

Biology and Ecology of Red Alder

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Abstract

Red alder is the most common hardwood in the Pacific Northwest with a range stretching from coastal southeast Alaska to southern California and east to isolated populations in Idaho. Soil moisture during the growing season influences where it grows and its growth rates; it can tolerate poor drainage but not droughty, hot sites. Due to its tolerance of wet soil conditions, alder is common in riparian areas. Alder can be injured by spring and fall frosts and is not found at elevations above 1100 m anywhere in its range. The species produces small, very light seeds that disperse over long distances; it is favored by disturbance and often increases in abundance after logging or burning. Alder establishment via seed is not assured, however, as drought and heat injury, pathogens, animals and other factors often destroy seedlings. Alder has nitrogen-fixing nodules on its roots that directly and indirectly increase nitrogen in forest ecosystems. Alder usually has a spreading fibrous root system when young and can root deeply if soil aeration is not limiting. When grown in dense stands, its shade intolerance results in rapid mortality of shaded stems and lower branches. It is a relatively short-lived, intolerant pioneer with rapid juvenile growth. This pattern of height growth—very rapid when young and slowing quickly at a relatively young age—means that if thinning is delayed, alder can not rapidly build crown and increase in diameter growth. Although alder wood stains and decays rapidly after death, live trees compartmentalize decay very efficiently,

and pruning and thinning are feasible operations. Stem rots do not result in high volumes of damage overall but can be locally important; ring shake can also be a serious problem in some stands. Insects and diseases are not generally a problem in young stands although insect defoliators, *Nectria* cankers, and alder bark beetles can cause problems. Meadow mice, voles, and beaver can also hinder stand establishment in some areas. Deer or elk may rub small alder saplings during the fall with their antlers but do not usually browse its leaves and twigs. Sapsucker damage is sporadic, but if stems are repeatedly damaged, their future log value will be greatly reduced. Mortality and top damage have been observed after ice or early snowstorms. Red alder is now being managed for a wider range of objectives and on many more sites than in the past; this is due to recent increases in wood value of alder relative to other species as well as its ability to fill specialized niches (e.g., add nitrogen to forest ecosystems, immunity to laminated root rot) and produce sawlogs on relatively short rotations. Management experience with the species, however, is still limited to a fairly narrow range of sites and management scenarios. Thus, information on the biology and ecology of the species should help guide managers until more direct experience is available.

Keywords: *Alnus rubra*, biology, ecology, damaging agents, growth, red alder, regeneration

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Introduction

Red alder (*Alnus rubra*), also called Oregon alder, western alder, and Pacific coast alder, is the most common hardwood in the Pacific Northwest. It is a relatively short-lived, intolerant pioneer with rapid juvenile growth, the capability to fix atmospheric nitrogen, and tolerance of wet soil conditions (although best growth is not on poorly drained sites, see below). The species is favored by disturbance and often regenerates after harvesting and burning. Because the commercial value of alder has traditionally been lower than that of its associated conifers, many forest managers have tried to eliminate the species from conifer stands. On the other hand, red alder is the major commercial hardwood tree species in the region; its wood is used for furniture, cabinets, pallets, and to make paper (Harrington 1984b). Its value has increased substantially in recent years which has led to greater interest in the management of the species, and thus, to a need for more information on its biology. This chapter is a revised version of Harrington et al. 1994; it summarizes published information as well as unpublished data and observations on the biology and ecology of red alder with emphasis on topics not covered by other authors in this volume and on information that has become available since previous summaries were published (Trappe et al. 1968, Briggs et al. 1978, Heebner and Bergener 1983, Hibbs et al. 1994).

Taxonomy and Genetics

Red alder (genus *Alnus*) is a member of the family Betulaceae. The most conspicuous feature that the North American genera in this family have in common is the presence of male catkins (compact aggregates of staminate flowers) (Brayshaw 1976) that disintegrate after pollen shed. The seed-bearing catkins in alder remain intact and attached to the plant during seed dispersal and for a time after dispersal is completed. More detailed information on the taxonomy and evolution of red alder is presented in Ager and Stettler (1994).

Genetic Variation

No races of red alder have been described, though they may exist, especially in disjunct populations or in the extremes of the range. One researcher divided the species into three populations (northern, central, and southern) based on vegetative and reproductive features from herbarium specimens (Furlow 1974).

Geographic variation in growth rates, sensitivity to frost, and other characteristics has been reported (DeBell and Wilson 1978, Lester and DeBell 1989, Ager and Stettler 1994). In one study, provenances from areas with cold winters (i.e., Alaska, Idaho, high elevations in Washington and Oregon) had the poorest growth but the

greatest resistance to frost damage. Specific gravity did not differ significantly among provenances, nor was it correlated with growth rate (Harrington and DeBell 1980). In another study that compared families from coastal sources, it was possible to identify families with high growth rates and low sensitivity to spring frosts (Peeler and DeBell 1987, DeBell et al. 1990); work on laboratory techniques to predict frost tolerance of alder families is ongoing (Johnson and Herman 1995). A 24-family progeny trial in western Washington also demonstrated family variation in height-growth response to water-table depth (Hook et al. 1987).

Phenotypic variation between trees is also high. Differences in form and in characteristics of branch, bark, and wood were assessed for eight stands in western Washington; only bark thickness, a branch diameter index, branch angle, and a crown-width index differed significantly among stands (DeBell and Wilson 1978). Variation among trees in seed production has also been reported (see discussion below).

A cut-leaf variety (*Alnus rubra* var. *pinnatisecta*) (fig. 1) was first reported near Portland, OR (Starker 1939); the cut-leaf variety has since been found in several other isolated areas in British Columbia, Washington, and Oregon. A single recessive gene causes the cut-leaf characteristic (Wilson and Stettler 1981); thus, this variety can be used as a marker in genetic breeding studies (Stettler 1978).

As forest managers plant red alder on increasing acreage, the need will increase for additional information on genetic variation in the species. Preliminary recommendations are available on seed zones for red alder (Hibbs and Ager 1989, Ager et al. 1994) and the major tree improvement options and long-term breeding prospects for the species have been discussed (Ager and Stettler 1994). Information, however, is lacking on the variation within the species in its tolerance of low nutrient or low soil moisture conditions and on the possible interactions among silvicultural practices, genotype, and wood quality characteristics.

Habitat

Native Range

Red alder occurs most commonly as a lowland species along the northern Pacific coast. Its range extends from southern California (lat. 34° N) to southeastern Alaska (60° N). Red alder is generally found within 200 km of the ocean and at elevations below 750 m. Tree development is best at elevations below 450 m in northern Oregon, Washington, and British Columbia. In Alaska, red alder generally occurs close to sea level. Farther south, scattered trees are found as high as 1100 m, but most stands are at much lower elevations. Red alder seldom grows east of the

Cascade Range in Oregon and Washington or the Sierra Nevada Mountains in California, although several isolated populations exist in northern Idaho (Johnson 1968a, 1968b).

Climate

Red alder grows in climates varying from humid to superhumid. Annual precipitation ranges from 400 to 5600 mm, most of it as rain in winter. Summers generally are warm and dry in the southern part of the range and cooler and wetter in the northern portion. Temperature extremes range from -30°C in Alaska and Idaho to 46°C in California. Low winter temperatures and lack of precipitation during the growing season appear to be the main limits to the range of red alder. For good development of trees, either annual precipitation should exceed 630 mm or tree roots should have access to ground water.

Soils and Topography

Red alder is found on a wide range of soils, from well-drained gravels or sands to poorly drained clays or organic soils. In Washington and Oregon it grows primarily on soils of the orders Inceptisols and Entisols but is also found on some Andisols, Alfisols, Ultisols, Spodosols, and Histosols (Harrington and Courtin 1994). In British Columbia, alder occurs on Brunisols, Gleysols, Organics, Podzols, and Regosols (Harrington and Courtin 1994). Best stands are found on deep alluvial soils in river and stream flood plains; however, some excellent stands are also found on upland sites on residual or colluvial soils derived from volcanic materials.

Soil moisture during the growing season appears to influence where the species grows. Alder can tolerate poor drainage conditions and some flooding during the growing season; consequently, it is common on soils where drainage is restricted—along stream bottoms or in swamps or marshes. It is not commonly found on droughty soils, however; and in areas of low precipitation, it seldom grows on steep south- or southwest-facing slopes. In Idaho and California, stands are usually limited to borders of streams or lakes.

Associated Forest Cover

Red alder grows in both pure- and mixed-species stands. Pure stands are typically confined to stream bottoms and lower slopes. Red alder is, however, much more widely distributed as a component of mixed stands. It is a major component of the Red Alder cover type (Society of American Foresters Type 221) and occurs as a minor component in most of the other North Pacific cover types (Eyre 1980).

Common tree associates are Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), grand fir (*Abies grandis*), Sitka

spruce (*Picea sitchensis*), black cottonwood (*Populus trichocarpa*), bigleaf maple (*Acer macrophyllum*), and willow (*Salix* spp.). Occasional tree associates include cascara buckthorn (*Fangula purshiana*), Pacific dogwood (*Cornus nuttallii*), Oregon ash (*Fraxinus latifolia*), bitter cherry (*Prunus emarginata*), and Pacific silver fir (*Abies amabilis*). Western paper birch (*Betula papyrifera* var. *commutata*) is an occasional associate in the northern and eastern portions of the range of alder, and redwood (*Sequoia sempervirens*) in the southern portion.

In the western hemlock and Sitka spruce zones, alder is most vigorous in plant associations dominated in the understory by western swordfern (*Polystichum munitum*) or redwood sorrel (*Oxalis oregana*) (Henderson et al. 1989). Common associations in British Columbia are: alder-salmonberry (floodplain), alder-swordfern (more upland) and alder-sedge (*Carex*). Common species in these plant associations include salmonberry (*Rubus spectabilis*), red elderberry (*Sambucus racemosa*), thimbleberry (*Rubus parviflorus*), red-osier dogwood (*Cornus stolonifera*), false lily-of-the-valley (*Maianthemum dilatatum*), oval-leaf huckleberry (*Vaccinium ovalifolium*) (especially on decaying woody debris), youth-on-age (*Tolmiea menziesii*), Siberian miner's lettuce (*Claytonia sibirica*), lady fern (*Athyrium filix-femina*), foamflower (*Tiarella trifoliata*), devil's club (*Oplopanax horridum*), and coastal leafy moss (*Plagiomnium insigne*) (D. Peter, P. Courtin, pers. comm. 2005). Salal (*Gaultheria shallon*), especially on raised surfaces, logs or stumps, is common in these plant zones, but increasing amounts on mineral soil indicate progressively drier and poorer sites for red alder. Increasing amounts of devil's club, skunk cabbage (*Lysichiton americanum*), and sedge indicate progressively wetter sites with greater potential for windthrow and ultimately poorer growth. Windthrow is not common in alder stands but can occur on poorly drained sites or where the root system has been undercut.

At higher elevations red alder is restricted by snow breakage. Increasing snow breakage potential is indicated by an increase in the occurrence of silver fir throughout much of the range of red alder with the notable exception of coastal rainforests in Washington and southern British Columbia. To the south, red alder is increasingly restricted to the Sitka spruce, redwood, and the wettest portions of the western hemlock zones, and especially to riparian areas. In these areas salmonberry is considered an especially good indicator of potential alder habitat (Atzet et al. 1996).

As is true in many plant communities worldwide, alder communities often contain non-native plants. This is particularly true in riparian areas as they are more open (many non-native plants that become problems are intolerant of shade) and water may serve as a transport path for seeds and other plant propagules. In addition, riparian areas are often disturbed by flooding, animals accessing water, and



Figure 1—(above) A cut-leaf alder growing in Capitol State Forest near Olympia, WA.

Figure 2—(below) Understory vegetation in alder stands can vary substantially. Shown are: A) swordfern understory with a red huckleberry just leafing out visible on a stump in the background; B) understory dominated by lady fern and devil's club on a fairly wet site; c) red elderberry and swordfern; and D) salmonberry in flower and indian plum on a riparian site.



in some areas by people recreating, so conditions may be favorable for non-native plant establishment. Japanese and giant knotweed (*Fallopia* (syn. *Polygonum*)) (fig. 3) and old man's beard (*Clematis vitalba*) are examples of three non-native species that can be very invasive in riparian areas. Disturbed or harvested alder sites are also favorable for rapid spread of nitrogen-loving species such as thistles (*Cirsium* spp.), grasses including bentgrass (*Agrostis* spp.) and velvet grass (*Holcus lanatus*), and groundsels (*Senecio* spp.). Other exotic plants that are common and vigorous on disturbed sites include cat's ear (*Hypochaeris radicata*), foxglove (*Digitalis purpurea*), evergreen blackberry (*Rubus laciniatus*) and Himalayan blackberry (*Rubus discolor*). Many exotic species are shade-intolerant and decline as the tree canopy closes, but particularly in riparian areas where flood disturbance may be chronic and the canopy more open, exotics such as the knotweeds may remain vigorous.

Alder is host to many epiphytes, especially lichens. Alder bark is brown, reddish brown, or greyish brown with white lenticels visible on the twigs; however, the bark often appears to be white or very light gray and patchy in color due to the presence of crustose lichens that can completely cover the bark and mask the underlying color (fig. 4). Common genera of crustose lichens on alder bark that give it a white or grey appearance are: *Arthothelium*, *Graphis*, *Lecanora*, *Lecidea*, *Ochrolechia*, *Rinodina*, and *Thelotrema* (T. Goward, F. Rhoades, pers. comm. 2005). Many other lichen genera are also present on alder trunks and branches; common species include: *Parmelia sulcata*,

Menegazzia terebrata, *Ramalina farinacea*, *Usnea wirthii*, *Hypotrachyna sinuosa*, *Evernia prunastri*, *Hypogymnia enteromorpha*, *Peltigera collina*, and *Usnea cornuta* (these were the 9 most common species out of 160 species of mostly foliose and fruticose species found on alder in western Washington, western Oregon, and northern California, L. Geiser and A. Ingersoll, pers. comm. 2005). Many lichen species are sensitive to air quality (Nash 1996, Stolte et al. 1993) and the bark of alder growing near pulp mills, coal-fired power plants or even in urban areas can be strikingly different in appearance from the bark of alders growing in areas of higher air quality (fig. 4).

Other Associates

General associations or interactions between red alder and wildlife species have been discussed previously (McComb 1994) and were discussed at this conference (McComb 2005). Interactions between red alder and animals, insects, and fungi that can result in tree damage are discussed later in this chapter.

Forest Succession

Red alder is a pioneer species favored by high light levels and exposed mineral soil. Its ability to fix atmospheric nitrogen permits establishment on geologically young or disturbed sites with low levels of soil nitrogen. It can form pure stands on alluvium, avalanche paths, and other disturbed sites. Harvesting and burning have favored alder; pollen records indicate that alder stands are more extensive in the twentieth century than they were for several centuries before that time (Heusser 1964, Davis 1973). Red alder pollen, however, was also abundant between 9000 and 4800 B.C.; the mix of species present in the pollen record for that time has been interpreted as indicating a somewhat warmer climate accompanied by an increase in fire frequency (Cwynar 1987).

Observations of mature forests in the Pacific Northwest suggest that alder stands are ultimately replaced by longer-lived, more tolerant conifers that have more sustained growth rates at older ages than does alder. This is undoubtedly true in most cases (see discussion below for exceptions), but the time required for this to occur in unmanaged forests is not well documented. Rapid growth and high stem densities of alder in younger stands make it difficult for conifers (especially shade-intolerant species) to regenerate and grow if they do not become established at the same time or shortly before alder invades a disturbed area. Douglas-fir can be easily eliminated in dense young alder stands while more tolerant species (western hemlock, western redcedar, and Sitka spruce) can survive and over time grow into the alder canopy and ultimately dominate the site.

Many alder stands in western Oregon have few associated conifers, leading some researchers to conclude

that those alder stands will be replaced by shrubs and that without disturbance a shrub-dominated community may persist for an extended period of time (Newton et al. 1968, Carlton 1988, Tappeiner et al. 1991, O'Dea 1992). Clonal shrubs, particularly salmonberry, but also thimbleberry and vine maple, often form a dense shrub canopy which makes it difficult for conifers to invade and become established from seed. These shrub species can expand rapidly by vegetative reproduction as space becomes available due to death of the alder overstory (Tappeiner et al. 1991, O'Dea 1992, Zasada et al. 1992).

Experience suggests that alder replacement by conifers will have a high degree of spatial and temporal variation if the process is left to proceed naturally. The density of alder stems and the presence and abundance of shade-tolerant tree species are obviously important in influencing which successional trajectory will be followed; however, the specific ecological factors that determine the successional sequence in alder stands are not known. This topic is discussed in more detail in Deal (2006).

Life History

Reproduction and Early Growth

Flowering and fruiting. Red alder reaches sexual maturity at age 3 to 4 years for individual trees and at age 6 to 8 for most dominant trees in a stand (Stettler 1978). The species is generally monoecious, with separate male and female catkins developing on the previous year's twigs (Hitchcock et al. 1964). Staminate catkins, which occur in pendulous groups and are usually in a terminal position on a short shoot, elongate in late winter, changing from green to reddish brown and from 2 to 3 cm long to about 7 or 8 cm. Pollen grains are small (20 to 23 μm in diameter, Owens and Simpson, N.d.), lightweight, and produced in abundance. Several pistillate catkins are borne per floral bud and are commonly located on a bud proximal to the staminate catkins. They are 5 to 8 mm long and reddish green when receptive. Both male and female catkins usually occur in groups of three to six; variation in the ratio of male to female catkins in terms of numbers and weights has been described for three elevational transects (Brown 1986). Flowering occurs in late winter or early spring; peak shedding of pollen generally precedes peak receptivity by a few days but synchrony in pollen shed and receptivity have been observed in some trees (Brown 1985). Pistillate catkins are upright at the time of flowering but become pendulous as they mature. Most alder seed is probably the result of outcrossing, but some self-pollination occurs (Stettler 1978).

Limited information is available on the effects of cultural practices on flowering of red alder. In an experimental plantation on a well-drained site near Olympia, Washington, both male and female flower production were decreased by irrigation during the growing season

(Harrington and DeBell 1994); this is consistent with observations for other species that moisture stress increases flowering (Owens 1991). Within an irrigation regime, flower production was generally concentrated on the larger trees; thus, the percentage of trees flowering was greatest at the widest spacing, and within each spacing, the percentage of trees flowering increased as tree size increased.

Seed production and dispersal. Seeds are small, winged nutlets borne in pairs on the bracts of woody, cone-like strobili (Schopmeyer 1974). The seeds are without endosperm and contain only small cotyledons (Brown 1986). The strobili are 11 to 32 mm long and 8 to 15 mm wide.

Red alder is believed to be a prolific and consistent producer of seed; however, there are no long-term records of red alder seed production. Seed production in red alder varies substantially among trees; Brown (1985) reported production rates for 45 mature trees of similar size from 0 to 5.4 million seeds per tree. She reported within-stand variation to be much greater than variation among stands. Based on a two-year study of seedfall on two sites in British Columbia, McGee (1988) reported substantial variation between sites and years. Maximum total production was 1550 seeds/m²; in the more productive year, production was four to seven times greater than in the less productive year. In the more productive year, one site produced 1.8 times more seed than the other, while in the less productive year seedfall was similar at both sites. Seed-crop quality (percent viable seeds) was similar between sites with 40 to 50 percent of the seeds viable in the good year and less than 10 percent in the poorer year. Worthington (1957) concluded that moderate seed crops are produced almost annually and bumper crops occur every three to five years; however, no specific studies were cited. Complete failure of a seed crop is rare, but after a severe freeze in 1955, almost no seed was produced in 1956 (Worthington 1957). Additional information on variation in red alder seed production is available (Ager et al. 1994). Information on seed production in other members of the Betulaceae (*Alnus* and *Betula*) is summarized in Harrington et al. 1994.

The annual pattern of red alder seed dispersal and how it varies over its range is not well documented. In general it is believed to begin in the middle of September in the center of its range and slightly earlier or later to the north and south respectively. McGee (1988), working in British Columbia, found that small amounts of seed were dispersed in September, but that the major dispersal events occurred from November to February. Lewis (1985) reported that major seedfall of red alder in Washington occurred during winter and spring, but that some seedfall was observed throughout the year. Major dispersal events occurred in consecutive months as well as in months separated by several months of low dispersal, a pattern similar to that in other members of the *Betulaceae* (McGee 1988, Zasada et al. 1991).

The nature of the catkin suggests that the timing of seed dispersal is regulated by factors similar to those regulating the release of seeds from the cones of conifers; that is, once catkins are mature, dispersal is determined by the occurrence of weather which dries them, thus opening the scales and allowing the seeds to be released. In general, wet weather keeps catkins closed and wet weather following dry weather closes catkins, thus terminating a dispersal event. Nonetheless, heavy seedfall can occur during wet weather under certain catkin conditions (Lewis 1985) and dispersal will not occur if ice freezes the seed in the catkin (Lewis 1985, Brown 1986). The dispersal patterns reported for red alder (Lewis 1985, McGee 1988) are consistent with the hypothesized mechanisms, but more frequent observations of seed dispersal in relation to weather and catkin condition need to be made. In coastal Alaska, drying trends brought by high-pressure weather systems are important to seed dispersal of Sitka spruce and western hemlock (Harris 1969), two common associates of alder. In addition, generally similar patterns of seed dispersal have been observed for alder and hemlock growing in the same stand in western British Columbia (McGee 1988).

Red alder seeds are very light, numbering 800 to 3000/g, and wind dissemination is effective over long distances. Lewis (1985) documented dispersal of red alder seeds for a two-year period and found amount of seed, seed weight, percentage of filled seed, and viability all to be inversely correlated with distance from the seed source. Amount of seedfall 100 m from the edge of an alder stand was 2 to 3 percent of the seedfall density inside the stand.

Although seeds are dispersed primarily by wind, some dispersal may occur by water (Brown 1986) and by birds or other animals. Birds are commonly seen around catkins, and alder seeds have been shown to be an important source of food for some species (White and West 1977). Birds play both passive and active roles in seed dispersal. Passive dispersal occurs simply by movement of the catkins as birds work in the crown of alders; active dispersal occurs as birds extract seeds from the catkins while feeding.

Germination, seedling survival and development. In normal germination of red alder seed, the radicle or root elongates first, followed by hypocotyl growth (hypogeal germination); this means that the root emerges first from the seed coat (fig. 5). When seed has been stored for an extended period of time, this process can be reversed and hypocotyl elongation occurs first, the cotyledons emerge from the seed coat and then root elongation begins (epigeal germination) (pers. obs., J. Kraft).

Seed germination in clearcut environments in the central Oregon Coast Range began in late February and early March and was completed by mid-April (Haeussler 1988, Haeussler and Tappeiner 1993). Differences between north and south aspects were small compared to the forested environments where the onset of germination was delayed,



Figure 4—(above) The lichen community on alder bark can result in very different appearances from smooth brown bark to brown bark with shaggy spots to white or light gray bark. Many lichen species are sensitive to air pollution; the tree on the left with almost no lichens on its bark was growing in the vicinity of a coal-fired power plant near Centralia, WA.

Figure 5—(right) Alder seed germination is rapid and hypogeal; the radicle develops root hairs almost immediately. Photo by J. Kraft, PNW.



Figure 3—(below) Exotic species can be a particular problem in riparian areas where light levels are high and disturbance from flooding or animal access occurs. This view shows Japanese knotweed (yellow-brown foliage) overgrowing Himalayan blackberry (shrub with dark green foliage) in a black cottonwood and red alder stand on the Snoqualmie River in western Washington. Photo by S. Reutebuch, PNW.



relative to that in clearcuts, for a month and continued into June. On average, the number of germinants emerging was higher on disturbed than on undisturbed seedbeds. There was no clear difference in germinant appearance between forested and clearcut environments for either seed-bed type. A positive relationship between spring soil moisture conditions and germinant appearance was stronger in the clearcut environment than in the modified light and temperatures prevailing under forested conditions (Haeussler 1988).

Seedling establishment. The number of seeds required to produce a seedling one growing-season old differed dramatically between westside and eastside Coast Range environments (Haeussler and Tappeiner 1993). Under the drier conditions on the eastside of the Coast Range, no seedlings survived through the growing season in either of the years of study. On the north aspect of the westside coast site, 1 seedling was produced per 32 seeds sown; on an adjacent south aspect, 1 seedling was produced per 181 seeds (Haeussler 1988). In another study on a southwest-facing coastal site, sowings in each of two years on newly created mineral soil seedbeds at a rate of 1000 to 1500 seeds/m² failed to produce any surviving seedlings at the end of one growing season (J. Zasada, pers. comm. 1994). In a third study, sowing of alder seed on dry Coast Range sites similar to those studied by Haeussler (1988) resulted in germinants but no surviving seedlings after one growing season (J. Tappeiner and J. Zasada, pers. comm. 1994). These three studies suggest that alder establishment is not assured even when large quantities of seeds are sown on what are believed to be desirable seedbeds.

A number of environmental factors result in high mortality of seeds and seedlings between the time seeds arrive on the seedbeds and the end of the first growing season (Haeussler 1988), and these certainly contribute to the temporal and spatial variation in alder regeneration. In unprotected microsites, seedling emergence was 75 percent on disturbed seedbeds and 38 percent on undisturbed seedbeds on protected microsites. Loss of seeds to soil biota was greater under forest conditions than in clearcuts. On undisturbed and mineral soil microsites, 60 and 20 percent of the seed population were destroyed by soil organisms, respectively. Causes of seedling mortality included drought and heat injury, pathogens, animals, erosion, frost and smothering by organic debris. Drought and heat-related mortality were the major causes of mortality in clearcuts, whereas damping-off fungi and other pathogens were most important under forest conditions (Haeussler 1988).

Alder seeds are most commonly described as having little or no dormancy. This is based on studies which have shown that germination of stored seeds under optimum germination temperatures is not improved by stratification (Radwan and DeBell 1981, Berry and Torrey 1985); however, one provenance from British Columbia

was reported as having a physiological dormancy that was released by stratification (Elliott and Taylor 1981a). Germination under sub-optimum temperatures, such as may prevail at the time of germination under field conditions, is enhanced by stratification (Tanaka et al. 1991). Based on germination of lots stored for several years, the need for stratification is not affected by storage but seed viability will decline over time.

Bormann (1983) and Haeussler (1988) demonstrated that alder seeds do not germinate in the dark and that the phytochrome system is very sensitive (i.e., germination is inhibited by exposure to far-red light). A field study by Haeussler (1988) strongly suggests that alder germination is controlled by light quality and that a type of light-enforced dormancy may prevent seeds from germinating when other conditions appear optimal; thus, a persistent alder seedbank may be present under some conditions. A buried seedbank is probably not important in alder because of the high seed mortality rate caused by soil organisms (Haeussler 1988); however, it can't be ruled out without study since seeds of some species of *Betula* remain viable in the soil for much longer than would be expected based on seedcoat structure and general seed germination characteristics (Granstrom 1982, Perala and Alm 1989).

Assuming that site conditions are suitable, red alder can initially be regenerated by any silvicultural system that provides moderate sunlight and exposed mineral soil. The species is an aggressive pioneer on avalanche paths, road cuts, log landings, skid trails, or other areas where mineral soil has been freshly exposed to seedfall. For example, shortly after a heavy thinning (removal of 50 percent of the basal area) in a 62-year-old Douglas-fir stand, an alder understory became established and grew rapidly (Berg and Doerksen 1975). Clearcutting and large-group selection are feasible regeneration systems. During harvesting or in a subsequent site preparation treatment, the site must be disturbed sufficiently to expose mineral soil. Fire probably can substitute for mechanical disturbance on most sites. To exclude red alder from the next rotation stand, some forest managers try to reduce the supply of alder seed by cutting possible alder seed trees in the vicinity before or at the time of final harvest; to avoid creating favorable seedbed conditions, they also disturb the site as little as possible during logging and, if feasible, do not burn the logging slash (Lousier and Bancroft 1990).

Artificial regeneration can be accomplished with either bare-root or containerized seedlings, and guidelines for producing planting stock are available (Berry and Torrey 1985, Radwan et al. 1992, Ahrens 1994). Survival and growth of planted seedlings are usually excellent (Radwan et al. 1992), but can vary significantly with slope, slope position, and aspect within a given clearcut. For example, Zasada (pers. comm. 1994) followed the fates of seedlings planted on different sites within a clearcut and observed nearly 100 percent survival on steep north aspects over a

three-year period while immediately adjacent south-facing and stream bottom sites (with higher soil moisture stress and a higher probability of early season frosts, respectively) suffered as much as 60 percent mortality.

Height growth of red alder seedlings is generally rapid. On favorable sites, seedlings can grow 1 m or more the first year, and on all but the poorest sites, seedlings surpass breast height (1.3 m) the second year (Smith 1968, Harrington and Curtis 1986). Maximum annual height growth of more than 3 m a year can be achieved by 2- to 5-year-old seedlings (Harrington and Curtis 1986).

Seasonal growth of red alder is under strong climatic control and consequently quite variable. The timing of radial growth is similar for red alder and its common associate Douglas-fir; in the Puget Sound area of Washington State, growth begins about mid-April and continues until mid-September (Reukema 1965). Substantial height growth (i.e., height growth other than that associated with initial bud break) begins slightly later in the season than radial growth. Red alder has indeterminate height growth; thus, height growth continues through the growing season until soil moisture, temperature, or light conditions become unfavorable (see DeBell and Giordano 1994). The specific environmental conditions that control root and shoot growth have not been determined.

Vegetative reproduction. Red alder sprouts vigorously from the stump when young. It can be repeatedly coppiced on short cycles but rootstock mortality increases with each harvest (Harrington and DeBell 1984). The likelihood of obtaining stump sprouts and the vigor of the sprouts are influenced by age, time of year, and cutting height (Harrington 1984a). Stumps sprout best when trees are cut in the winter and when stump height exceeds 10 cm. Older trees rarely sprout and coppice regeneration cannot be expected after pole-size or sawlog-size material is harvested (Harrington 1984a). Because of reduced vigor of sprouting, manual cutting of alder as a means of competition control in conifer plantations can be an effective vegetation management practice (DeBell and Turpin 1989); however, results from cuts at different times during the summer can be variable (Pendl and D'Anjou 1990).

Other vegetative methods of propagation that have been successfully used include: rooting greenwood cuttings from young trees (Monaco et al. 1980); rooting of cuttings of succulent new spring growth from shoots of young trees and epicormic sprouts from 30-year-old trees (Radwan et al. 1989), and rooting of sprouts propagated by mound layering (Wilson and Jewett, unpub. data, see Harrington et al. 1994 for a more complete description.).

Sapling and Pole Stages to Maturity

Growth and yield. Alder growth form is strongly excurrent during the period of rapid height growth. Crown

form becomes moderately to strongly deliquescent as the trees mature. Growth of vegetative shoots is primarily monopodial (e.g., branching with the apical bud forming a persistent leader and new branches arising laterally below the apex, Swartz 1971); however, shoots producing flowers exhibit sympodial growth (e.g., the terminal bud withers and the main axis of branching is made up of a series of lateral branches, Swartz 1971).

Alder produces three types of branches: sylleptic (developed from a bud formed during the current year), proleptic (developed from a bud formed the previous year), and epicormic (developed from suppressed buds). Sylleptic branches are important in rapid development of leaf area but are short lived. Proleptic branches are persistent and form primarily from buds at the upper end of the height increment for the year; thus, the pattern of proleptic branches on the main stem can often serve as a rough method of determining past height increment. Epicormic branches are produced when suppressed buds are triggered to develop by injury or a change in plant environment. They are commonly seen after top breakage, a major increase in exposure (e.g., road construction, logging), or in response to injury (e.g., flooding, girdling). The physiological factors that determine the amount of apical control on branch growth and angle have not been studied for alder.

Growth of primary shoots of alder can be phototropic (i.e., differential elongation of cells resulting in growth toward light; Zimmerman and Brown 1971). Alder trees can exhibit substantial amounts of lean when grown in irregularly spaced stands or when located along roads, streams, stand boundaries, or other areas with unequal light distribution on all sides of the tree; the lean is probably caused primarily by greater crown development on the sunnier sides of the tree rather than by phototropism per se (DeBell and Giordano 1994). Other changes in stem form may occur as the result of heavy snow or if gravity causes all or part of the tree to shift abruptly (e.g., as a result of soil slumping or high winds when soils are saturated). If juvenile red alder is grown at wide and fairly even spacing, however, lean and sweep will be minimized (Bormann 1985, DeBell and Giordano 1994).

Red alder has rapid juvenile growth. Among its associates, only black cottonwood grows as much or more during the juvenile phase. On good sites, alder trees may be 9 m at age 5, 16 m at age 10, and 24 m at age 20. One tree was 9.8 m tall and 16.3 cm in dbh 5 years from seed (Smith 1968).

Growth slows after the juvenile stage, the decrease beginning much sooner on poor sites. Site index, as determined at base-age 20 years, ranges from 10 to 25 m (Harrington and Curtis 1986); at base age 50, it ranges from 18 to 37 m (Worthington et al. 1960). Associated conifers have much slower juvenile growth, but they sustain height growth years longer than alder. On an average upland site,

both Douglas-fir and red alder can attain the same height at about age 45 (Williamson 1968). Beyond that age, Douglas-fir surpasses red alder in height. Because the two species have different site tolerances, their relative performances will be site-specific as well as age-specific (Deal 2005, Harrington and Courtin 1994).

Red alder is a relatively short-lived species, maturing at about 60 to 70 years; maximum age is usually about 100 years (Worthington et al. 1962). On favorable sites, trees can be 30 to 40 m tall and 55 to 75 cm in diameter. The American Forests Big Trees national champion red alder in Oregon measured 198 cm in dbh (www.odf.state.or.us; last updated Aug.25, 2004) and the largest red alder in Washington measured 158 cm in diameter (Van Pelt 1996), but trees over 90 cm in diameter are rare. In pure stands on good sites, it has been estimated that red alder can achieve mean annual cubic volume growth rates of 21 m³/ha in pulpwood rotations of 10 to 12 years, and 14 m³/ha in sawlog rotations of 30 to 32 years (DeBell et al. 1978). Most of the existing alder volume is in naturally regenerated mixed-species stands where growth and yield are variable. Several reports have indicated that maximum cubic volume in alder stands is about 500 m³/ha at age 50 to 70 (DeBell et al. 1978, Worthington et al. 1960, Chambers 1983); however, volumes of 700 m³/ha and even 1000 m³/ha have been measured on small inventory plots in fully stocked natural stands 70 years or older in the Queen Charlotte Islands or islands in the Johnston Straits (N. Hughes, pers. comm. 2005). These extremely high volumes are very unusual and may not be possible on larger areas.

Rooting habit. Red alder forms extensive, fibrous root systems. Root system distribution is primarily controlled by soil drainage, soil structure, and compaction. In poorly drained soils, most rooting is surface-oriented, and rooting is often prolific in the boundary between the lower organic layer and the uppermost mineral horizon. In wet soils, the uppermost mineral horizon usually is rooted heavily, as is the lower part of the surface organic layer if it is thick enough. On well-drained sites, root distribution is strongly influenced by water availability; increased rooting is common at horizon boundaries where changes in soil texture slow downward water movement through the profile. Because rooting also follows the path of least resistance, it is greater in old root channels or, especially if the soil is compacted and soil structure well developed, between units of soil structure. Root system extent is a function of soil characteristics and tree size. Smith (1964) showed tree diameter and average root length to be significantly correlated; larger trees also tended to have deeper roots than smaller trees.

Red alder, especially when young, forms adventitious roots when flooded. In a greenhouse study, alder seedlings previously growing under well-drained conditions produced adventitious roots when the soil was saturated (Harrington 1987). These roots emerged at or near the root collar and

grew on top of the saturated soil surface; when the soil was drained, the root exteriors suberized and many of the longer roots turned downward into the soil where they continued to grow. Minore (1968) also reported formation of adventitious roots when seedlings in pots were flooded, noting that seedlings that did not form adventitious roots did not survive. Although it has not been documented, formation of adventitious roots may be an important adaptive trait on floodplain sites.

The sensitivity of red alder root growth to environmental conditions is not well known, but recent studies provide some information (also see Shainsky et al. 1994). Under soil moisture stress, red alder saplings shifted carbon allocation from leaf and stem biomass to root biomass (Chan 1990). In a companion study, root biomass decreased with increasing density of alder stems (Shainsky et al. 1992). Ratios of root to shoot were significantly affected by stand density; however, most of the variation in root biomass was directly attributable to variation in shoot biomass. When grown in pots in a growth chamber, these ratios were decreased by fertilization and were lower in sandy soil than in loam or sandy loam (Elliott and Taylor 1981b).

Red alder roots are commonly ectomycorrhizal, although only a few species of fungi form ectomycorrhizal associations with alder. Fungal symbionts include alder-specific fungi and fungi capable of mycorrhizal associations with other hosts (Molina 1979, Molina et al. 1994).

Red alder also has root nodules that fix atmospheric nitrogen (fig. 6). The nodules are a symbiotic association between the tree and an actinomycete (*Frankia* spp.). In natural stands nodulation occurs soon after seed germination; root systems of seedlings a few months old commonly have dozens of visible nodules. Nodule sizes on young trees range from the size of a pinhead up to 25 mm in diameter. Mature trees have nodules on both the large woody roots and the smaller new roots. The large compound nodules found mature trees can be 80 or 90 mm in diameter. Rates of nitrogen fixation and the effects of these nitrogen additions on soil chemistry have been discussed by others (Binkley et al 1994, Bormann et al. 1994).

Reaction to competition. Red alder requires more light than any of its tree associates except black cottonwood and is classed as intolerant of shade (Minore 1979). Light quality has been shown to be important in germination (Bormann 1983, Haeussler 1988); however, its role in seedling development has not been documented. Young seedlings can withstand partial shade for a few years but will grow very little; if not released, they will die. The only trees that survive are those that maintain dominant or codominant crown positions. Self-thinning or mortality caused by competition is rapid in red alder stands; densities in natural stands may be as high as 124,000 seedlings/ha at age 5 (DeBell 1972) and fully stocked stands at age 20 averaged 1665 trees/ha (Worthington et al. 1960).

Red alder also self-prunes extremely well when grown in dense stands. Shaded lower branches rapidly die and fall off, resulting in clear and slightly tapered boles. Live crown ratios in crowded, pure stands are very low, and narrow, domelike crowns are characteristic. As would be expected for a shade-intolerant species, branch retention and crown shape are strongly related to light levels in the canopy. Trees grown at low densities develop large lower branches (c.f., fig. 7) that live longer and take much longer to decay after death than do branches that develop under higher stand densities.

Early control of spacing is necessary to keep live crown ratios high enough to maintain good growth beyond the juvenile phase. Sawlog yields might be maximized on short rotations by combining early spacing control with pulpwood thinnings (DeBell et al. 1978). Thinnings in previously unthinned stands are most effective in stimulating growth of residual trees if done before height growth slows—about age 15 to 20 (Warrack 1949, Olson et al. 1967, Smith 1978). Thinning in older stands can salvage mortality and help maintain the vigor of residual trees, but usually does not accelerate diameter growth (Lloyd 1955, Warrack 1964).

Epicormic branching has been reported after thinning, especially when thinning has been late or drastic (Warrack 1964, Smith 1978). If epicormic sprouting occurs after thinning, it is most common on the south or west side of stressed trees; however, trees drastically opened up (e.g., via clearcutting or construction activities) may have epicormic branches on any or all sides. Epicormic branches appearing after early thinning may be ephemeral, but this has not been documented and is likely to be dependent on stand density. Epicormic branches were reported after pruning 21-year-old trees (Berntsen 1961), but those trees were heavily thinned and overstory conifers had been girdled at the same time as pruning (H. Rapraeger, 1949 report on thinning and pruning alder at Cascade Head Experimental Forest, on file at Olympia Forestry Sciences Laboratory) so it was not possible to separate the effects of pruning on epicormic branches from those of the other cultural practices. Very few epicormic branches developed after pruning of young trees (Brodie and Harrington 2006).

Red alder can be managed in pure stands or as part of a mixture with other intolerant species, such as Douglas-fir and black cottonwood (or *Populus* hybrids), or with more shade-tolerant species, such as western redcedar, western hemlock, or Sitka spruce. Knowledge of site-specific growth rates and relative shade tolerances of each component in a mixture is critical to achieving the potential benefits from mixed stands. Alder must be kept in the upper canopy to survive in mixed stands. Even if alder is shaded out in a mixed stand, however, it may make substantial contributions to soil nitrogen prior to that time (Berg and Doerksen 1975, Tarrant and Miller 1963). The benefit of alder to the other species is dependent on site

conditions as well as the relative density of the tree species (Courtin and Brown 2001, Deal et al. 2004, Miller 2005, Miller and Murray 1978, Miller et al. 1993, Miller et al. 1999). The proportion of alder and Douglas-fir in mixed plantations has been shown to influence the stem quality of both species (Grotta et al. 2004). In addition, the richness of shrubs, ferns, herbs, and mosses in mixed-species stands is increased over that found in conifer stands (Deal 1997).

Reaction of alder to competition is influenced by many factors including the size, species composition, and density of the competing vegetation (other alder stems, non-alder stems in the upper canopy, and plants in the understory) as well as soil and site factors. For example, growth of closely spaced, dominant alder was decreased with increasing density of subordinate Douglas-fir (Shainsky and Radosevich 1991, Shainsky et al. 1994). Rectangularity of spacing also influences growth and development of alder (DeBell and Harrington 2002).

Damaging Agents

There are relatively few instances where damaging agents kill enough red alder trees to result in large openings in a natural stand. Frost pockets or unseasonable heavy frosts may be an exception. Forest managers may also be concerned, however, at lower levels of mortality, when growth rates are depressed, or tree form or wood quality is affected. In addition, problems will likely increase as management is intensified, particularly in nurseries and plantations.

Leaf and Stem Fungi. Red alder is fairly free from most disease problems, especially when young and uninjured (Worthington et al. 1962, Hepting 1971). Many species of fungi have been reported growing in association with alder (Lowe 1969, Shaw 1973, Farr et al. 1989), but few have been shown to cause ecologically or economically important levels of damage in natural stands. *Nectria distissima* can be a serious bark canker in young stands (Fig. 8) and *Cytospora* spp. can develop following sunscald or winter damage (W. Littke, pers. comm. 2005). Several other canker-causing stem diseases—*Didymosphaeria oregonensis*, *Hymenochaete agglutinans* and *Botrytis cinerea*—cause some damage but overall their impact is slight. Nonetheless, the potential exists for more damaging levels of disease should conditions occur that favor their rapid development and spread. For example, naturally occurring weak pathogens have been used as biocontrol agents for juvenile red alder (i.e., to kill unwanted alder) (Dorworth 1995), thus, indicating their ability to cause mortality under certain conditions.

The primary disease of concern in nursery production is *Septoria alnifolia*, a disease that causes leaf spots and stem cankers (some experts believe that *Septoria alnifolia* only causes a leaf spot and another species or another stage of the same species with a separate name is responsible for the

canker). Although some infected seedlings grow over stem cankers caused by *S. alnifolia* (see note above), on other seedlings the cankers result in top dieback, stem breakage, reduced growth, or mortality. Thus, infected nursery stock should be graded out as cull (i.e., discarded). This disease can be controlled with monthly applications of Benlate® (a fungicide) and by locating alder nursery beds in areas not adjacent to alder stands (W. Littke, pers. com. 1992).

Fungi diseases of alder catkins (*Taphrina occidentalis* and *T. alni*) cause enlargements of the bracts of female catkins (Mix 1949), which prevent or hinder normal fertilization and seed development. Although currently these fungi are not important economically, they could become so if alder seed orchards or seed production areas were established.

Compared with other hardwood species, living red alder trees have very little decay. In a study on Vancouver Island, Allen (1993a) examined 383 alder trees ranging from 20 to 120 years old. Decay losses of merchantable volume were less than 4 percent in all trees sampled. The incidence of decay (number of decay columns per tree) was not correlated with age in the Vancouver Island study and thus, susceptibility to decay in older trees does not appear to be as severe as suggested in previous reports (Johnson et al. 1926, Worthington 1957).

Much of the decay present in living alder results from injury to standing trees due to broken tops and branches, or scars from falling trees (Allen 1993a). Once trees are injured, decay organisms gain entry through the damaged tissue. Alder, however, is very efficient in its ability to compartmentalize decay, and most decay events do not spread much beyond the injured tissue. For example, the dead tissue of stubs formed from self-pruned branches was colonized by fungi and sometimes developed into a decay column in the main stem. Most branch stubs, however, were overgrown by healthy wood with no further decay development (see additional information on this topic in DeBell et al. 2006). In general, individual decay columns were not large, with a median volume of 0.0024 m³.

The wood of red alder is a light, creamy-white color prior to exposure. Once trees are cut or the wood is exposed by breakage, the exposed wood develops a reddish orange or reddish brown stain. This stain is the basis for the species name (*rubra* meaning red). It is not known definitively what causes the color change but a compound, oregonin (a diarylheptanoid xyloside) was extracted from alder bark and demonstrated potential for stain development in the presence of peroxidase and hydrogen peroxide; i.e., the stain appears to be the result of oxidation but its exact mechanism is not known (Karchesy 1974). In addition, a more intense red stain can develop in response to fungal infection by *Ceratostyis picea* (a vascular wilt fungus) (Morrell 1987). Fungal spores land on freshly exposed surfaces of alder logs, germinate and grow into the wood, and the response

of the living cells is an intense red stain (Allen 1993b). The rate of stain development is influenced by season of harvest and conditions after harvest (Allen 1993b). Wood producers use several techniques to reduce the stains due to both oxidation and those due to fungal infection; in addition, new techniques are being evaluated to determine their efficacy to reduce stain development in logs and sawn wood products.

A number of decay fungi have been isolated from living alder trees in British Columbia, including *Heterobasidion annosum*, *Sistotrema brinkmannii*, *Pholiota adiposa*, *Trametes* sp., and *Meruliopsis corium*. From a log buyer's standpoint, "redheart" and "black knot" are common defects but multiple fungal species could be associated with these general terms; one species that causes red heart rot in alder is *Stereum sanguinolentum* (Omdal, pers comm. 2005). A previous report suggested that white heart rot, caused by *Phellinus* (syn. *Fomes*) *igniarius*, is the most destructive disease of living alder trees (Worthington 1957). This statement seems to have originated from Johnson et al. (1926), who made a similar claim that was unsupported by data or reference citation. *Phellinus igniarius* has been found only rarely on living alder in British Columbia, although the pathogen may be more common in other parts of the alder range. As indicated above, these decay fungi do not appear to result in serious losses in most living trees.

Wood stain and decay proceed rapidly in cut alder trees. Losses due to stain resulting from fungal infection that occurs during the time *between* harvesting and milling are much greater than losses from decay in living trees (Allen 1993a). For this reason, logs should be processed as soon as possible after harvest, particularly in warm summer months. The development of stain and decay is retarded in winter months and in logs stored in fresh water (Worthington 1957).

In the past, some foresters have suggested that red alder would have to be managed on short rotations due to increasing disease problems with age (so-called pathological rotations) or that thinning and pruning were risky due to the increased probability of inducing stem damage; based on our current information on alder's ability to compartmentalize decay, these suggestions appear unwarranted. During intermediate cuts, however, care should be taken to avoid injuring residual trees. There are good reasons for short rotations, such as the species' growth pattern with age and economics; however, sensitivity to decay does not appear to be a reason to suggest short rotations.

Root rots. The root rot pathogen *Heterobasidion annosum* has been observed growing on alder in mixed-species stands in which both alder and conifers were present (Allen 1993a). Since the fungus infects both hardwoods and softwoods, it is possible that alder could become infected when planted on sites previously occupied

by infected conifers. In addition, infected alder could serve as an inoculum source for subsequently planted conifers. Thus, preharvest surveys for root-rot fungi should be considered for sites where alder is a possible species to manage as well as on sites where conversion from alder to other species is being considered.

Red alder is subject to root rot by *Armillaria mellea* but it is not considered to be a major disease (Hepting 1971).

All hardwoods are immune to *Phellinus weirii* (a widespread conifer root rot) and red alder occurs naturally and has been planted on sites where *P. weirii* infection levels are high. The absence of susceptible species will eventually “starve-out” the fungus as suitable substrates decay and are not replaced. It has been hypothesized that red alder alters the soil environment to the detriment of *P. weirii* by enhancing the growth of microbes (e.g., *Trichoderma*) antagonistic to the pathogen (Nelson et al. 1978) and/or by inhibiting the growth of the fungus (Li et al. 1969, 1972; Hansen 1979).

Many foresters, following the suggestion that alder may serve as a biological control agent for *Phellinus weirii* (Trappe 1972, Nelson et al. 1978), have recommended planting alder as a root-rot control measure. This may have contributed to increased planting of red alder on some lands, but the interactions between red alder and *P. weirii* are not fully understood and therefore caution should be exercised in making management decisions. For example, Hansen (1979) observed vigorous and extensive development of *P. weirii* ectotrophic mycelium on infected roots of very large, old-growth Douglas-fir stumps in a 20-year-old alder stand that established following logging of the Douglas-fir. He concluded that red alder apparently “does not shorten the time required to reduce the inoculum.”

Long-term trials are underway to quantify the long-term effects of alder stands on *Phellinus weirii*. At this time all I can say is that alder should be considered as one of several immune species to plant on sites with high levels of *P. weirii*. Foresters planting red alder on sites with high levels of *P. weirii* inoculum that are considered poor or unsuitable sites for alder should expect alder growth to be poor and problems with damaging agents to increase.

Insects. Numerous insects have been reported feeding on or associated with red alder (Furniss and Carolin 1977, Gara and Jaeck 1978, Dolan 1984). Insect pests are not usually a major concern, but serious outbreaks of some defoliators can cause growth reductions. The forest tent caterpillar (*Malacosoma disstria*), western tent caterpillar (*M. californicum*), alder woolly sawfly (*Eriocampa ovata*), striped alder sawfly (*Hemichroa crocea*), the alder flea beetle (*Altica ambiens*), and a leaf beetle (*Pyrrhalta punctipennis*) have caused substantial damage, but reports of mortality are rare (Worthington et al. 1962, Furniss and Carolin 1977, Briggs et al. 1978). Mortality, however, has been observed when tent caterpillar outbreaks overlapped

drought periods (Russell 1991, K. Ripley pers. com. 2005) and the mortality from the combined stresses was probably substantially greater than would have occurred if only one stress had been present.

A flatheaded wood borer (*Agrilus burkei*) can kill twigs and branches (Furniss and Carolin 1977, Briggs et al. 1978). The alder leaf miner, *Lithocolletis alnicolella*, can cause necrotic spots up to 30 mm in diameter on leaves but does not apparently affect growth (W. Littke, pers. com. 1992). An epidemic of grasshoppers was reported to only slow growth slightly (Russell 1986). The fall webworm (*Hyphantria cunea*) skeletonizes or consumes leaf blades, but its damage is usually minor (Furniss and Carolin 1977). The alder bark beetle (*Alniphagus aspericollis*) breeds primarily in slash and in young stressed trees; however, healthy trees can be attacked when bark beetle populations are high (Gara and Jaeck 1978).

The alder aphid (*Pterocaulis alni*) feeds on tender shoots (Furniss and Carolin 1977) and on foliage with high nitrogen content (Dolan 1984). Aphids are common associates in many young alder stands and generally are not considered to cause much damage, although severe aphid epidemics have been reported in young alder plantations planted on droughty soils (Dolan 1984, DeBell pers. comm. 2005).

Ambrosia beetles (*Gnathotrichus retusus*, *Trypodendron lineatum*, *Xyleborus saxeseni*) attack logs and slash left on the ground, thus, log quality can rapidly degrade. Insect holes can also serve as entry sites for fungi. Merchantable material should be removed rapidly, and large accumulations of slash should be avoided.

Animals. In general, animals cause only minor damage in alder stands; however, under some circumstances animal damage can be significant. Alder is not a highly preferred browse species for black-tailed deer (*Odocoileus hemionus columbianus*) or Roosevelt elk (*Cervus elaphus roosevelti*) during most of the year. Young trees are occasionally browsed by deer and elk, especially during the late summer and fall (Brown 1961), and browsing begins earlier in the summer when weather conditions are dry or when other food sources are not available.

Abscising or freshly abscised leaves were documented as being a major component of deer and elk diets in old-growth forests on the Olympic Peninsula (Leslie et al. 1984) and penned black-tailed deer have been observed eating freshly abscised alder leaves in the fall when other food sources were available (D. L. Campbell, pers. com. 1992). Seasonal changes in deer and elk browsing may be related to changes in foliar chemical composition; alder foliage in the fall is higher in crude fat content and lower in total phenols than during the summer (Radwan et al. 1978). Elk repeatedly browsed red alder planted on a debris flow associated with the 1981 eruption of Mt. St. Helens

(Russell 1986) when alternative food sources were limited. Most browsed trees resprouted vigorously and very little mortality was associated with the heavy browse damage; however, the repeated browsing resulted in trees with shrub-like forms.

Deer and elk can cause stem deformation, reduce growth, and provide entry sites for decay organisms when they rub their antlers against tree trunks; in localized pockets this type of damage can be common. In a young spacing trial near Centralia, Washington, the incidence of stem rubbing was greatest in the narrowest spacings, presumably because the closer spacings had higher rates of branch mortality that resulted in easier access to the main stems. Others, however, have observed greater damage in wide spacings (Newton and Cole 1994). The relationship between spacing and damage may change with age or other factors. Deer and elk occasionally strip and eat alder bark, especially during winter and spring.

Mountain beaver (*Aplodontia rufa*) clip small alder stems and branches; only the bark is eaten from stems 5 to 20 mm in diameter while smaller pieces are consumed whole (D. L. Campbell, pers. com. 1992). Although mountain beaver only clip small-diameter pieces, they climb trees and can continue to clip branches and terminals as trees increase in size. In an artificial feeding trial in which several plant species were made available at the same time, mountain beaver consistently selected alder stems all months of the year (data on file, USDA APHIS Animal Damage Research Unit, Olympia, Washington). Thus, alder appears to be a regular item in mountain beaver diets and problems in stand establishment should be anticipated on sites with established mountain beaver populations (D. L. Campbell, pers. com. 1992). Mountain beaver use of alder *foliage* for food is minor except when other food sources are not available or in late September when use is fairly heavy (Voth 1968).

Observations of other animals damaging red alder are limited. Beaver (*Castor canadensis*) will cut any species of tree near their ponds to support their construction activities. As a food source, beaver prefer red alder over Douglas-fir, but other plants are selected before alder if they are equally available (D. L. Campbell, pers. com. 1992). In years of high populations, meadow mice (*Microtus sp.*) girdle young stems; this type of damage has been most commonly observed in grassy or very wet areas. Deer mice (*Peromyscus maniculatus*) eat alder seed from the surface of snowpacks when other food is difficult to obtain (Moore 1949); however, alder seed is not usually a preferred food source. Individual trees can be heavily damaged (fig. 9) by red-breasted sapsuckers (*Sphyrapicus ruber*); if the damage encircles all or most of the stem, the top may break off during periods of wind or snow. Ring shake can create a serious problem of log quality in some stands. The causes of ring shake in alder are not known but it has been linked to sapsucker damage in eastern species (Baumgrass et al. 2000, Shigo 1963).

Extremes in physical factors. Extremes in temperature, wind, or fire can damage red alder. Mortality and top damage have been documented in natural stands after ice storms or unseasonable frosts (Duffield 1956, Worthington et al. 1962). Widespread cold damage (terminal dieback and mortality) has been observed in bare-root nurseries in several years after unseasonably cold frost events in October and early November. Frost protection in nursery beds via watering is effective in preventing damage and the stems that bend over with the ice resulting from watering usually recover well (N. Khadduri, pers. com. 2005). Recently planted trees are also susceptible to cold damage; late spring frosts and early fall frosts have caused top dieback and mortality (DeBell and Wilson 1978, Peeler and DeBell 1987). When grown at a common location, alder sources from northerly locations or higher elevations set bud and became cold tolerant earlier in the fall than sources from more southerly locations or lower elevations (Cannell et al. 1987, Ager and Stettler 1994); geographic variation in spring budbreak and frost hardiness were more complex. Variation in budbreak has been predicted from growing season thermal sums (Ager 1987, Ager and Stettler 1994). The winter dormancy requirement for red alder has not been studied, however, and the causal factors controlling timing of spring budbreak are not known. Presumably, once chilling requirements (if any exist) are met or day length is permissive, budbreak is temperature dependent. This assumption is consistent with the observation of Peeler and DeBell (1987) that cold damage occurred when late frosts followed a period of warmer-than-normal temperature.

Other temperature-related problems observed on alder are sunscald and frost cracks. As is generally true for other species, this type of damage is most common on the south and west side of exposed trees and both sunscald and frost cracks occur during the winter. As noted above, stem cankers may develop after this type of damage.

Fire is rarely a damaging agent because of the scarcity of flammable debris in alder stands; in fact, the species has been planted as a firebreak to protect adjacent conifers (Worthington et al. 1962). Alder bark is thin but sufficiently fire-resistant to prevent damage during light surface fires (Worthington 1957). Alder stands are also likely to be somewhat more fire resistant than most conifer stands because many alder stands are in riparian areas or on generally moister microsites.

Windthrow is not common in alder because of the intermingling of roots and branches, the absence of leaves during winter storms when soils can be waterlogged, and the relatively deep-rooting habit of the species on well-drained soils. Uprooted trees are most commonly observed along cutting boundaries or where flooding or erosion has undercut established root systems. High winds, heavy snow, and ice storms will break alder tops and branches, but these problems are generally less for alder than for associated species that are foliated during the winter. Exposed windy

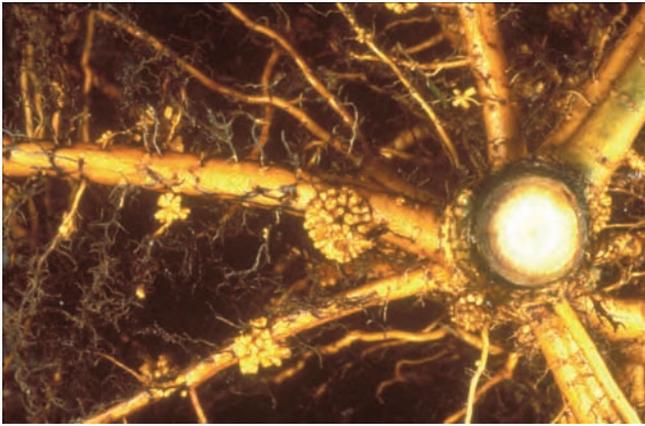


Figure 6—(above) Nitrogen-fixing nodules on the root system of a red alder seedling. Photo by J. Kraft, PNW.



Figure 8—(right-top) *Nectria distissima* can cause cankers on young alder. Photo by W. Littke, Weyerhaeuser Company.

Figure 9—(right-bottom) Red-breasted sapsuckers can cause substantial damage to individual alder stems. This tree near Olympia, WA was repeatedly damaged by sapsuckers several years after it was pruned.

Figure 7—(below) Alder trees grown at low density, such as this tree near Cape Disappointment, WA, will develop large-diameter branches that do not die or abscise quickly. Note the difference in stem form, branching and bark color between this tree and those shown in figs. 2 and 4.



sites, however, such as those near the ocean or mountain passes, have top breakage and reductions in height growth consistently enough to reduce site index (Harrington 1986). Top breakage due to snow, ice, or wind can be a serious problem under some conditions. For example, young trees re-spaced from high to lower densities can be very susceptible to breakage after thinning (P. Courtin, pers. comm. 2005). This occurs because the lower crown ratios that resulted from the higher density growing environment result in a small stem diameter at the base of the live crown and the thinning changes wind sway (or snow or ice loading) from a whole-stand phenomenon to one where individual trees primarily sway or flex with the base of the live crown as the pivot point. Damage is particularly severe if wet snow or ice occur in the late fall when the foliage is still on the branches.

Red alder has evolved to survive in climates with low summer rainfall. The greater stomatal control of red alder as compared to black cottonwood (Harrington 1987) is probably a key feature that allows the species to grow on upland sites. In general, however, red alder is probably not as drought tolerant as most of its coniferous associates (Shainsky et al. 1994).

During the summer of 1987, rainfall in the Puget Sound area of Washington was less than one-third of normal; for red alder this resulted in widespread leaf yellowing and premature abscission, terminal dieback, and, on droughty sites or new plantings, mortality (Russell 1991). Prior to 1987, the Puget Sound area experienced several decades without back-to-back dry summers and many years of above-normal rainfall. Combining these weather patterns with high levels of harvesting activity that created seedbed conditions favorable to alder establishment may have increased the percentage of alder stands growing on drought-sensitive sites (K. Russell, pers. com. 1992). Every summer (1 June to 30 September) from 1987 through 1992, the Puget Sound region had below-normal precipitation. Thus trees stressed by the extreme drought in 1987 may have been further stressed in subsequent years; presumably these back-to-back dry summers are one of the causes of the wide-spread instances of alder top dieback and mortality in the Puget Sound region in the late 1980s and early 1990s (K. Russell, pers. com. 1992).

The sensitivity of red alder to stress factors other than those discussed above is not documented. Alder is found on sites close to the ocean and presumably is fairly tolerant of salt spray. Alder has also been observed adjacent to pulp mills and other industrial plants and thus exhibits tolerance for at least some components of air pollution.

Future Research Needs

More than 25 years ago Minore (1979) commented on the surprising lack of information on autecological characteristics of red alder. Although available information has increased since then, much of our knowledge of the biology of red alder is still based on casual or short-term observations and not on detailed life histories or controlled experiments. Additional research on the biology and ecology of red alder is warranted to provide a firm knowledge base from which to make management recommendations. Specific topics of interest include the physiological or ecological factors that control: (1) forest succession, (2) alder seed production, dispersal and germination, (3) spatial distribution, timing of, and interrelationships between root and shoot growth, (4) tree responses to changes in light, nutrients, moisture, or temperature regimes, and (5) the occurrence and significance of biotic damaging agents.

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Red Alder Stand Development and Dynamics

Robert L. Deal¹

Abstract

This paper synthesizes information on the development of natural pure red alder stands and dynamics of mixed alder-conifer stands. Early research on red alder growth and yield focused on developing stand volume and normal yield tables for alder in the Pacific Northwest. Recent site-index estimation and height-growth curves were developed on a 20-year site base age. These height-growth and site-index curves were a significant improvement over earlier work and are widely used today. Red alder exhibits rapid early height growth with much more rapid height growth than for conifer associates. On good sites, trees may be 9 m at age 5, 16 m at age 10 and 24 m at age 20. Height growth then quickly declines, and by age 15 alder will reach more than half its total height and nearly all of its mature height by the age of 40. Alder height growth essentially stops by age 50.

Long-term successional sequences of red alder stands are not well understood. Red alder frequently occurs in mixed stands with conifer associates including Douglas-fir, western hemlock, Sitka spruce and western redcedar. Mixed species dynamics is more complex and variable than for pure stands and depends on a number of factors including forest composition, establishment and survival of understory

conifers, timing of alder mortality, abundance and composition of shrubs, and geographic location. Red alder is short lived (approximately 100 years) compared with its conifer associates. In some sites, alder may succeed to brush dominated communities with few if any conifers to replace the alder. In other sites, succession to more shade tolerant trees such as western hemlock and Sitka spruce is certain but the sequence of events is unknown. On some nitrogen deficient sites red alder has been shown to increase growth of conifer associates but in other cases red alder has been shown to suppress and even kill less shade tolerant conifers. Other conifer species such as western hemlock, Sitka spruce and western redcedar can survive as lower strata species and eventually grow above the alders but it may take several decades for this to occur. Height growth and long-term stand dynamics in mixed stands are highly variable and long-term succession is difficult to predict. More work is needed to understand the long-term successional sequence of events.

Keywords: *Alnus rubra*, red alder, stand development, stand dynamics, mixed alder-conifer stands, forest succession

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Introduction

Red alder (*Alnus rubra* Bong.) has become an increasingly important species both as a commercial forest product and for its recognized ecological role in forests. However, many questions remain about the growth potential, stand development, and long-term succession of alder stands. Forest land owners and managers have only recently begun to manage alder plantations and preliminary results suggest that these plantations have different growth potential and possibly shorter rotations than natural stands. These alder plantations also appear to have different tree height and diameter growth patterns than natural alder stands. In natural stands, red alder frequently occurs in species mixtures and common conifer associates include Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). These mixed stands are quite different than pure stands of either red alder or conifer species.

Red alder has often been considered as a weed species and in the past alder was commonly eliminated from conifer stands. However, the potential value of red alder as a commercial forest product has been recognized for decades. An article published in the 1930s (Munger 1938) discussed the increase of red alder in cut over and burned areas of the Pacific Northwest and the emergence of sawmills that were using the wood of red alder as a substitute for other hardwoods such as birch, mahogany or walnut. Munger described the wood of red alder as “among other desirable qualities it turns well, takes glue and paint satisfactorily, and does not incline to warp, check or shrink if properly handled.” Other papers entitled “Alder comes of Age” (Clark 1955), and “Don’t call red alder a weed!” (Morse 1967) highlight the difficulty for alder to become recognized as an important commercial species in the Pacific Northwest. Despite this information on the potential of red alder, forest managers continued to discourage alder in managed forests for decades. However, the recent premium value for alder sawlogs has led to widespread interest in red alder as a commercial forest product. Current sawlog prices for red alder now equal or exceed those for Douglas-fir and red alder is now recognized as a premium value tree. In a region that has witnessed many saw mill closures and a major reorganization of the timber industry, new sawmills are being opened that are focusing almost exclusively on red alder. The commercial value of red alder now appears firmly established in the Pacific Northwest, with increasing demand for domestic lumber, furniture supply and a significant increase in lumber exports to countries such as China (Forestry Source 2005).

Red alder’s important ecological role in both aquatic and terrestrial systems is also widely recognized. Red alder has been shown to increase the abundance of invertebrates for fish and other aquatic resources in its immediate vicinity

and in downstream reaches (Wipfli 1997, Piccolo and Wipfli 2002). Within red alder stands, vegetation for both invertebrate and vertebrate herbivores was increased by the presence of red alder, an observation consistent with previous work in southeastern Alaska (Hanley 1996, Hanley and Barnard 1998, Deal 1997, Wipfli 1997, Piccolo and Wipfli 2002). Increased prey availability likely affects many more species, such as bats and other small mammals, birds, and other wildlife in these young forested ecosystems. Results suggest that red alder has an important ecological function in forested ecosystems (Pechanec and Franklin 1968, Tarrant et al. 1983, McComb et al. 1993, Deal 1997, Wipfli 1997, Hanley and Barnard 1998). Rather than viewing red alder as an undesirable, early-successional tree and managing it accordingly, managers are planting alder or manipulating existing vegetation to favor the maintenance of red alder.

Most available information on red alder growth and yield comes from natural unmanaged red alder stands (Worthington et al. 1960, Curtis et al. 1968, Harrington and Curtis 1986). New preliminary information from alder plantations suggest different stand and tree growth patterns in these plantations as compared with natural stands (Bluhm and Hibbs 2006). Little information is available on long-term stand development and forest succession of red alder, and most of the literature is from descriptive studies with speculation on successional sequences of red alder stands. Mixed alder-conifer stands are also very different than either pure red alder or conifer forests and show highly variable development patterns and differences among species compositions such as red alder – Douglas fir and red alder – Sitka spruce stands. This paper will briefly summarize some of the key findings and synthesize the state of knowledge about red alder stand development and dynamics of mixed alder-conifer stands. The major objectives of this paper include:

- Describe stand development and growth of natural pure red alder stands, and compare and contrast development with common conifer associates including Douglas-fir, western hemlock and Sitka spruce,
- Describe stand dynamics of mixed red alder-conifer forests focusing on red alder/Douglas-fir stands and red alder/Sitka spruce/western hemlock stands.

Finally, forest succession of red alder stands will be discussed and some specific future research needs for red alder management will be identified.

Development of Natural Pure Red Alder Stands

Some clarification of terms is necessary to define the scope and content of this section. Pure stands are those stands that are essentially composed of only red alder and are contrasted with mixed species stands which will be described in a later section. Natural stands are those stands that established following natural disturbances or harvesting without artificial aid and have never received any management practices including planting, vegetation control, thinning or pruning. These natural stands are contrasted with artificial plantations and/or stands that have received weeding, thinning or other density management or stand-tending practices.

Red alder growth and yield

Early research on red alder growth and yield focused on developing stand volume and normal yield tables for alder in the Pacific Northwest. Tree taper equations were developed (Curtis et al. 1968), site curves constructed (Johnson 1949, Bishop et al. 1958, Skinner 1959) and yield tables produced (Worthington et al. 1960, Chambers 1973). This research provided baseline information on red alder volume, growth and yield of natural unmanaged stands. Height growth models in the past were based on site-index equations (Bishop et al. 1958, Worthington et al. 1960). These equations were developed to predict site index from stand height, however, and were probably not the best means to predict stand height (Curtis et al. 1974). Another concern for using these equations was using a site index based on the top height at age 50 when alder rotations were becoming increasingly shorter in length. To address these concerns, Harrington and Curtis (1986) expanded the database to include younger stands and developed separate height growth equations for red alder. They sampled twenty three natural red alder stands in western Washington and Oregon across a range of geographic locations, site quality and soil conditions. They supplemented this data with red alder stem analysis data from earlier red alder height growth curves (Johnson and Worthington 1963). Harrington and Curtis (1986) developed site-index estimation curves for red alder and developed new height-growth curves based on a 20-year site-base age (fig. 1). The height growth and site index curves they developed were a significant improvement over earlier work and are still widely used today.

Most available information on growth and yield comes from natural unmanaged stands. A number of variables including initial stand density, mortality, site factors such as soils, moisture and nutrients, and management regimes such as planting density, thinning, and vegetation control can significantly affect stand growth. Some important considerations for growth and yield are summarized by Puettmann (1994) and include information on height and diameter growth, mortality, site-index and height-growth

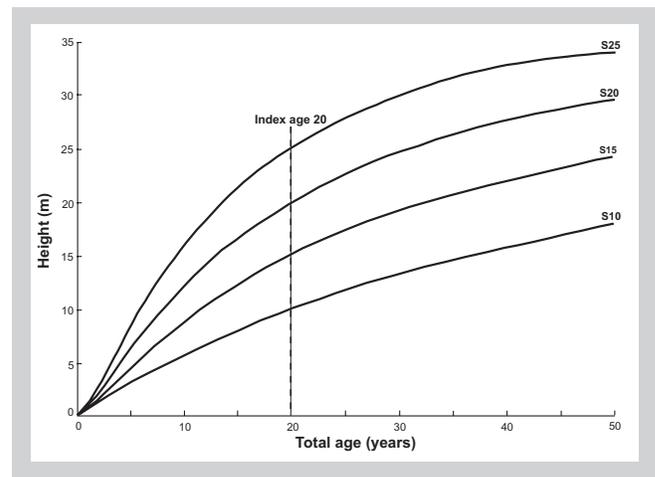


Figure 1—Red alder height-growth curves based on a 20-year site base age (Figure modified from Harrington and Curtis, 1986).

equations, yield tables, growth models and stand density guides. Red alder plantations appear to have different tree height, diameter and stand growth than natural stands (Bluhm and Hibbs 2006) and the need for further investigation of plantations led to the establishment of the Hardwood Silviculture Cooperative (HSC). The first plantations from the HSC were established in 1989 and efforts are underway to use this information to develop new stand growth models for red alder. In particular, there is a need to use new tree taper data from plantations to develop volume equations and growth models more appropriate for red alder plantations.

Height growth of red alder stands

Red alder exhibits rapid early height growth and then growth slows considerably after age 15-20 (fig. 1). Height growth of seedlings is exceptionally rapid and on favorable sites seedlings can grow 1 m or more the first year, and on all but the poorest sites, seedlings surpass breast height (1.3 m) by the second year (Harrington 1990). Maximum annual height growth of more than 3 m per year can be achieved by 2- to 5- year-old seedlings. On good sites, trees may be 9 m at age 5, 16 m at age 10 and 24 m at age 20 (Harrington and Curtis 1986, Harrington 1990). Height growth rate decreases substantially beyond age 20. Dominant tree heights range from 10-25 m at age 20 and at age 50 range from 18-37 m (Worthington et al. 1960). By age 15, red alder has reached more than half of its total height and height growth attains nearly all of its mature height before age 40 (Newton and Cole 1994).

Total height and total age possible for red alder is unknown. Red alder height can reach 25-30 m on many sites and the tallest red alder is listed as 32 m (http://en.wikipedia.org/wiki/Alnus_rubra). As previously mentioned, alder height growth essentially stops by age 40 or 50. Red alder is a short lived tree but individuals can



Figure 2—Four-year-old red alder plantation planted at about 2950 trees ha⁻¹.

live to be more than 100 years old, however, pure red alder stands frequently begin to “break up” at around age 80 (Newton and Cole 1994, Smith 1968). Red alder is shade intolerant and highly susceptible to suppression. When slower growing but longer lived conifers eventually overtop alders, these alders can die, and alders are not reestablished without new disturbances. Long-term succession for alder stands is not clearly understood and depends on the establishment of conifer associates, shrub development, geographic location and specific site factors. More discussion on succession is presented below in the section on mixed species stand dynamics.

Potential site productivity or site quality for alder is indicated by height-growth and site-index curves. Site index or height at a specified age is the most commonly used index of site quality. Site index estimates will be most reliable when stand age is within 10 years of the index age and estimates are unreliable for stands less than 5 years of age or at stands much older than 50 years. Site-index curves were developed by Harrington and Curtis (1986) and later adapted to a 50 year base to compare with conifer associates (Mitchell and Polsson 1988, Thrower and Nussbaum 1991). Site quality is also closely associated with other measures of productivity other than tree height. Site quality was related to several environmental factors and published by Harrington (1986) and summarized later by Harrington and Courtin (1994). Harrington found that elevation, physiographic position, and other soil site characteristics could be used to predict potential site index. This information has been useful to predict potential site index for red alder from soil data and other environmental factors when reliable tree height data was not available.

Management activities also can influence apparent site quality as measured by tree height. Spacing experiments have indicated that alder height growth is influenced by initial density and maximum height growth occurs at



Figure 3—Nine-year-old red alder plantation planted and thinned later to about 246 trees ha⁻¹.

intermediate spacings (DeBell and Giordano 1994, Knowe and Hibbs 1996). Recent findings from the Hardwood Silviculture Cooperative indicate that plantations established at high densities appear to be growing faster than natural plantations with more rapid height, diameter and volume growth than expected (Bluhm and Hibbs 2006, figs. 2 and 3). Density appears to have an important effect on early height growth with most rapid height growth in stands of moderate to moderately high densities. The site index and height growth curves developed from natural stands (Harrington and Curtis 1986) may underestimate potential height and volume growth of plantations at moderate to moderately high densities.

Height growth and stand development of conifer associates

This section compares early and later height growth of pure conifer stands with pure red alder stands. It is important to make the distinction between height growth of pure conifer and pure alder stands, and the development of mixed species stands. Competition between tree species with different growth development patterns produces more variable and complex mixed species stands and will be described in the last section on dynamics of mixed alder-conifer stands. This section will describe juvenile and mature height growth of common conifer associates of red alder including Douglas-Fir, Sitka spruce, western hemlock and western redcedar (*Thuja plicata* Donn ex D. Don).

Young red alder height growth is more rapid than all other tree associates with the exception of black cottonwood (*Populus trichocarpa* Torr. and Gray) (Harrington 1990). The available height growth information for conifers is much better than for red alder and the data for Douglas-

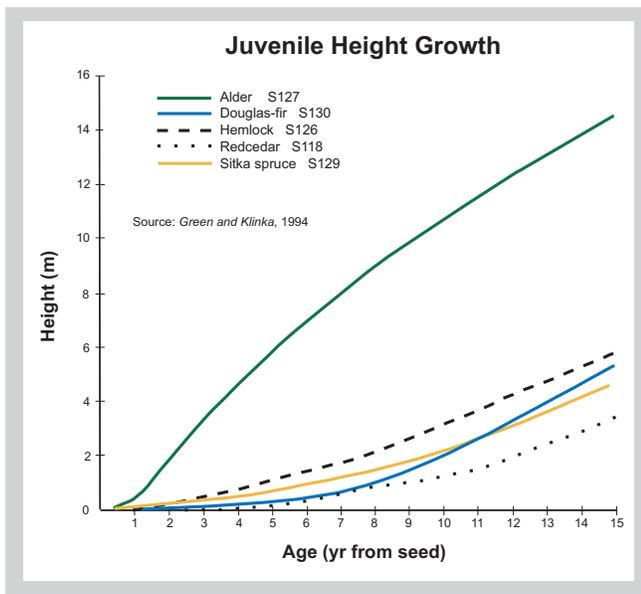


Figure 4—Comparison of juvenile height growth of red alder and associated conifers to age 15. Height curves are based on median values for conifers on Site Class II (King 1966). (Figure modified from Green and Klinka 1994).

fir is particularly robust. Red alder juvenile height growth is much more rapid than any of its conifer associates. On the best sites, Douglas-fir may be 12 m at age 10, 18 m at age 15, and 24 m at age 20 (King 1966). Even on the best Douglas-fir sites, juvenile height growth of red alder is more rapid than for Douglas-fir, and total height of dominant alder are greater than dominant Douglas-fir until about age 20.

It is probably more useful to compare height growth of alder and conifers on average sites. Alder has significantly greater early height growth than any of the common conifer associates. On average sites, Douglas-fir height is only 1 m at age 5, 2 m at age 10 and 4 m at age 15 compared with 5 m at age 5, 11 m at age 10 and 15 m at age 15 for red alder (fig. 4). Green and Klinka (1994) report that early height growth is slightly higher for western hemlock followed by Douglas-fir and Sitka spruce, with the slowest height growth for western redcedar. Other researchers (Omule 1987) report Douglas-fir with the most rapid early height growth, with redcedar height growth significantly slower than these other conifers. However, differences in early height growth are small among the four most common conifer associates with each species lagging behind red alder (Omule 1987, Green and Klinka 1994).

Longer-term height growth and stand development shows very different height growth patterns for alder and conifers. As previously reported, alder height growth rapidly declines after age 20 whereas height growth increases and is sustained for Douglas-fir, hemlock and spruce. Coastal Douglas-fir attains the largest height increments between ages 20-30, and has the ability to maintain a fairly rapid rate of height growth over a long period (Hermann and

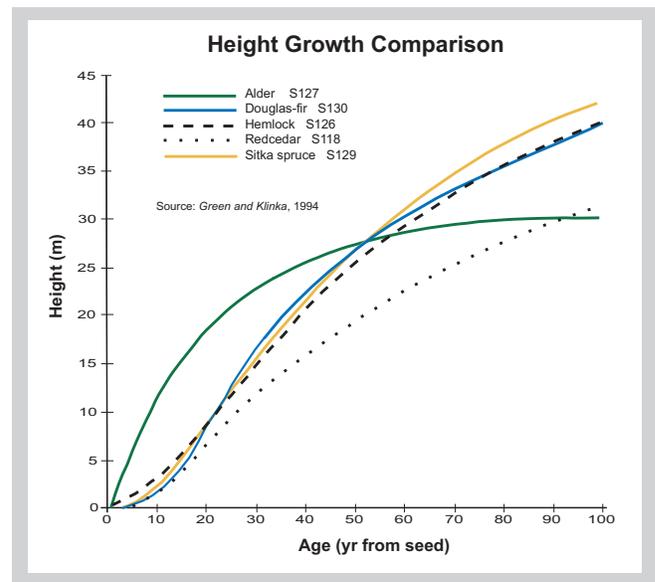


Figure 5—Comparison of height growth of red alder and associated conifers to age 100. Height curves are based on median values for conifers on Site Class II (King 1966). (Figure modified from Green and Klinka 1994).

Lavender 1990). On average sites, Douglas-fir, Sitka spruce and western hemlock all surpass red alder at about age 50 (fig. 5, Green and Klinka 1994). Another study (Williamson 1968) reports that Douglas-fir and red alder attain the same height at about age 45. Western redcedar height growth is somewhat slower and may take as long as 80 years to achieve the same height as red alder (Green and Klinka 1994). Again, it is worth noting that these projections are for pure stands and not for mixed alder-conifer stands where tree species interact. Mixed stands can be quite different and have extremely variable growth patterns.

Dynamics of mixed red alder – conifer stands

Growth and development of mixed red alder-conifer stands is different than patterns observed in either pure alder or pure conifer stands. Mixed species stand development is more complex and variable than for pure stands and depends on a number of factors including establishment and species composition, early height growth, species shade tolerance, initial species dominance and the spatial distribution of species. This section will discuss dynamics of mixed alder-conifer stands using some examples of mixed red alder/Douglas-fir stands and mixed red alder/Sitka spruce/western hemlock stands. Discussions of stand dynamics will focus on stand growth and development and some of the effects of mixed stand structure on other forest resources including understory plants.

Mixed red alder – Douglas-fir stands

A well-documented study of mixed red alder-conifer stands at Wind River in southwestern Washington compared a nitrogen-deficient stand of mixed Douglas-fir and red alder with adjacent pure stands of Douglas-fir (Tarrant 1961, Tarrant and Miller 1963, Miller and Murray 1978). After 48 years, mixed alder-conifer stands had significantly greater stand growth with overall wood production nearly double that of adjacent pure Douglas-fir stands. Douglas-fir site index was increased by an average of 6.4 meters. Improved soil fertility was suggested to be largely responsible for the improved growth of these stands (Bormann et al. 1994). Other authors have indicated that on poor sites alder may increase growth and production in Douglas-fir plantations (Atkinson et al. 1979, Tarrant et al. 1983).

Research from a mixed alder-conifer stand at Cascade Head in coastal Oregon reported different results in productivity. At Cascade Head, researchers found no appreciable difference in productivity between the mixed alder-conifer stand and an adjacent pure conifer stand. Both biomass and net primary productivity were higher in the pure conifer stand than in the mixed stand (Binkley et al. 1992). On fertile sites such as this stand, where growth was less limited by nitrogen, availability of nitrogen also increased, but with no corresponding increase in productivity (Binkley et al. 1992). The mixed alder-conifer site at Cascade Head has also been used to investigate effects of alder on stand structure and understory vegetation (Franklin and Pechanec 1969, Pechanec and Franklin 1968). Franklin and Pechanec found that the species richness and cover of herbaceous plants was greatest under pure alder and least under pure conifer, with mixed stands intermediate.

Several studies suggest that red alder can inhibit Douglas-fir growth (Newton et al. 1968, Miller and Murray 1978, Miller et al. 1999). In a reconstruction study of red alder and Douglas-fir in the Pacific Northwest, Newton et al. (1968) assessed height growth of red alder and Douglas-fir in 39 nearly pure red alder stands in western Oregon. They determined that red alder remained dominant for 25 to 35 years on most sites, and 40 years or more on wetter sites. Emergence of Douglas-fir from beneath red alder depends on its ability to grow while being suppressed and the intensity of suppression. Newton et al. (1968) reported that under all environmental conditions the initial growth of red alder was substantially better than for Douglas-fir. On some sites they suggested that Douglas-fir could not be expected to reach the overstory unless it was established 3 to 8 years before the alder. Newton concluded that Douglas-fir would be unable to maintain height growth while being suppressed, but more shade-tolerant species might be able to do so. In another study, Miller and Murray (1978) assessed growth in four mixed red alder – Douglas-fir stands. Conifers showed reduced growth in heavily stocked mixed alder – Douglas-fir stands on higher quality sites. Douglas-fir generally

emerged from the alder canopy and attained dominance in mixed stands by 25 to 35 years on drier sites and about 10 years later on wetter sites. They suggested that to attain full stocking of Douglas-fir, the stocking and distribution of red alder would need to be controlled either by thinning the alder and recommended uniformly stocking the stand with 50 to 100 alder trees ha⁻¹.

Mixed red alder – Sitka spruce – western hemlock stands

A series of studies was established in 45-year-old mixed red alder/Sitka spruce/western hemlock stands on Prince of Wales Island, Alaska (Wipfli et al. 2002, Deal et al. 2004, Orlikowska et al. 2004). Nine stands were sampled across a compositional range from 0-86% alder. Alder height growth was initially rapid then slowed considerably, whereas, conifer height growth was initially slow then rapidly increased. Dominant conifers emerged from the alder overstory in 18-25 years after logging, and at age 45, conifers were 4-9 m taller than the associated alders (Deal et al. 2004). Red alders were relatively evenly distributed with most trees in a narrow diameter and height range. Conifers were more variable in size than the alders and included numerous small trees and a few of the tallest trees in the stand. Stands containing both red alders and conifers provided a broader and more even tree-size distribution than is typically found in pure conifer stands. These mixed alder-conifer stands created a multi-layered forest canopy with a few tall overstory conifers, a mid-canopy level of red alder and a lower canopy level of small diameter conifers. This pattern of development has also been reported in other mixed red alder/Sitka spruce/western hemlock stands in Alaska (Hanley and Hoel 1996, Deal 1997). Overall, these mixed alder-conifer stands provided more heterogeneous structures than is typically found in pure conifer stands of the same age.

Stand development in these mixed alder-conifer stands is highly dynamic and tree height and stand structure is different then it was at earlier stages. In mixed alder-conifer stands in Alaska (Deal et al. 2004), dominant spruces and hemlocks emerged from the slower growing alder overstory at about 18-25 years after logging. This species change in overstory canopy position has been reported by other authors (Newton et al. 1968, Miller and Murray 1978, Stubblefield and Oliver 1978) in mixed red alder and Douglas-fir stands in the Pacific Northwest. Increased Sitka spruce height growth, however, occurred earlier and appeared to release more quickly than for Douglas-fir. Other conifer species such as western hemlock and western redcedar survived as lower strata trees and eventually grew above the alders, however, it took several decades for these conifers to release (Stubblefield and Oliver 1978).

Forest succession of red alder stands

Red alder is relatively short-lived compared to its associated conifers (Smith 1968, Harrington 1990). Worthington et al. (1962) suggested a maximum age for red alder of about 100 years. Smith (1968) notes that by 50 years of age, pure alder stands on highly productive Douglas-fir sites in British Columbia were “breaking up.” Individual trees showed dieback as early as 40 years of age. On less productive sites, mortality occurred at stand age 60 to 70, with few red alder stands remaining intact beyond 100 years. In Washington, Oregon, and British Columbia, mortality of red alder increases rapidly in stands over 90 years old, and little alder remains by the age of 130 years (Newton and Cole 1994).

Successional sequences of alder stands are not well understood. Observation of mature forests in the Pacific Northwest suggests that where seed sources are present, alder is replaced by longer-lived, more shade-tolerant conifers that sustain growth rates for longer periods. Alder’s rapid early growth and high stem densities make it difficult for other shade-intolerant species to regenerate and grow if they do not become established at the same time alder invades a disturbed area. Douglas-fir can be eliminated in dense, young alder stands while more shade-tolerant species such as western hemlock, Sitka spruce and western redcedar can survive, grow into the canopy, and ultimately dominate the site (Harrington et al. 1994). Other scenarios have been reported where following initial dominance by alder, understory shrub cover increases after about age 20, and in the absence of understory conifers, shrubs may completely dominate the site after senescence of alder at age 80-100 (Peterson et al. 1996, Hibbs and Bower 2001).

Long term stand dynamics of mixed alder-conifer forests are uncertain. Red alder is expected to die out of these stands but it is unclear how long this will take. The mechanism of alder mortality is also unknown but it is likely due competition with conifers and/or tree disease. Red alder is short lived and some researchers have reported that by 50 years most alder stands were breaking up and few stands remain intact beyond 100 years (Smith 1968). Newton and Cole (1994) report for stands in Oregon that the last alder will succumb in less than 130 years. It is unlikely that any of the alder stands in southeast Alaska will be replaced by shrubs as has been observed in some sites in the Oregon Coast Range (Newton et al. 1968, Hibbs and Bower 2001). The abundance of shade tolerant conifers such as Sitka spruce and western hemlock suggests that a treeless shrub succession is highly unlikely. Also, when alders die out they may create more gaps in the canopy and lead to a later stage of stand development that is either more open or invaded by a new cohort of conifers. Where alder forms a more continuous canopy with few conifers, alder trees compete with one another, often forming a continuous

canopy height, and they may persist for much longer. In summary, the successional sequences of alder depend on a combination of factors including forest composition, establishment and survival of understory conifers, timing of alder mortality, abundance and composition of shrubs and geographic location.

Future Research Needs

Most of the available information for red alder on stand development, growth and yield comes from natural unmanaged stands. Red alder plantations, however, appear to have different tree height and diameter and stand growth than natural stands. As new information becomes available from red alder plantations it will be essential to use these data to construct new tree taper and volume equations and develop growth models based on plantations. A number of factors including initial planting density, mortality, thinning, vegetation control and other management practices significantly affect stand growth. Preliminary results suggest that early height growth of alder plantations is closely related to initial stand density. Longer term data is needed to determine if this reported early height growth in red alder plantations results in shorter rotations and/or increases in overall stand growth. If so, then new growth models will need to be developed that reflect these changes in stand growth projections. Growth and development of mixed red alder-conifer stands is quite different than patterns observed in pure stands and successional sequences of alder stands are not well understood. Stand development of mixed-species stands is highly variable and depends on a number of factors including species composition, establishment, initial species dominance, shade tolerance, disturbance frequency, geographic location and other factors that influence long-term successional sequences. Although it would be difficult to control experimentally, better information is needed on the relative importance of these factors and their role for successional sequences of different alder-conifer compositional mixtures.

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