *(4)*. Stem dissection of trees on the east side of the Oregon Cascades shows that growth to breast height in natural stands is slower on sites thought to have a late-lying snowpack than on warmer sites.

Mountain hemlock is generally slow to regenerate after disturbances such as logging, site preparation, or wildfire. Most burned areas in the mountain hemlock zone on the Olympic Peninsula do not have adequate stocking for commercial forests (600 trees/ha 1,500/acre) even 55 to 88 years after wildfires *(3)*. Reproduction is greater during normal-to-wet growing seasons, than during dry growing seasons, and greater in areas near live trees at the edge of fires and near trees that survive the fires than in areas farther from seed sources. In the parkland subzone, reproduction is limited to the margins of tree clumps *(48,72)*, except when successive years with earlier than normal snowmelt allow invasion of subalpine meadows *(3,23)*.

Young stands 20 to 40 years old (some in burned areas) in southern Oregon and northern California may be pure mountain hemlock and quite dense (9,900 to 24,700 trees/ha, or 4,000 to 10,000/acre) *(11)*.

In Oregon, mountain hemlock forests typically regenerate slowly after they are clearcut. In a study of 25 clearcuts, 5 to 11 years were required to reach 60-percent stocking on 0.0012-ha (0.003-acre) subplots *(56)*. Establishment of seedlings during the first 2 years in an Oregon shelterwood cut was very low because germinants were few at low residual basal areas (less than 11.5 m^2/ha or 50 ft^2/acre) and all seedlings died at all higher basal areas *(69)*.

Figure 3—*Forest-grown mountain hemlock, showing good form, pruning, and height.*

The normally slow restocking process is retarded by slash treatment. On the east side of the Cascade Range in Oregon, treated (generally piled and burned) clearcuts had lower stocking (33 percent based on 0.0004-ha (0.001-acre) subplots) than untreated clearcuts (57 percent) because of destruction of advance regeneration and a 50-percent decrease in the number of subplots stocked with natural, postharvest reproduction *(61)*. These clearcuts ranged from 3 to 19 years old. Stocking of mountain hemlock and its associates near Willamette Pass, OR, in 13-

Figure 4—*Well-stocked pure mountain hemlock stand in the central high Cascades of Oregon with canopy trees 300 to 400 years old.*

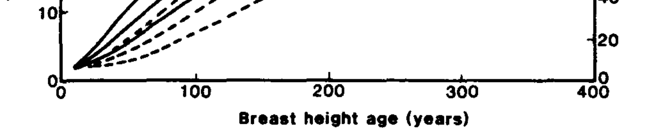

Figure 5—*Height growth curves for two mountain hemlock communities on the east side of the Cascade Range in central Oregon (adapted from* 43). *Mean site index (base age 100 years) and form of height growth curve differ markedly between communities.*

year-old strip cuts with unburned slash was 95 percent (on subplots of 0.0012 ha or 0.003 acre), compared with 82 percent in units that had been burned. The difference was due to advance regeneration of silver fir and mountain hemlock in the unburned clearcuts. These studies indicate that stocking in clearcuts in the mountain hemlock zone is typically made up of postharvest naturally seeded trees, such as mountain hemlock, Shasta red fir *(Abies magnifica* var. *shastensis)*, silver fir, lodgepole pine, and western white pine *(Pinus monticola)*; and advance regeneration of mountain hemlock and Shasta red fir *(56,67)*. Planting has been relatively ineffective in speeding regeneration on these cold, snowy sites compared with advance and postharvest natural regeneration that slowly provide adequate to abundant stocking.

Healthy mountain hemlock saplings (mean d.b.h. 4.5 cm, 1.8 in) respond well to release, in both diameter and height growth *(68)*. Understory saplings with crown ratios greater than 50 percent and growing fastest before release will likely be the best crop trees *(68)*.

Regeneration of mountain hemlock varies in response to environmental gradients. In six strip cuts at Willamette Pass, OR, it decreases from the south (shaded) side to the north (unshaded) side. In the Cascade Range in central Oregon, it decreases with increasing cover of grass and forbs *(67)*. Near Windigo Pass, OR, mountain hemlock makes up an increasing proportion of tree regeneration as elevation and pumice depth increase *(56)* and so becomes increasingly important for reforesting these harsher sites. In Oregon, the proportion of mountain hemlock to other species in clearcuts and burned areas typically is lower than that in surrounding mature stands, whereas the proportion of lodgepole pine, western white pine, and Shasta red fir reproduction is relatively higher.

Seedlings and small saplings of mountain hemlock tolerate heavy snowpacks well. Bent boles and branches spring erect after snowmelt. Leader replacement by axial buds is less frequent than in other North American hemlocks, and the drooping leaders take 3 or more years to become erect *(40)*.

Vegetative Reproduction—Layering is an important method of reproduction on muskegs and krummholz in Alaska but is insignificant in subalpine tree clumps in the north Cascades of Washington *(48)* and in forested areas in general.

Sapling and Pole Stages to Maturity

Growth and Yield—Mature trees range in height from 15 m (50 ft) on poor sites to 46 m (150 ft) on the best sites (figs. 3, 4). Depending on stocking, diameters of old trees range from 30 cm (12 in) on poor sites to 150 cm (60 in) on good sites (fig. 4). The record tree of the American Forestry Association's list of big trees is 34.4 m (113 ft) tall and 224 cm (88 in) in d.b.h. Mountain hemlocks 700 to 800 or more years old are reported in British Columbia *(9)* and at Mount Rainier National Park, WA.

Mountain hemlock grows slowly in height (fig. 5) and in diameter. Three investigators found that stem-dissected trees in Oregon and southern Washington without signs of impeded height growth were only 7 to 28 m (23 to 91 ft) tall at 100 years *(39,43,54)*. Height growth of mountain hemlock is initially slower than that of western hemlock but continues at a moderate rate to greater age. As a result, use of western hemlock site curves in old mountain hemlock stands leads to large overestimates of growth and yield *(39)*.

Site index (base age 100 years) and the form of the height growth curve are different in different plant communities in the central Oregon Cascades (fig. 5) *(43)*. The mountain hemlock/smooth woodrush *(Tsuga mertensiana/Luzula hitchcockii)* and mountain hemlock/prince's-pine-pinemat manzanita *(T. mertensiana/Chimaphila umbellata—Arctostaphylos nevadensis)* communities have ranges in site index of 7 to 14 m (23 to 46 ft) and 13 to 19 m (43 to 62 ft), respectively. In the Coast Mountains of British Columbia, site index (base age 100 years) ranges from less than 6 m (20 ft) on xeric sites to 34 m (110 ft) on the best sites *(46)*.

Mountain hemlock stands at least 200 years old can have high basal areas and volumes; the highest values are in mixed species stands. In the mountain hemlock zone in British Columbia, stands in which that species makes up more than half the volume (59 to 79 percent) have volumes of 125 to 924 m^3/ha (1,786 to 13,204 ft^3/acre); volumes are much higher (range 588 to 1348 m^3/ha, 8,397 to 19,260 ft^3/acre) in stands where mountain hemlock makes up less than half the volume (9 to 36 percent) *(9)*. These more productive mixed-species stands usually grow on deeper soils irrigated by seepage and have a slightly longer average snow-free period, whereas the communities in which mountain hemlock forms a majority of the stocking occupy the poorer, colder sites.

A similar pattern occurs in the Cascade Range in southern Oregon *(42)*. The mountain hemlock/grouse whortleberry community (nearly pure mountain hemlock) produces an estimated 1.0 m^3/ha (14 ft^3/acre) per year, and the Shasta red fir–mountain hemlock/pinemat manzanita/long-stoloned sedge community produces an estimated 3.8 to 9.8 m^3/ha (54 to 140 ft^3/acre) per year *(42)*. The latter community tends to grow on warmer sites, and most of the productivity is by Shasta red fir, not mountain hemlock. Basal areas of both communities are high, 76 and 62 m^2/ha (330 and 270 ft^2/acre), respectively. Mountain hemlock communities in the western Cascades of Oregon and Washington commonly have a mixture of other tree species; estimated productivity ranges from 3.8 to 7.6 m^3/ha (54 to 108 ft^3/acre) per year *(8,38)*. Volume tables are available for mountain hemlock for Alaska *(32)* and the central Oregon Cascades *(6)*. Volume growth, biomass, and leaf area equations are also available *(1,26,71,81,87)*.

Leaf area index (all sides), like volume productivity, is lower in nearly pure mountain hemlock forest (10 m^2/m^2 or 10 ft^2/ft^2) *(25)* than in mixed species forest (35 m^2/m^2 or 35 ft^2/ft^2) *(88)* in the Cascade Range.

Rooting Habit—Mountain hemlock is usually shallow rooted. In British Columbia, roots are mainly confined to the forest floor *(9,45)*. This is not surprising because of the high proportion of soil nutrients in the forest floors of these forests. Mountain hemlock will root adventitiously when, for example, 10 to 20 cm (4 to 8 in) of volcanic tephra is added to the soil surface *(91)*.

Two-thirds to three-quarters of the net primary productivity (NPP) is allocated below ground, according to the available data on three stands 130 to 280 years old dominated by silver fir but with significant mountain hemlock components *(30,84)*. This high allocation below ground is probably caused by the need to obtain sufficient nutrients in these infertile soils *(30)*. Mycorrhizae were found to be important sinks for carbon and components of nutrient cycles in one stand *(84)*.

Reaction to Competition—Mountain hemlock is classed as tolerant of shade and other forms of competition *(10,48,55)* and, based on synecological studies, is more tolerant than all its associates except Pacific silver fir *(46)*, western hemlock, and Alaska-cedar.

Mountain hemlock is considered a minor climax species on most of its habitats; however, it pioneers on glacial moraines in British Columbia and Alaska *(11)* where it is nevertheless considered indicative of the climax forest *(46)*; also see references in *19*). Pacific silver fir is a major climax species in many communities of the mountain hemlock forest subzone in British Columbia *(9)* and Washington and northern Oregon *(20)*. Alaska-cedar, western redcedar *(Thuja plicata)*, and western hemlock *(Tsuga heterophylla)*, however, are climax associates on some sites. Mountain hemlock is more commonly the major climax species in the mountain hemlock zone south of central Oregon where Pacific silver fir does not occur.

Mountain hemlock often succeeds lodgepole pine or subalpine fir when these species pioneer on drier sites *(20)*. It also tends to replace Engelmann spruce when the two species occur together, possibly because hemlock is better able to withstand the allelopathic effects of spruce than are other associated species *(76)*.

Damaging Agents—The most striking damage to mountain hemlock is probably that caused by laminated root rot *(Phellinus weiri)* in the high Cascades of central Oregon *(49)*. This fungus spreads from centers of infection along tree roots so that all trees are killed in circular areas that expand radially. Mountain hemlock is the most susceptible tree in these forests *(18,49)*, and *Phellinus* moves faster (34 cm/yr; 13.3 in/yr) through nearly pure mountain hemlock (91 percent hemlock) than through a more heterogeneous conifer (74 percent hemlock) stand (23 cm/yr; 9.1 in/yr) *(49)*. Growth and coalescence of *Phellinus* pockets have produced infected areas of more than 40 ha (100 acres). The low levels of available nitrogen in the forest floor and mineral soil *(51)* stress mountain hemlock, increasing its susceptibility to infection by *Phellinus*, as indicated by a seedling growth chamber study *(52)*.

Seedlings of mountain hemlock and associated species recolonize disease-killed areas immediately behind the advancing mortality front. These seedlings are apparently not susceptible to reinfection by *P. weiri* for 80 to 120 years *(89)*. This may be due to greater vigor caused by higher levels of available nitrogen (up to a 4-fold increase), higher temperatures, and more growing-season moisture in this regrowth zone *(7,89)*.

Other common fungal pests of mountain hemlock include several heart rots *(Heterobasidion annosum, Phellinus pini, Fomitopsis pinicola,* and *Phaeolus schweinitzii) (11,72)*, of which Indian paint fungus *(Echinodontium tinctorum)* is perhaps the most common and damaging *(42)*. Several needle diseases and a snow mold *(Herpotrichia nigra)* also attack mountain hemlock but are not considered serious pests *(11)*.

The mountain hemlock race of hemlock dwarf mistletoe *(Arceuthobium tsugense)* is a potentially damaging parasite that causes witches' broom, reduction in vigor, and occasionally death *(11,50)*. It is found throughout most of the range of mountain hemlock, but reported infection of mountain hemlock decreases from Washington north *(36)*. Dwarf mistletoe rarely infects mountain hemlock in Alaska, though western hemlock is often infected. Several defoliating insects, bark beetles, and wood-boring insects attack mountain hemlock but do not cause extensive damage *(11)*.

Before effective fire suppression, many mountain hemlock stands south of Alaska probably succumbed to fire, as is indicated by the many young stands *(11,20)*. The species is considered susceptible to fire because it often retains branches almost to the ground, grows in clusters, and, in Oregon, often has well-developed forest floors that dry out in the summer *(72)*.

Wind commonly destroys trees in the coastal strip of British Columbia *(45)* and Alaska where fire is not important *(35)*. As cutting is increased in mountain hemlock forests, wind damage will probably become a more common cause of mortality of this shallow-rooted species. Periodic snow breakage may remove 2 to 6.5 percent of the foliage mass *(29)*.

After the eruption of Mount St. Helens and deposition of tephra on foliage and soil (18 cm, 7 in), growth slowed but trees did not die *(41)*.

Special Uses

Perhaps the most important use of mountain hemlock is for watershed protection and the scenic beauty it adds to subalpine landscapes. It is well adapted to produce attractive forest on the more extreme subalpine sites. The Mount Jefferson (fig. 2) and Three Sisters Wildernesses, heavily used year-round recreation areas in Oregon, provide excellent examples. Stands of this species are said to be well suited to the conservation of snow (see references in *19)*. Its slow growth contributes to its attractive, dense foliage and usually balanced form so that it is a desirable ornamental, including the cultivars that make fine dwarf specimens or have silvery foliage *(76)*.

Some mountain hemlock forest types are important deer summer range on Vancouver Island *(34)*. A shrubby plant association (Mountain Hemlock—Copperbush) there provides abundant browse in old stands as well as in early seral conditions, so harvesting does not significantly affect food availability.

Genetics

Mountain hemlock has several morphological characteristics that separate it from most other species of *Tsuga*, including branchlets not all in one plane; needles radially arranged, relatively thick, with stomata on both surfaces; cones generally larger with more scales; and pollen with air bladders. Because of these spruce-like characteristics, the genetic background of mountain hemlock was under some question *(11,13)* until recently. Mountain hemlock was proposed as a hybrid between western hemlock and Sitka spruce *(Picea sitchensis)* by several French taxonomists and assigned to the new genus *Tsugo–Picea* (see references in *11,13*). Recent studies of pollination mechanisms *(59)*, embryology *(61)*, and leaf pigment chemistry *(74)*, however, place the species firmly in the genus *Tsuga*. These studies are consistent with the proposal by Taylor *(74)* that *Picea* and *Tsuga* are closely related genera, and mountain hemlock is more similar to *Picea* than are other *Tsuga* species *(59,74)*.

Individuals morphologically intermediate between western hemlock and mountain hemlock are occasionally found where the two species occupy the same site. These populations have been given hybrid status *(Tsuga × jeffreyi* (Henry) Henry) *(11,13,47)*. A study of leaf pigment chemistry of 43 morphologically intermediate individuals collected from throughout western Washington indicated, however, that only three (all from Corral Pass near Mount Rainier) were chemically intermediate and so were potentially of hybrid origin *(74)*. Six leaf cuticle characteristics of *Tsuga × jeffreyi* in Britain were similar to mountain hemlock and dissimilar to western hemlock *(70)*, also not supporting hybrid status. The limited overlap in the timing of pollen release *(14)* and failure of all known controlled pollinations to produce filled seeds (in British Columbia *(53)* and in Oregon (cited in *74)* support the conclusion that true hybrids are probably much rarer than the morphological intermediates on which hybrid status is based, if such hybrids occur at all.

A California form of mountain hemlock has been given specific status *(Tsuga crassifolia* Flous) and is proposed as a hybrid between Engelmann spruce and mountain hemlock *(13)*. The hybrid swarms expected from backcrosses with the parent taxa have not been observed *(13)*, however, and this specific status and phylogeny are not generally recognized by taxonomists *(17,47,57)*.

All mountain hemlock in the Siskiyou Mountains from the Oregon–California border south were recently given subspecific status as *Tsuga mertensiana* (Bong.) Carr. ssp. *grandicona* Farjon, in recognition of the generally larger cones of trees in this region *(17,63)*. This classification is less ambitious than the new species *T. crassifolia*.

Clausen *(10)* studied the mountain hemlock phenotypes of erect simple stems and prostrate krummholz (elfinwood) over a gradient in elevation (3050 to 3350 m; 10,000 to 11,000 ft) in the Sierra Nevada and described them as genetic races. It has not been determined, however, whether these growth forms have different genotypes or result solely from different environments.

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