

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 (Furrow 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.

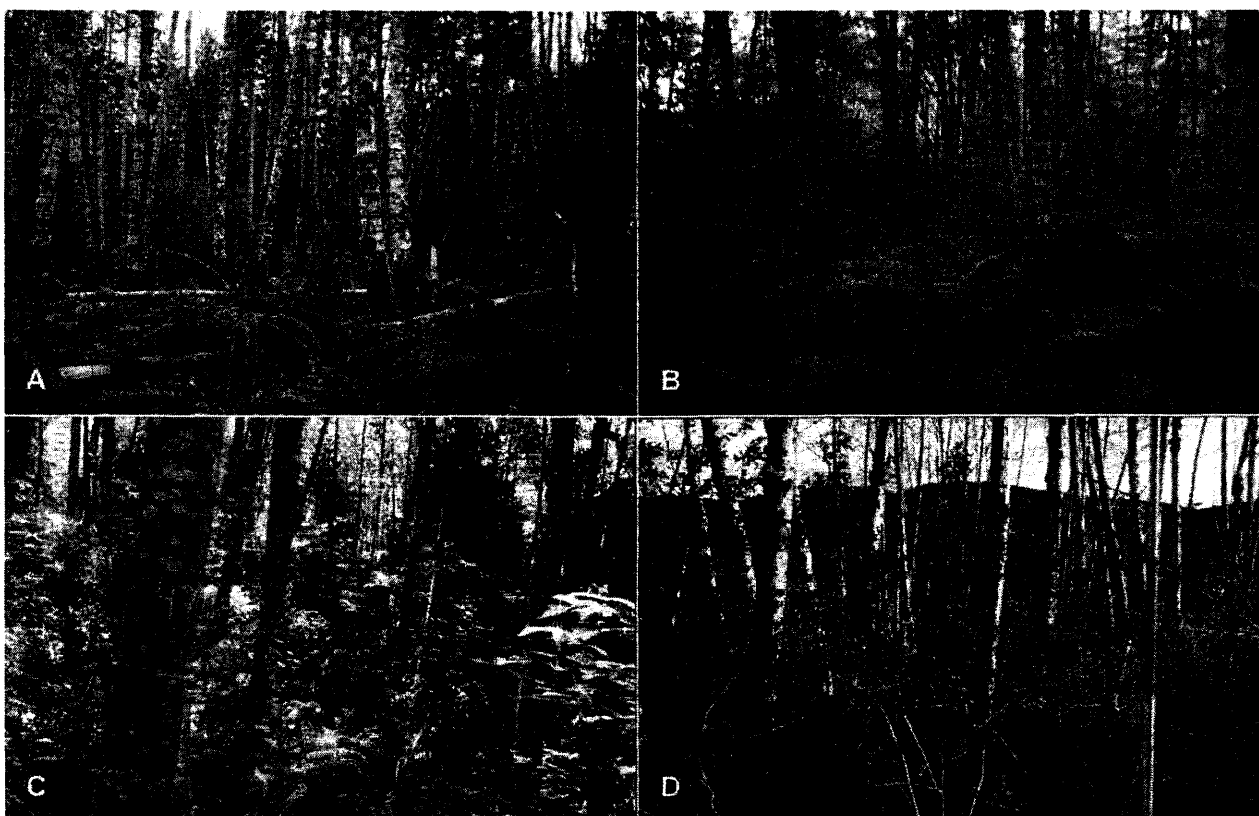
At higher elevations red alder is restricted by snow breakage. Increasing snow breakage potential is indicated by an increase in the occurrence of silver fir throughout much of the range of red alder with the notable exception of coastal rainforests in Washington and southern British Columbia. To the 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 depend 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. Litke, 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 *Ceratosystis 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 Jaek 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 Jaek 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

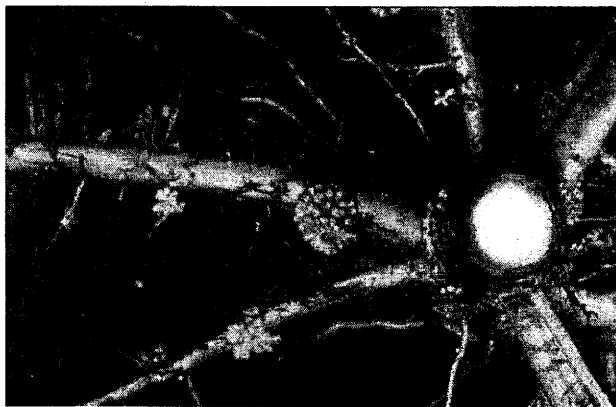


Figure 6—(above) Nitrogen-fixing nodules on the root system of a red alder seedling. Photo by J. Kraft, PNW.



Figure 8—(right-top) *Nectria distissima* can cause cankers on young alder. Photo by W. Litke, 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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Literature Cited

- Ager, A.A. 1987.** Genetic variation in red alder (*Alnus rubra* Bong.) in relation to climate and geography in the Pacific Northwest. Ph.D. thesis. Seattle, WA: University of Washington.
- Ager, A.A.; Stettler, R.F. 1994.** Genetics of red alder and its implications for future management. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 92-105.
- Ager, A.A.; Tanaka, Y.; McGrath, J. 1994.** Biology, ecology, and utilization of red alder seed. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 159-169.
- Ahrens, G. 1994.** Seedling quality and nursery practices for red alder. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 170-185.
- Allen, E.A. 1993a.** Decay in living red alder trees. Research Memo No. 216. FRDA. Victoria, BC: British Columbia Ministry of Forests. 7 p.
- Allen, E.A. 1993b.** The development of stain and decay in harvested red alder logs. Research Memo No. 217. FRDA. Victoria, BC: British Columbia Ministry of Forests. 4 p.
- Atzet, T.; White, D.E.; McCrimmon, L.A. [et al.] 1996.** Field guide to the forested plant associations of southwestern Oregon. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.
- Baumgras, J.E.; Sendak, P.E.; Sonderman, D.L. 2000.** Ring shake in eastern hemlock: frequency and relationship to tree attributes. In: McManus, K.A.; Shields, K.S.; Souto, D.R.; eds. Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. General Technical Report GTR-NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 156-160.
- Berg, A.; Doerksen, A. 1975.** Natural fertilization of a heavily thinned Douglas-fir stand by understory red alder. Res. Note 56. Corvallis, OR: Forest Research Laboratory, Oregon State University.
- Berntsen, C.M. 1961.** Pruning and epicormic branching in red alder. Journal of Forestry. 59(9): 675-676.
- Berry, A.M.; Torrey J.G. 1985.** Seed germination, seedling inoculation and establishment of *Alnus spp.* in containers in greenhouse trials. Plant and Soil 87(1):161-173.
- Binkley, D.; Cromack, K., Jr.; Baker, D.D. 1994.** Nitrogen fixation by red alder: biology, rates, and controls. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 57-72.
- Bormann, B.T.; Cromack, K., Jr.; Russell, W.O., III. 1994.** Influences of red alder on soils and long-term ecosystem productivity. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 47-56.
- Bormann, B.T. 1983.** Ecological implications of phytochrome mediated seed germination in red alder. Forest Science 29: 734-738.
- Bormann, B.T. 1985.** Early wide spacing in red alder (*Alnus rubra* Bong.): effects on stem form and stem growth. Res. Note PNW-423. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Brayshaw, T.C. 1976.** Catkin-bearing plants (*Amentiferae*) of British Columbia. Occasional papers No. 18. British Columbia Provincial Museum.
- Briggs, D.G.; DeBell, D.S.; Atkinson, W.A., comps. 1978.** Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Brodie L.C.; Harrington, C.A. 2006.** The response of young red alder to pruning. In: Deal, R.L. and C.A. Harrington, eds. Red alder—a state of knowledge. General Technical Report PNW-GTR-669. Portland, OR: U.S. Department of Agriculture, Pacific Northwest Research Station: 95-102.
- Brown, E.R. 1961.** The black-tailed deer of western Washington. Biol. Bull. 13. Olympia, WA: Washington State Department of Game.
- Brown, S.M. 1985.** A study of reproductive biology of *Alnus rubra* along three elevational transects in Washington and Oregon. Report on file, U.S. Department of Agriculture, Forest Service, Olympia Forest Sciences Laboratory, Olympia, WA.
- Brown, S.M. 1986.** Sexual allocation patterns in red alder (*Alnus rubra* Bong.) along three elevational transects. M.S. thesis. Seattle, WA: University of Washington.
- Cannell, M.G.R.; Murray, M.B.; Sheppard, L.J. 1987.** Frost hardiness of red alder (*Alnus rubra*) provenances in Britain. Forestry 60: 57-67.

- Cara, R.I.; Jaeck, L.L. 1978.** Insect pests of red alder: potential problems. In: Briggs, D.G.; DeBell, D.S.; Atkinson, W.A., comps. Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 265-269.
- Carlton, G.C. 1988.** The structure and dynamics of red alder communities in the central Coast Range of western Oregon. M.S. thesis. Corvallis, OR: Oregon State University.
- Chambers, C.J. 1983.** Empirical yield tables for predominantly alder stands in western Washington. 4th print. DNR Rep. 31. Olympia, WA: Washington State Dept. of Natural Resources.
- Chan, S.S. 1990.** Effects of light and soil moisture availability on Douglas-fir and red alder sapling development, carbon allocations, and physiology. Dissertation. Corvallis, OR: Oregon State University.
- Courtin P.J.; Brown, K.R. 2001.** The use of red alder to enhance Sitka spruce growth in the Queen Charlotte Islands. Forest Research Extension Note EN-008. Nanaimo, BC: British Columbia Ministry of Forests. 4 p.
- Cwynar, L.C. 1987.** Fire and the forest history of the North Cascade Range. Ecology 68(4):791-802.
- Davis, M.B. 1973.** Pollen evidence of changing land use around the shores of Lake Washington. Northwest Science 47(3): 133-148.
- Deal, R.L. 1997.** Understory plant diversity in riparian alder-conifer stands after logging in southeast Alaska Res. Note PNW-RN-523. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 8 p.
- Deal, R.L. 2006.** Red alder stand development and dynamics. In: Deal, R.L. and C.A. Harrington, eds. Red alder—a state of knowledge. General Technical Report PNW-GTR-669. Portland, OR: U.S. Department of Agriculture, Pacific Northwest Research Station: 45-54.
- DeBell, D. S. 1972.** Potential productivity of dense, young thickets of red alder. For. Res. Note 2. Camas, WA: Crown Zellerbach.
- DeBell, D.S.; Giordano, P.A. 1994.** Growth patterns of red alder. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 116-130.
- DeBell, D.S.; Harrington, C.A. 2002.** Density and rectangularity of planting influence 20-year growth and development of red alder. Canadian Journal of Forest Research. 32: 1244-1253.
- DeBell, D.S.; Harrington, C.A.; Singleton, R.; Gartner, B.L. 2006.** Time and distance to clearwood in pruned red alder saplings. In: Deal, R.L. and C.A. Harrington, eds. Red alder—a state of knowledge. General technical Report PNR-GTR-669. Portland, OR: U.S. Department of Agriculture, Pacific Northwest Research Station: 103-113.
- DeBell, D.S.; Radwan, M.A.; Harrington, C.A., et al. 1990.** Increasing the productivity of biomass plantations of cottonwood and alder in the Pacific Northwest. Annual technical report submitted to the U. S. Dept. of Energy, Woody Crops Program.
- DeBell, D.S.; Strand, R.F.; Reukema, D.L. 1978.** Short-rotation production of red alder: some options for future forest management. In: Briggs, D.G.; DeBell, D.S.; Atkinson, W.A., comps. Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 231-244.
- DeBell, D.S.; Turpin, T.C. 1989.** Control of red alder by cutting. Res. Pap. PNW-414. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- DeBell, D.S.; Wilson, B.C. 1978.** Natural variation in red alder. In: Briggs, D.G.; DeBell, D.S.; Atkinson, W.A., comps. Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 193-208.
- Dolan, L.S. 1984.** The cultural treatment of selected species for woody biomass production in the Pacific Northwest. Final report prepared by Seattle City Light Dept. for U.S. Department of Energy. Grant DE-FG-79-78BP35773.
- Dorworth, C.E. 1995.** Biological control of red alder (*Alnus rubra*) with the fungus *Nectria ditissima*. Weed Technology 9: 243-248.
- Duffield, J.W. 1956.** Damage to western Washington forests from November 1955 cold wave. Res. Note 129. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Elliot, D.M.; Taylor, I.E.P. 1981a.** Germination of red alder (*Alnus rubra*) seed from several locations in its natural range. Canadian Journal of Forest Research 11: 517-521.
- Elliot, D.M.; Taylor, I.E.P. 1981b.** The importance of fertility and physical characteristics of soil in early development of red alder seedlings grown under controlled environmental conditions. Canadian Journal of Forest Research 11: 522-529.
- Eyre, F.H., ed. 1980.** Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters.

- Farr, D.F.; Bills, G.F. Chamuris, G.P.; Rossman, A.Y. 1989. Fungi on plants and plant products in the United States. American Phytopathological Society Press: 92-97.
- Furrow, J. 1974. A systematic study of the American species of *Alnus* (Betulaceae). Ph.D. thesis. Lansing, MI: Michigan State University.
- Furniss, R.; Carolin, V.M. 1977. Western forest insects. Misc. Publ. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service.
- Granstrom, A. 1982. Seed viability of fourteen species during five years of storage in forest soil. Journal of Ecology. 75:321-331.
- Grotta, A.T.; Gartner, B.L.; Radosevich, S.R. 2004. Influence of species proportion and timing of establishment on stem quality in mixed red alder-Douglas-fir plantations. Canadian Journal of Forest Research 34: 863-873.
- Haeussler, S. 1988. Germination and first-year survival of red alder seedlings in the central Coast Range of Oregon. M.S. thesis. Corvallis, OR: Oregon State University.
- Haeussler, S.; Tappeiner, J.C., II. 1993. Effect of the light environment on seed germination of red alder (*Alnus rubra*). Canadian Journal of Forest Research 23: 1487-1491.
- Hanley, T.A.; Barnard, J.C. 1998. Red alder, *Alnus rubra*, as a potential mitigating factor for wildlife habitat following clearcut logging in southeastern Alaska. Canadian Field-Naturalist 112(4): 647-652.
- Hansen, E.M. 1979. Survival of *Phellinus weirii* in Douglas-fir stumps after logging. Canadian Journal of Forest Research 9: 484-488.
- Harrington, C.A. 1984a. Factors influencing sprouting of red alder. Canadian Journal of Forest Research 14(3): 357-361.
- Harrington, C.A. 1984b. Red alder: an American wood. Publ. FS-215. Washington DC: U.S. Government Printing Office.
- Harrington, C.A. 1986. A method of site quality evaluation for red alder. Gen. Tech. Rep. PNW-192. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Harrington, C.A. 1987. Responses of red alder and black cottonwood seedlings to flooding. Physiol. Plant. 69: 35-48.
- Harrington, C.A.; Courtin, P.J. 1994. Evaluation of site quality for red alder. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 141-158.
- Harrington, C.A.; DeBell, D.S. 1995. Effects of irrigation, spacing and fertilization on flowering and growth in young *Alnus rubra*. Tree Physiology 15: 427-432.
- Harrington, C.A.; Zasada, J.C.; Allen, E.A. 1994. Biology of red alder (*Alnus rubra* Bong.). In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The Biology and Management of Red Alder. Corvallis, OR: Oregon State University Press: 3-22.
- Harrington, C.A.; Curtis, R.O. 1986. Height growth and site index curves for red alder. Res. Pap. PNW-358. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Harrington, C.A.; DeBell, D.S. 1980. Variation in specific gravity of red alder (*Alnus rubra* Bong.). Canadian Journal of Forest Research 10(3):293-299.
- Harrington, C.A.; DeBell, D.S. 1984. Effects of irrigation, pulp mill sludge, and repeated coppicing on growth and yield of black cottonwood and red alder. Canadian Journal of Forest Research 14(6): 844-849.
- Harris, A. S. 1969. Ripening and dispersal of a bumper western hemlock-Sitka spruce seed crop in southeast Alaska. Res. Note PNW-105. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Heebner, C.F.; Bergener, M.J. 1983. Red alder: a bibliography with abstracts. Gen. Tech. Rep. PNW-161. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Henderson, J.A.; Peter, D.H.; Leshner, R.D.; Shaw, D.C. 1989. Forested plant associations of the Olympic National Forest. R6-ECOL-TP 001-88, Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. Agric. Handb. 386. Washington, DC: U.S. Department of Agriculture, Forest Service.
- Heusser, C.J. 1964. Palynology of four bog sections from the western Olympic Peninsula, Washington. Ecology 45: 23-40.
- Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. 1994. The biology and management of red alder. Corvallis, OR: Oregon State University Press. 256 p.
- Hibbs, D.E.; Ager, A.A. 1989. Red alder: guidelines for seed collection, handling, and storage. Spec. Publ. 18. Forest Research Laboratory, Corvallis, OR: Oregon State University.
- Hitchcock, C.L.; Cronquist, A.; Ownbey, M.; Thompson, J.W. 1964. Vascular plants of the Pacific Northwest. Part 2: *Salicaceae* to *Saxifragaceae*. Seattle, WA: University of Washington Press.

- Hook, D. D.; Murray, M.D.; DeBell, D.S.; Wilson, B.C. 1987.** Variation in growth of red alder families in relation to shallow water-table levels. *Forest Science*. 33: 224-229.
- Johnson, F.D. 1968a.** Disjunct populations of red alder in Idaho. In: Trappe, J.M.; Franklin, J.F.; Tarrant, R.F.; Hansen, G.M., eds. *Biology of alder*. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station. 1-8.
- Johnson, F.D. 1968b.** Taxonomy and distribution of northwestern alders. In: Trappe, J.M.; Franklin, J.F.; Tarrant, R.F.; Hansen, G.M., eds. *Biology of alder*. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 9-22.
- Johnson, H.M.; Hanzlik, E.J.; Gibbons, W.H. 1926.** Red alder of the Pacific Northwest: its utilization, with notes on growth and management. U.S. Department of Agriculture, Dept. Bulle. 1437.
- Johnson, J.D.; Herman, B. 2005.** Assessing frost tolerance in red alder [Abstract]. In: *Red Alder: a state of knowledge, meeting program and abstracts*. Seattle, WA: University of Washington: 23-24.
- Karchesy, K. 1975.** Polyphenols of red alder: chemistry of the staining phenomenon. Ph.D. Dissertation. Corvallis, OR: Oregon State University. 103 p.
- Leslie, D.M., Jr.; Starkey, E.E.; Vaura, M. 1984.** Elk and deer diets in old-growth forests in western Washington. *Journal of Wildlife Management* 48(3): 762-775.
- Lester, D.T.; DeBell, D.S. 1989.** Geographic variation in red alder. Res. Pap. PNW-RP-409. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Lewis, S.J. 1985.** Seedfall, germination, and early survival of red alder. M.S. thesis. Seattle: University of Washington.
- Li, C. Y.; Lu, K.C.; Nelson, E.E. [et al.] 1969.** Effect of phenolic and other compounds on growth of *Poria weirii* *in vitro*. *Microbios* 3: 305-311.
- Li, C. Y.; Lu, K.C.; Trappe, J. M.; Bollen, W.B. 1972.** *Poria weirii*-inhibiting and other phenolic compounds in roots of red alder and Douglas-fir. *Microbios* 5: 65-68.
- Lloyd, W.J. 1955.** Alder thinning—progress report. West Area Woodland Conservation Tech. Note 3. Portland, OR: U.S. Department of Agriculture Soil Conservation Service.
- Lousier, J.D.; Bancroft, B. 1990.** Guidelines for alder seed tree control. FRDA Memo No. 132. Canadian Forestry Service and British Columbia Ministry of Forests.
- Lowe, D.P. 1969.** Checklist and host index of bacteria, fungi, and mistletoes of British Columbia. Environment Canada Publ. BC-X-32. Canadian Forestry Service, Forest Research Laboratory. 241-244.
- McComb, W.C. 1994.** Red alder: interactions with wildlife. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. *The biology and management of red alder*. Corvallis, OR: Oregon State University Press: 131-158.
- McGee, A. B. 1988.** Vegetation response to right-of-way clearing procedures in coastal British Columbia. Ph.D. thesis. Vancouver, BC: University of British Columbia.
- Miller, R.E.; Obermeyer, E.L.; Anderson, H.W. 1999.** Comparative effects of precommercial thinning, urea fertilizer, and red alder in a site II, coast Douglas-fir plantation. Res. Pap. PNW-RP-513. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 25 p.
- Miller, R.E.; Anderson, H.W.; Murray, M.; Leon, R. 2005.** Comparative effects of urea fertilizer and red alder in a site III, coast Douglas-fir plantation in the Washington Cascade Range. Res. Pap. PNW-RP-565. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 28 p.
- Miller, R.E.; Reukema, D.L.; Max, T.A. 1993.** Size of Douglas-fir trees in relation to distance from a mixed red alder - Douglas-fir stand. *Canadian Journal of Forest Research* 23: 2413-2418.
- Miller, R.E.; Murray, M.D. 1978.** The effects of red alder on growth of Douglas-fir. In *Utilization and management of alder*. Gen. Tech. Rep. PNW-GTR-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 283-306.
- Minore, D. 1968.** Effects of artificial flooding on seedling survival and growth of six northwestern species. Res. Note PNW-92. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Minore, D. 1979.** Comparative autecological characteristics of northwestern tree species—a literature review. Gen. Tech. Rep. PNW-87. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Mix, A.J.A. 1949.** A monograph of the genus *Taphrina*. Sci. Bulle. 33. Lawrence, KA: University of Kansas 1: 3-167.
- Molina, R. 1979.** Pure culture synthesis and host specificity of red alder mycorrhizae. *Canadian Journal of Botany* 57(11): 1223-1228.
- Monaco, P.A.; Ching, T.M.; Ching, K.K. 1980.** Rooting of *Alnus rubra* cuttings. *Tree Planters' Notes* 31(3): 22-24.

- Moore, A.W. 1949.** Forest tree-seed-eaters and methods used to measure their populations in the Pacific Northwest Douglas-fir region. Washington State University: Forest Club Quarterly 23(1): 7-11, 25.
- Morrell, J. 1987.** A reddish purple stain of red alder by *Ceratocystis picea* and its prevention. Forest Products Journal 37(2): 18-20.
- Nash, T.H., III. 1996.** Lichen biology. Great Britain: Cambridge University Press. 303 p.
- Nelson, E.E.; Hansen, E.M.; Li, C.Y.; Trappe, J.M. 1978.** The role of red alder in reducing losses from laminated root rot. In: Briggs, D.G.; DeBell, D.S.; Atkinson, W.A., comps. Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 273-282.
- Newton, M.; Cole, E.C. 1994.** Stand development and successional implications: pure and mixed stands. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 106-115.
- Newton, M.; El Hassan, B.A.; Zavitkovski, J. 1968.** Role of red alder in western Oregon forest succession. In: Trappe, J.M.; Franklin, J.F.; Tarrant, R.F.; Hansen, G.M., eds. Biology of alder. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 73-84.
- O'Dea, M.E. 1992.** The clonal development of vine maple during Douglas-fir development in the Coast Range of Oregon. M.S. thesis. Corvallis, OR: Oregon State University.
- Olson, R.; Hintz, D.E.; Kittila, E. 1967.** Thinning young stands of alder. West Area Woodland Conservation Tech. Note 122. Portland, OR: U.S. Department of Agriculture, Soil Conservation Service.
- Owens, J.N. 1991.** Flowering and seed set. In: Raghavendra, A.S., ed. New York: Wiley: Physiology of Trees: 247-271.
- Owens, J.N.; Simpson, S.J. [n. d.]** Manual of conifer pollen from British Columbia conifers. Victoria, BC: Biology Department, University of Victoria.
- Peeler, K.C.; DeBell, D.S. 1987.** Variation in damage from growing-season frosts among open-pollinated families of red alder. Res. Note PNW-464. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Pendl, F.; D'Anjou, B. 1990.** Effect of manual treatment timing on red alder regrowth and conifer release. FRDA Rep.112. Victoria, BC: British Columbia Ministry of Forests.
- Perala, D.A.; Alm, A. 1989.** Regenerating paper birch in the Lake States with the shelterwood method. Northern Journal of Applied Forestry 6: 151-153.
- Radwan, M.A.; DeBell, D.S. 1981.** Germination of red alder seed. Res. Note PNW-370. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Radwan, M.A.; Ellis, W.D.; Crouch, G.L. 1978.** Chemical composition and deer browsing of red alder foliage. Res. Pap. PNW-246. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Radwan, M.A.; Max, T.A.; Johnson, D.W. 1989.** Softwood cuttings for propagation of red alder. New Forests 3: 21-30.
- Radwan, M.A.; Tanaka, Y.; Dobkowski, A.; Fangen, W. 1992.** Production and assessment of red alder planting stock. Res. Pap. PNW-450. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Reukema, D.L. 1965.** Seasonal progress of radial growth of Douglas-fir, western redcedar, and red alder. Res. Pap. PNW-26. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Russell, K. 1986.** Revegetation trials in a Mount St. Helens eruption debris flow. In: Proceedings of a Symposium. Mt. St. Helens: five years later. Cheney, WA: Eastern Washington University: 231-248.
- Russell, K. 1991.** Drought injury to trees related to summer and winter weather extremes. Forest Health Alert #3. Olympia, WA: Washington State Department of Natural Resources.
- Schopmeyer, C.S. 1974.** *Alnus B. Ehrh.*—alder. In: Schopmeyer, C.S., tech. coord. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: 206-211.
- Shainsky, L.J.; Newton, M.; Radosevich, S.R. 1992.** Effects of intra- and inter-specific competition on root and shoot biomass of young Douglas-fir and red alder. Canadian Journal of Forest Research 22: 101-110.
- Shainsky, L.J.; Radosevich, S.R. 1991.** Analysis of yield-density relationships in experimental stands of Douglas-fir and red alder seedlings. Forest Science 37: 574-592.
- Shainsky, L.J.; Yoder, B.J.; Harrington, T.B.; Chan, S.S.N. 1994.** Physiological characteristics of red alder: water relations and photosynthesis. In: Hibbs, D.E.; DeBell, D.S.; Tarrant, R.F., eds. The biology and management of red alder. Corvallis, OR: Oregon State University Press: 73-91.

- Shaw, C.G. 1973.** Host fungus index for the Pacific Northwest, vol. 1, Host. Bulle. 766. Pullman, WA: Washington State University, Washington Agriculture Experiment Station. 14-15.
- Shigo, A. L. 1963.** Ring shake associated with sapsucker injury. Res. Pap. NE-8. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 10 p.
- Smith, J.H.G. 1964.** Root spread can be estimated from crown width of Douglas fir, lodgepole pine, and other British Columbia tree species. Forestry Chronicle 40: 456-473.
- Smith, J.H.G. 1968.** Growth and yield of red alder in British Columbia. In: Trappe, J.M.; Franklin, J.F.; Tarrant, R.F.; Hansen, G.M., eds. Biology of alder. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 273-286.
- Smith, J.H.G. 1978.** Growth and yield of red alder: effects of spacing and thinning. In: Briggs, D.G.; DeBell, D.S.; Atkinson, W.A., comps. Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 245-263.
- Stettler, R.F. 1978.** Biological aspects of red alder pertinent to potential breeding programs. In: Briggs, D.G.; DeBell, D.S.; Atkinson, W.A., comps. Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 209-222.
- Stolte, K.; Mangis, D.; Doty, R.; Tonnessen, K., tech. coords. 1993.** Lichens as bioindicators of air quality. Gen. Tech. Rep. RM-GTR-224. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. 131 p.
- Swartz, D. 1971.** Collegiate dictionary of botany. New York: Ronald Press Co.
- Tanaka, Y.; Brotherton, P.J.; Dobkowski, A.; Cameron, P.C. 1991.** Germination of stratified and non-stratified seeds of red alder at two germination temperatures. New Forest 5: 67-75.
- Tappeiner, J.; Zasada, J.; Ryan, P.; Newton, M. 1991.** Salmonberry clonal and population structure: the basis for a persistent cover. Ecology 72(2): 609-618.
- Tarrant, R.F.; Miller, R.E. 1963.** Accumulation of organic matter and soil nitrogen beneath a plantation of red alder and Douglas-fir. Soil Science Society America Proceedings 27(2): 231-234.
- Trappe, J.M. 1972.** Regulation of soil organisms by red alder—a potential biological system for control of *Poria weirii*. In: Berg, B., ed. Managing young forests in the Douglas-fir region. Corvallis, OR: Oregon State University: 35-46.
- Trappe, J.M.; Franklin, J. F.; Tarrant, R.F.; Hansen, G.M., eds. 1968.** Biology of alder. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Voth, E.H. 1968.** Food habits of the Pacific mountain beaver, *Aplodontia rufa pacifica* Merriam. Ph.D. thesis. Corvallis, OR: Oregon State University.
- Warrack, G. 1949.** Treatment of red alder in the coastal region of British Columbia. Res. Note 14. Victoria, BC: British Columbia Forest Service.
- Warrack, G.C. 1964.** Thinning effects in red alder. Victoria, BC: British Columbia Forest Service, Research Division.
- White, C.M.; West, G.C. 1977.** The annual lipid cycle and feeding behavior of Alaskan redpolls. Oecologia 27: 227-238.
- Williamson, R.L. 1968.** Productivity of red alder in western Oregon and Washington. In: Trappe, J.M.; Franklin, J. F.; Tarrant, R.F.; Hansen, G.M., eds. Biology of alder. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station: 287-292.
- Wilson, B.C.; Jewett, N.W.** Propagation of red alder by mound layering. Unpublished report. On file at the Washington State Department of Natural Resources, Olympia, WA.
- Wilson, B.C.; Stettler, R.F. 1981.** Cut-leaf red alder. Unpublished report. On file at the University of Washington, Seattle, WA.
- Worthington, N.P. 1957.** Silvical characteristics of red alder. Silvical Series 1. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Worthington, N.P.; Johnson, F.A.; Staebler, G.R.; Lloyd, W.J. 1960.** Normal yield tables for red alder. Res. Pap. PNW-36. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.
- Worthington, N.P.; Ruth, R.H.; Matson, E.E. 1962.** Red alder: its management and utilization. Misc. Publ. 881. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Range and Experiment Station.

Zasada, J. 1986. Natural regeneration of trees and tall shrubs on forest sites in interior Alaska. In: Van Cleve, K.; Chapin, F.S., III; Flanagan, P.W.; Viereck, L.A.; Dyrness, C.T., eds. Forest ecosystems in the Alaska taiga: a synthesis of structure and function. Springer-Verlag: 44-73.

Zasada, J.; Sharik, T.; Nygren, M. 1991. The reproductive process in boreal forest trees. In Shugart, H.H.; Leemans, R.; Bonan, G.B., eds. A systems analysis of the global boreal forest. Cambridge, UK: Cambridge University Press: 85-125.

Zasada, J.; Tappeiner, J.; O'Dea, M. 1992. Clonal structure of salmonberry and vine maple in the Oregon Coast Range. In: Clary, W.; McArthur, E.; Bedunah, D.; Wambolt, C., comps. Proceedings: Ecology and management of riparian shrub communities. Gen. Tech. Rep. INT-289. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 56-61.

Zimmerman, M.H.; Brown, C.L. 1971. Trees: structure and function. New York: Springer-Verlag.

ABSTRACT

Deal, Robert L.; Harrington, Constance A., eds. 2006. Red alder—a state of knowledge. Gen. Tech. Rep. PNW-GTR-669. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 150 p.

In March 23-25, 2005, an international symposium on red alder was held at the University of Washington Center for Urban Horticulture in Seattle, WA. The symposium was entitled “Red alder: A State of Knowledge” and brought together regional experts to critically examine the economic, ecological and social values of red alder. The primary goal of the symposium was to discuss new advances in the understanding of red alder biology and silviculture, changing market and non-market values, and the current regulatory climate for management of alder. This proceedings includes 14 papers based on oral presentations given at the symposium. These papers highlight some of the key findings from the history, ecology, biology, silviculture and economics sessions presented at the red alder symposium.

KEYWORDS: Red alder, *Alnus rubra*, history, biology and ecology, mixed-species stands, silviculture, pruning, plantation establishment, economics, inventory, supply.