NOTE / NOTE

Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder

Dan Binkley

Abstract: Early insights on the effects of N_2-fixing red alder (*Alnus rubra* Bong.) on conifer forests came largely from two case studies dating from the 1920s at Wind River, Washington (low soil N), and Cascade Head, Oregon (high soil N). These classic experiments were remeasured after 70 years of stand development. The pure conifer stand at Wind River showed near-zero net increment in stem mass for the past 20 years, with stem mass remaining near 120 Mg/ha. Conifer stem mass in the mixed stand continued to increase at 4.5 $Mg \cdot ha^{-1} \cdot year^{-1}$, reaching 230 Mg/ha at age 72. The alder mass declined over this period from about 70 Mg/ha near age 50 to just 10 Mg/ha at age 72 as a result of increasing dominance of tall Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees. The pure conifer plot at Cascade Head reached a stem mass of 600 Mg/ha at age 74 years compared with 312 Mg/ha in the mixed stand (conifers, 200 Mg/ha; alder, 112 Mg/ha) and 173 Mg/ha in the pure alder plot. The long-term impacts of alder appeared to remain very strong after seven decades, greatly increasing ecosystem productivity at the N-poor Wind River site and reducing productivity at the N-rich Cascade Head site.

Résumé : Les premières données sur les effets de l'aulne rouge (*Alnus rubra* Bong.), une espèce fixatrice de N_2, sur les forêts de conifères proviennent principalement de deux études datant des années 1920, l'une à Wind River dans l'État de Washington (sol pauvre en N) et l'autre à Cascade Head en Oregon (sol riche en N). Ces dispositifs ont été mesurés de nouveau après 70 ans. Le peuplement pur de conifères à Wind River a montré un accroissement net presque nul pour la masse des tiges au cours des derniers 20 ans, avec une masse des tiges stables à près de 120 Mg/ha. La masse des tiges de conifères dans le peuplement mixte a continué de s'accroître de 4,5 $Mg \cdot ha^{-1} \cdot an^{-1}$, atteignant 230 Mg/ha à l'âge de 72 ans. Durant cette période, la masse de l'aulne a diminué, passant de 70 Mg/ha à l'âge de 50 ans à seulement 10 Mg/ha à l'âge de 72 ans, résultant d'une dominance accrue des grands sapins de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco). La masse des tiges de la parcelle de conifères purs à Cascade Head a atteint 600 Mg/ha à l'âge de 74 ans, comparé à 312 Mg/ha dans le peuplement mixte (200 Mg/ha de conifères, 112 Mg/ha d'aulne) et 173 Mg/ha dans la parcelle pure d'aulne. Les impacts à long terme de l'aulne restent très importants après sept décennies, augmentant grandement la productivité du site pauvre en N de Wind River, et réduisant la productivité du site riche en N de Cascade Head.

[Traduit par la Rédaction]

Introduction

The presence of N_2-fixing trees in forests substantially alters soil fertility, tree production, and nutrient cycles. Some of these effects seem to be consistent across many sites and species. For example, the pools of soil N and C are consistently greater in forests with N_2-fixing trees (for a recent example, see Resh et al. 2002). Some other effects of N_2-fixing trees differ among forests, such as the effect on soil P supply, soil cation concentrations, and the growth of non-N_2-fixing trees. For example, the two oldest case studies with N_2-fixing red alder (*Alnus rubra* Bong.) and conifers showed opposite effects. The experiment at Wind River, Washington, showed substantially increased growth and conifer biomass in the stand mixed with alder, whereas a similar experiment at Cascade Head, Oregon, showed lower overall growth as well as conifer biomass in the mixed-species stand (Binkley and Greene 1983; Binkley et al. 1992; Kelty et al. 1992). The divergent effects of alder probably depend strongly on initial soil fertility (the soil at Wind River was much less fertile than that at Cascade Head) and on the early relative dominance of the species (conifers remained co-dominant in the mixed stand at Wind River). A variety of more recent studies have examined the influence of N_2-fixing trees in mixtures with other species in tropical forests, and some of these fast-growing forests have now covered a full rotation (cf. DeBell et al. 1997; Parrotta 1999; Binkley et al. 2003). Less experimentation is available for temperate

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D. Binkley. Department of Forest, Rangeland, and Watershed Stewardship, Natural Resource Ecology Laboratory, and Graduate Degree Program in Ecology; Colorado State University, Ft. Collins, CO 80523, U.S.A. (e-mail: dan@cnr.colostate.edu).

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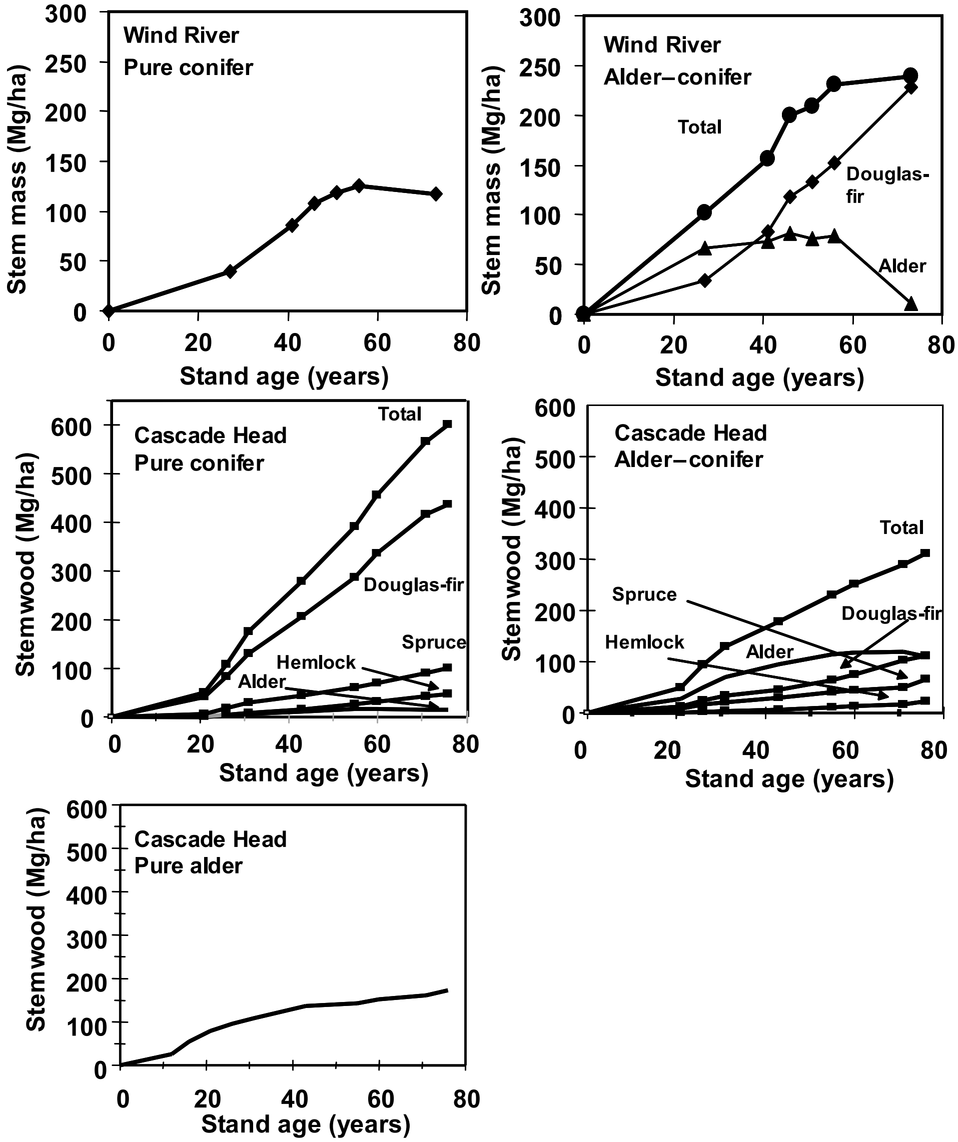
Fig. 1. Stem mass with stand age for the pure and mixed stands at the Wind River and Cascade Head sites.

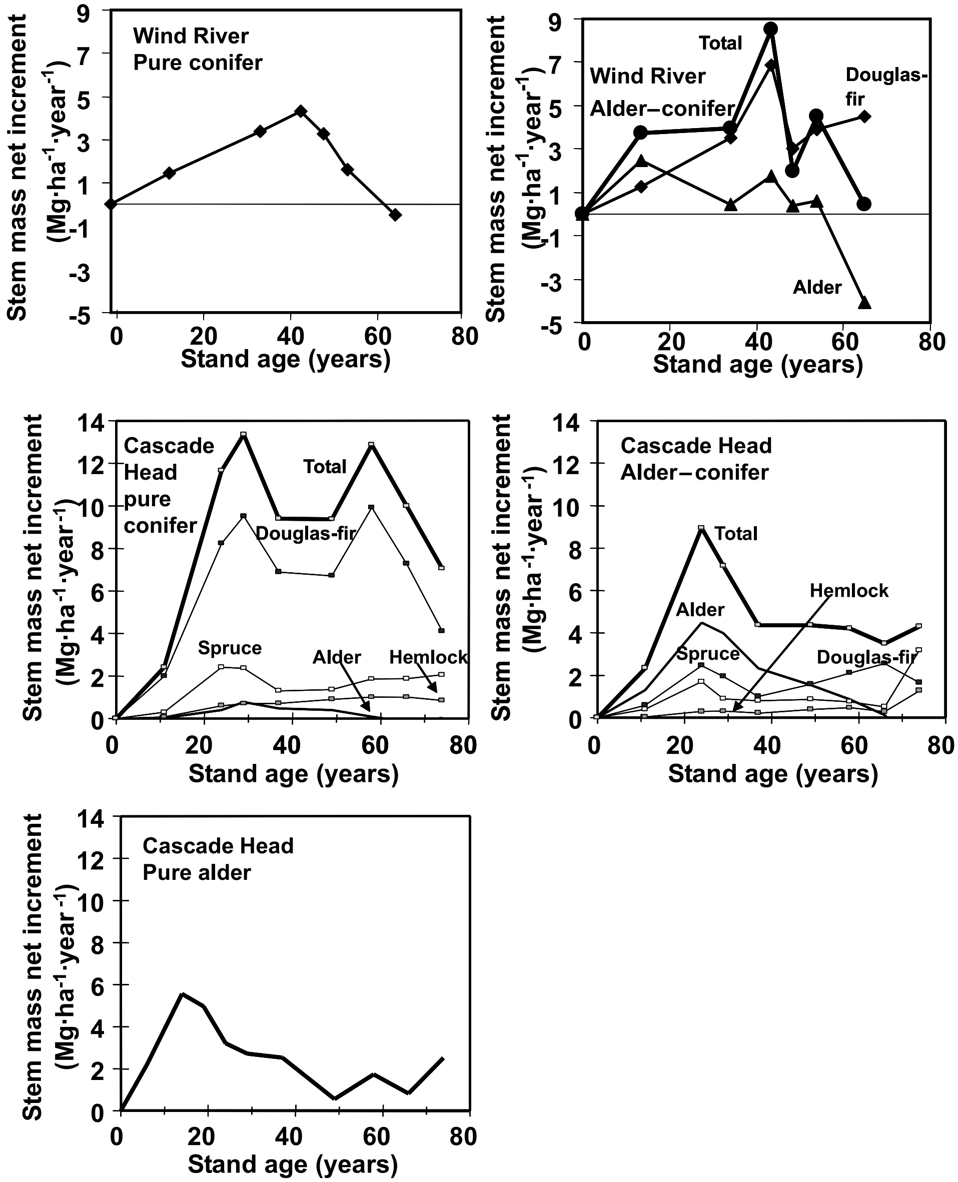


forests, where some intensive experimental plantations have not reached a midrotation point (Miller et al. 1999; Rothe et al. 2003). The Wind River and Cascade Head sites remain the only temperate forest experiments that are past the midrotation point of stand development. The biomass and production of these classic experiments were last reported through stand age 55 (Binkley et al. 1992); this paper updates the stand development situation for these forests for an additional 16–18 years.

Site description and methods

The Wind River stands were planted with 2-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings (1700/ha) in 1929 following a series of three fires earlier in the century. Four years later, seedlings of red alder were interplanted with the Douglas-fir in a long strip (20 m × 1600 m, 3000 alder/ha). The pure conifer plot also contained some naturally regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), accounting for about 4% of the total stem mass at age 72. The plantation without alder was very N deficient, containing only 2200 kg N/ha in the vegetation and soil to 0.9 m at age 55 years (Binkley et al. 1992); inclusion of alder increased ecosystem N content to 5100 kg N/ha. Site index for Douglas-fir without alder was about 25 m at 50 years, or Site Class IV (Miller and Murray 1978). The data presented here are from Tarrant's (1961) set of 12 paired plots in the conifer and alder–conifer stands (stand age 27) and Miller and Murray's (1978) set of four plots in each type (stand age 46). More recent sampling (stand age 50 and 55; Binkley et al. 1992) (age 72 in the spring of 2003) used variable-radius prism plots (1.86 m^2/ha basal area factor) with 10 (age 50 and 55) or 20 (age 72) plots at random intervals along a 200-m transect in each type. The transects ran down the middle of the alder–conifer strip (100 m in each direction from the section corner (sections 24, 19, 25, and 30 of T4N R7E)), with a parallel transect 50 m into the pure conifer stand beyond the western edge of the alder–conifer strip. Tree diameters were converted to stem biomass using the same equations as in Binkley et al. (1992) (from the Oregon State University Forest Science Data Bank; Means et al. 1994):

Fig. 2. Net stem increment with stand age for the pure and mixed stands at the Wind River and Cascade Head sites.



$$\log_e(\text{alder mass in kg}) = -2.669 + (2.463 \times \log_e(\text{diameter in cm}))$$

$$\log_e(\text{Douglas-fir mass in kg}) = -3.0396 + (2.5951 \times \log_e(\text{diameter in cm}))$$

$$\log_e(\text{hemlock mass in kg}) = -2.681 + (2.447 \times \log_e(\text{diameter in cm}))$$

The Cascade Head stands developed after pasture abandonment in 1925. Natural regeneration of alders and conifers led to very high stem densities (4500 conifers plus 3000 alder at age 8). Plots were established in the mid-1930s, including a control (Plot 11, 0.4 ha), and plots thinned to provide a pure plot of conifers (2800/ha, Plot 17, 0.2 ha) and another of alder (3100/ha, Plot 11, 0.2 ha). The pure conifer plot was N rich, with 9500 kg N/ha at age 55 (vegetation and soil to 0.9 m) compared with 14 500 kg/ha in the alder–conifer plot (Binkley et al. 1992). Berntsen (1961) considered the site to be Site Class II for conifer growth, although later stand growth showed productivity at the border between Site Classes II and I (site index of about 40 m at 50 years). Early stand development was reported by Berntsen (1961) and Binkley and Greene (1983) based on complete tallies of all trees (>2.5 cm diameter at breast height) in each plot, with no border area reserved between plots. The most recent measurement was in 2001, when the stands were about 75 years old. Stem mass was estimated with the equations listed above; Sitka spruce (*Picea sitchensis* (Bong.) Carrière) was estimated as

$$\log_e(\text{spruce stem mass in kg}) = -8.55 + (2.457 \times \log_e(\text{diameter in mm}))$$

Results and discussion

The total stem increment in the mixed stand (conifer and alder) at Wind River was greater than in the pure conifer stand at all ages. The pure conifer plot showed greater stem increment than the conifers in the mixed stand for the first 40 years of stand development (Figs. 1 and 2). Conifer growth was similar in both stands for the subsequent 10 years, but after age 50, the pure conifer stand's net increment approached 0, while conifer growth remained high in the mixed stand. The dramatic decline in net increment of Douglas-fir in the mixed stand between age 45 and 50 resulted from mortality of many dominant trees following girdling by black bears. With increasing dominance by Douglas-fir in the mixed stand, alder biomass plummeted from about 70 Mg/ha at age 55 to 10 Mg/ha at age 72. The pattern of alder mortality was spatially variable in the mixed stand, and at age 72 the biomass of Douglas-fir in the prism plots declined with increasing biomass of the surviving alder (Douglas-fir stem mass = 263 Mg/ha – 2.31 × alder stem mass; $r^2 = 0.33$, $P < 0.01$). Apparently the long-term benefit of alder on Douglas-fir growth was more pronounced at age 72 where the alder had died at some earlier point in stand development; recent competition with remaining alders appeared to remain important.

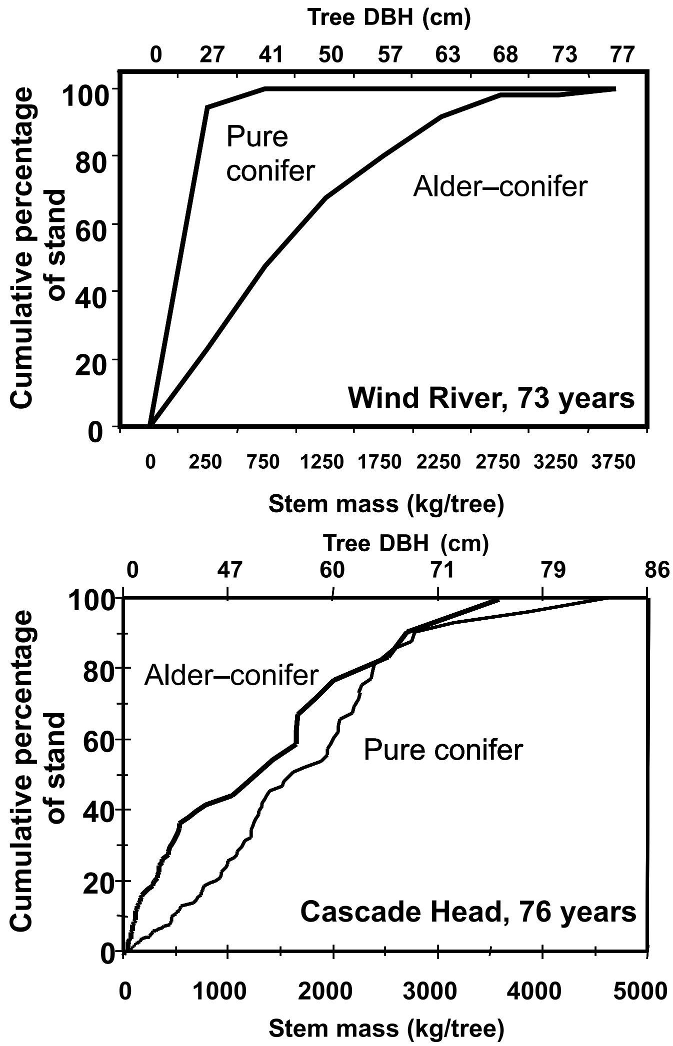
The pure conifer stand at Cascade Head had greater conifer stem mass and total stem mass than the mixed stand or the pure alder stand for all ages (Figs. 1 and 2). In fact, this plot's biomass of 600 Mg/ha rivaled the mass of stems in a 450-year-old Douglas-fir – mixed conifer forest on a less fertile site in the Cascade Mountains of Oregon (Grier and Logan 1977). The mass of the conifer plot at Cascade Head is probably overestimated owing to the likely effect of edges with the surrounding mixed forest that had lower biomass. The effects of alder might extend 5–15 m into adjacent forests (Rhoades and Binkley 1992; Miller et al. 1993; Lavery 2000); if the edge effect extended just 5 m into the pure conifer stand (with dimensions of about 35 m × 60 m) at Cascade Head, this zone of edge influence would constitute about 40% of the plot.

Alder growth was notably slower than conifer growth at the N-rich Cascade Head site, and the interactions of alder with conifers appeared to be purely competitive with no facilitation benefit for the conifers. Alder stems comprised about 40% of the stem mass in the mixed plot at age 75, but the net increment of alder had dropped to -1.8 Mg·ha^{-1}·year^{-1} in the most recent measurement interval. These values are probably not biased by edge effects, as the mixed plot was twice the size of the pure plots, and species composition was similar in the surrounding forest matrix.

The pure stand of alder at Cascade Head continued to accumulate stem mass at a slow but steady rate. The mass and growth of this plot may also have been influenced by the edge effect; in this case, the values may be underestimated, as the surrounding forest matrix contained large conifers.

The stand-level averages for all of these plots result from the combined patterns of stem density per hectare and tree size. At Wind River, the pure conifer stand comprised relatively small trees; over 90% weighed less than 250 kg (about 27 cm diameter at breast height) (Fig. 3). The Douglas-fir in the mixed stand were much larger, with half of the trees weighing more than 750 kg (about 41 cm diameter at breast height). This pattern was reversed at Cascade Head, where the size distribution of conifers was larger in the pure conifer stand than in the mixed stand. At both locations, the plots with greater conifer stem mass per hectare also had the largest individual tree sizes. The economic value of each kilogram of conifer stem mass may be much greater for larger stems, further enhancing the value (at Wind River) or cost (at Cascade Head) of inclusion of alder in the stands.

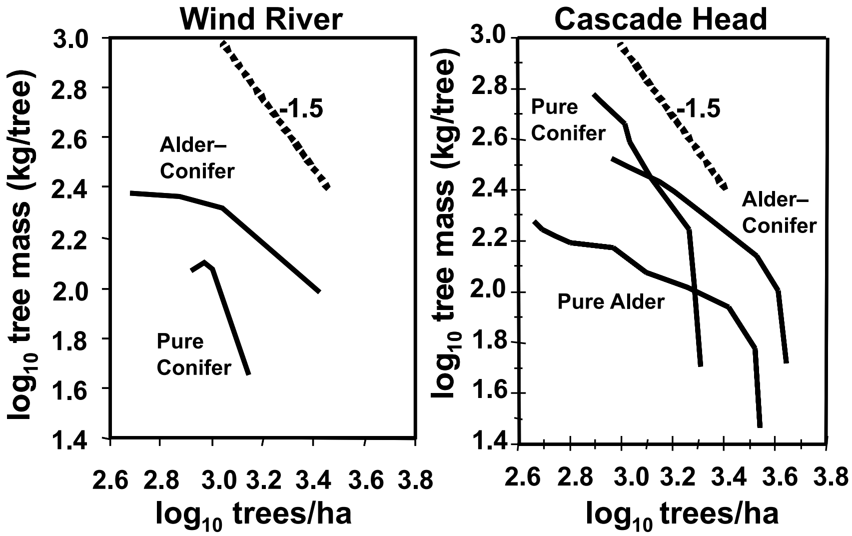
Fig. 3. Cumulative stem mass distributions for conifers at Wind River and Cascade Head. Conifers were much larger in the mixed stand at Wind River than in the pure conifer stand, whereas the opposite pattern developed at Cascade Head.



All the stands experienced substantial mortality over seven decades of stand development, and each stand appeared to follow a unique trajectory of tree density per hectare and average tree size (Fig. 4). The pure conifer stand at Cascade Head appeared to follow a classic trend of self-thinning, with a slope near –1.5. The other plots showed a variety of patterns, either with slopes of less than –1.5 (mixed at Wind River, pure alder and mixed at Cascade Head) or a pattern that probably reflects severe nutrient deficiency (and competition with understory shrubs) (Wind River conifers).

Overall, the latest remeasurement of these classic experiments yielded no major surprises. The increasing dominance

Fig. 4. Average tree size as a function of density over the course of stand development for Wind River and Cascade Head.



of Douglas-fir in the mixed stand at Wind River was apparent before age 50 (Miller and Murray 1978), and the death of most of the alder by age 72 was expected. The pattern of growth of the conifers may have been a bit unexpected, with near-zero net increment in the pure conifer stand and sustained high net increment in the mixed stand. Indeed, the conifer increment in the Wind River mixed stand (4.5 $Mg \cdot ha^{-1} \cdot year^{-1}$) had reached the rate of the conifers in the mixed stand at the much more productive Cascade Head site and about 60% of the rate of conifer increment in the pure conifer stand at Cascade Head. Stand development at Cascade Head simply demonstrated continued development of trends that were apparent at age 30 (Berntsen 1961) and 53 (Binkley and Greene 1983).

The long-term development of these classic experiments continued to support the idea that inclusion of codominant N_2-fixing alders in conifer stands should increase stand production on poor soils and increase the yield of conifers late in a rotation. Inclusion of alders in conifer stands on N-rich sites should lower both total stand growth and conifer yield (Binkley and Greene 1983). The optimal balance of alders in a mixture with conifers on N-deficient sites probably varies with relative tree dominance and spatial patterning of the stand; more recent experiments with species-replacement designs will provide some insights into this balance, and a greater range of insights might be obtained by analyzing the spatial pattern in tree species, size, and soil fertility in a variety of stands that have developed as unplanned mixtures.

What proportion of the forest landscape of the northwest region might benefit from mixtures of conifers and red alder? The Site Class IV productivity of the Wind River site (without alder) represents about one-quarter of the forest lands in western Oregon and Washington, whereas the Site Class II or I productivity of the Cascade Head site (without alder) represents about 45%–50% of the forest land (Isaac 1949; Azuma et al. 2002). Nitrogen limitation of Douglas-fir growth is generally greater on poorer sites (Chappell et al. 1992), and industrial forest management typically places the highest priority on fertilization of Site Class IV and III forests (Briggs et al. 2001). Based on these characteristics, I estimate that red alder may have the potential to increase conifer growth and total forest growth on about one-quarter (the Site Class IV lands) of the forest lands of western Washington and Oregon. The operational impacts of alder in these forests would depend in large part on the silvicultural treatments that allowed conifers to remain codominant and on special cases where other resources (such as water supply) may exacerbate competition between species. Red alder would probably decrease both total stand growth and conifer growth on about one-half of the forest lands in the same region (Site Class II and I lands). Site Class III lands commonly respond strongly to N fertilization, but the balance between competition and facilitation of alder on conifers might be highly variable in these intermediate-productivity lands.

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