Stand dynamics of mixed red alder – conifer forests of southeast Alaska

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Abstract: Stand structure and dynamics were evaluated in mixed red alder (*Alnus rubra* Bong.) – conifer forests of southeast Alaska. We assessed stand development, tree density, total basal area, diameter distribution of live and dead trees, height distribution of live trees, and mean diameter of all and largest conifers in 40-year-old red alder – conifer stands that developed following logging. Forty-five plots were established in nine stands sampled across a compositional range of 0%–86% alder. Alder height growth was initially rapid then slowed considerably, whereas conifer height growth was initially slow then rapidly increased with conifers now being 4–9 m taller than associated alders. Most alder diameters were 20–30 cm and conifer diameters were more variable with numerous small (3–10 cm) and a few large (>25 cm) trees. Total stand basal area significantly decreased (p = 0.013) with increasing proportions of alder, but density of live and dead trees was not closely associated with alder composition. More than 60% of all dead trees died standing regardless of size or species. Overall, these mixed red alder – conifer stands provided more heterogeneous structures than pure conifer stands, with more even diameter distributions, multiple canopy layers, and similar numbers of large diameter conifers.

Résumé : La structure et la dynamique des peuplements ont été évaluées dans les forêts mélangées d'aulne rouge (*Alnus rubra* Bong.) et de conifères du sud-est de l'Alaska en estimant le développement du peuplement, la densité des tiges, la surface terrière totale, la distribution diamétrale des arbres morts et vivants, la distribution de la hauteur des arbres vivants et le diamètre moyen de tous les plus gros conifères dans des peuplements d'aulne rouge et de conifères âgés de 40 ans qui se sont développés après une coupe. Quarante-cinq places-échantillons ont été établies dans neuf peuplements représentant une gamme de composition allant de 0 à 86 % d'aulne. La croissance en hauteur de l'aulne qui était rapide au début ralentissait considérablement par la suite alors que la croissance en hauteur des conifères qui était lente au début augmentait rapidement par la suite de telle sorte que les conifères étaient maintenant 4–9 m plus hauts que les aulnes avec lesquels ils étaient associés. Le diamètre de la plupart des aulnes était de 20–30 cm et celui des conifères était plus variable avec plusieurs petites tiges (3–10 cm) et quelques grosses tiges (>25 cm). La surface terrière totale diminuait significativement (p = 0,013) avec une augmentation de la proportion d'aulne mais la densité des arbres morts et vivants n'était pas étroitement reliée à la composition en aulne. Plus de 60 % de tous les arbres morts sont morts debout peu importe la dimension ou l'espèce. Dans l'ensemble, ces peuplements mélangés d'aulne et de conifères ont une structure plus hétérogène que les peuplements purs de conifères avec des distributions diamétrales plus régulières, plusieurs strates de végétation et un nombre similaire de conifères de fort diamètre.

[Traduit par la Rédaction]

Introduction

Intensive logging practices since the 1950s in southeast Alaska have increased the amount of red alder (*Alnus rubra* Bong.) in forests that develop after logging, particularly in areas where heavy soil disturbance resulted from tractor and cable-logging operations. Red alder, the most common hardwood tree in the Pacific Northwest, is a relatively short-lived, shade-intolerant pioneer species with rapid juvenile height growth (Harrington 1990). Red alder requires high light levels to regenerate and is frequently found on exposed mineral soil. In Alaska, red alder is commonly found along beaches and streams, on avalanche tracks, landslides, and logging skid trails, and as a pioneer species with Sitka spruce (*Picea sitchensis* (Bong.) Carriére) where mineral soil has been freshly exposed to seedfall (Harris and Farr 1974; Harrington et al. 1994). There is considerable information on red alder in the Pacific Northwest (Trappe et al. 1968; Hibbs et al. 1994), and alder commonly occurs in both pure and mixed stands with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) (Harrington 1990; Newton and Cole 1994). In Alaska, pure stands of red alder are rare and alder occurs primarily in mixed stands with shade-tolerant conifers including Sitka spruce, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar *Thuja plicata* Donn ex D. Don). Basic silvicultural information on red alder in Alaska is scarce, and it is unknown whether the development of alder in mixed stands with shade-tolerant conifers is similar to patterns observed with shade-intolerant species such as Douglas-fir.

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The coastal old-growth rain forests of southeast Alaska have simple tree composition but complex forest age and size structure. The predominant tree species, Sitka spruce and western hemlock, comprise over 90% of the region's total growing stock volume (Hutchison 1967). Abundant precipitation occurs throughout the year along with occasional hurricane-force winds, and wind-caused disturbances are common (Harris 1989; Nowacki and Kramer 1998). Complex multi-aged stands have been created by high-frequency, small-scale natural disturbances, such as endemic tree disease and wind-related disturbances (Brady and Hanley 1984; Deal et al. 1991; Kramer et al. 2001). These multi-aged stands contain complex, heterogeneous forest structures with many forest canopy layers, large trees and snags, heart rot cavities in live trees, logs and large woody debris, abundant understory vegetation, and other important ecological characteristics of old-growth forests (Franklin et al. 1981; Alaback 1982*b*; Alaback and Juday 1989; Franklin and Spies 1991).

In southeast Alaska, forest development following stand-replacing disturbances such as clear-cutting and windthrow is different than typical forest development following natural small-scale disturbances. Postharvest conifer regeneration is frequently abundant (>10 000 trees/ha), and the forest canopy closes in 15–25 years followed by a dense, long-lasting stage of stem exclusion (Alaback 1982*a*; Deal et al. 1991). These dense, young-growth stands have relatively uniform tree height and diameter distributions and notably lack the multi-layered, diverse structures of old-growth forests. Tree mortality in the densely stocked, conifer-dominated young-growth stands of southeast Alaska leads to many small diameter dead stems primarily originating from suppression mortality (Tait et al. 1985). By contrast, dead trees and the resulting woody debris in old-growth stands can be large and variable because internal heart rot is abundant, some dominant trees die, and tree death commonly leaves trees standing, broken-stemmed, or uprooted (Hennon and McClellan 2003).

Recent studies of young alder–conifer stands in southeast Alaska indicate different successional pathways following clear-cutting than the previously described development patterns of pure conifer stands. These mixed alder–conifer stands generally appear to have lower tree stocking and stand density (Deal 1997) than pure conifer stands of a similar age (40–50 years), with more open forest canopies especially during seasons when alder trees are leafless. Other studies in the region have reported increases in plant species richness and understory vegetation in mixed alder–conifer stands (Hanley and Hoel 1996; Deal 1997; Hanley and Barnard 1998). Longer-term forest succession in mixed alder–conifer stands, however, is not well understood.

There is increasing interest in developing forest management practices that maintain or enhance biodiversity and assure long-term sustainability of forest products, wildlife, and other forest resources. This study is part of a broadly integrated research project that examined the role of red alder to help achieve multiple resource compatibility in managed young-growth ecosystems in southeast Alaska (Wipfli et al. 2002). Our component of the overall study assessed the relationship of alder with stand density, structure, and development of mixed alder–conifer young-growth forests. This paper includes the following specific study objectives:

- Evaluate whether differences in tree density, basal area, and diameter distribution of both live and dead trees are associated with the proportion of alder in young-growth stands.
- Evaluate whether important forest structures such as large, live conifers; internal decay of live trees; and dead tree type are associated with the presence of alder.
- Interpret stand dynamics in mixed alder–conifer young-growth forests by using height growth reconstructions, size distribution of live and dead trees in current stands, and knowledge about the shade tolerance of different tree species.

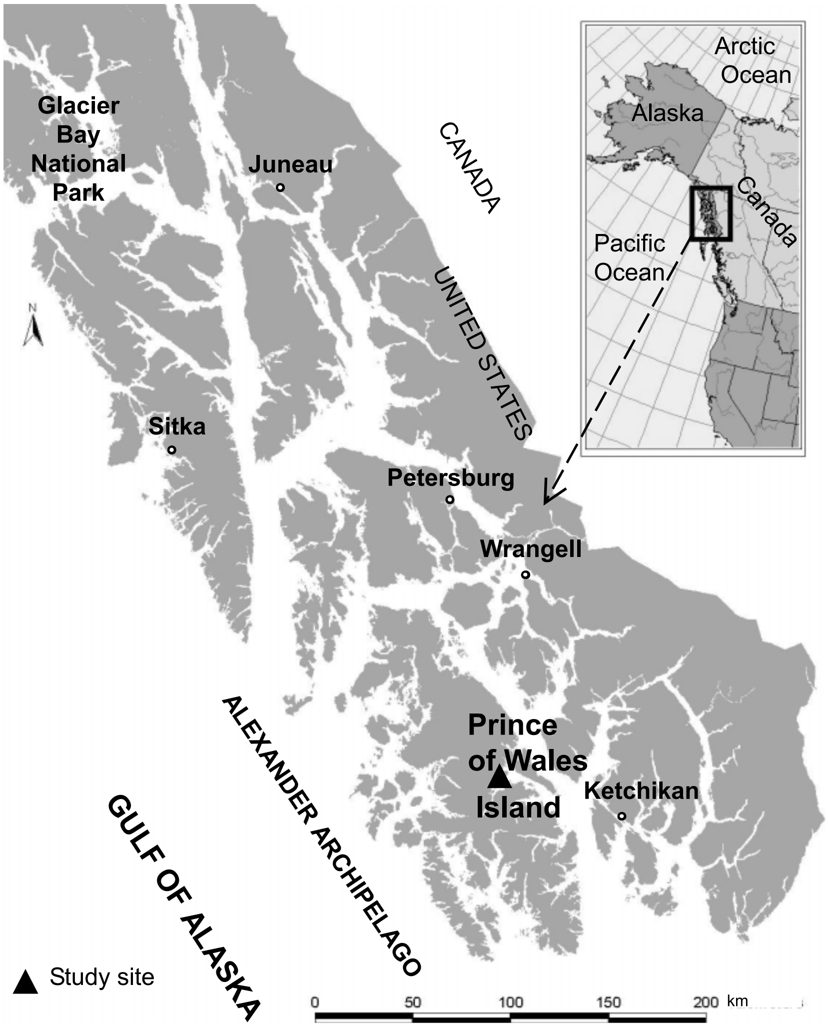
Materials and methods

Study areas and stand selection

Study sites are located in the Maybeso and Harris watersheds on Prince of Wales Island (55°49′N, 132°67′W) in southeast Alaska (Fig. 1). These watersheds are approximately 46 km^2 and 108 km^2 in size, respectively. The rugged mountains of central Prince of Wales Island are dissected by broad, deglaciated, U-shaped valleys. Metasedimentary mudstones, shales, conglomerates, and metavolcanic diorites dominate the study area (Swanston 1967; Nowacki et al. 2001). Sites are in depositional zones located on complex slopes and alluvial fans in mountain flank or mountain base geomorphic positions (Table 1). Soils are primarily derived from colluvial and alluvial sediments from glacial till and bedrock from the upper slopes. The climate is maritime-cool and moist, with an annual precipitation of 2500–3000 mm and average temperature of 6 °C (Western Regional Climate Center 2002). Sites are moderately to highly productive for forest growth (50-year spruce site index of 27–35 m; Farr 1984). Well-drained sites are occupied by western hemlock and Sitka spruce forests, whereas wetter sites contain mixed conifer stands with greater amounts of western redcedar. All sites were cable logged without using higher suspension cable-logging systems that have been in practice in the region since the early 1970s. Soil disturbance from these cable-logging operations and natural disturbances (Johnson and Edwards 2002) favored red alder regeneration and led to a higher component of alder in these stands than is currently found in more recently logged young-growth stands.

The proportion of alder in total stand basal area was the main criterion for stand selection, with an increasing proportion of alder sampled across a compositional range from pure conifer to alder-dominated stands. There were no pure alder sites available and predominantly alder sites were rare; hence, our mixed stands generally had more conifer than alder. Potential study areas were selected from a pool of sites identified by aerial photographs and USDA Forest Service district files. To reduce variability among sites, we selected stands in two adjacent watersheds having large contiguous areas that were clear-cut using cable-logging systems about 40 years ago. We selected nine stands during the summer of 2000 for intensive sampling (Table 1). Site selection criteria included stands that were logged and naturally regenerated, average stand size of 5–10 ha, elevation less than 150 m,

Fig. 1. The research study area of southeast Alaska.



moderate slopes of 10%–40%, and no intermediate management activities (e.g., no thinning, planting, or alder girdling). We installed a systematic grid of 20 variable-radius plots throughout each stand to determine average stand composition and to ensure our selection of sites provided a wide range of alder–conifer mixtures.

Plot data collection

Fixed-area plots were installed at five randomly selected, variable-radius plot locations in each stand. A total of 45 fixed-area plots in the nine stands were used to measure stand density, tree size distribution, patterns of tree mortality, tree height growth patterns, and to assess the relationship of increasing proportions of alder on stand density, tree mortality, and tree size, including the growth of large-diameter conifers. Each fixed-area plot consisted of four nested circular plots (Avery and Burkhart 1994): one large 0.05-ha plot (radius 12.62 m) to sample larger live and dead trees and three small 0.0025-ha plots (radius 2.82 m) to sample all trees. One small plot was located at the center of the large plot and two others at 8 m from plot center in randomly selected directions. Live and dead trees ≥20 cm DBH (diameter at breast height, 1.3 m) were measured in the 0.05-ha plots, and all live and dead trees ≥3 cm DBH were measured in the 0.0025-ha plots.

On each fixed-area plot, tree species, crown class, DBH, and total tree height were measured for all live trees to provide current stand structural information. Species, DBH, and type of dead tree structure (standing, uprooted, broken bole, or broken at the root collar) were recorded for all dead trees. We also noted the type of wood decay (i.e., white or brown rot (Gilbertson and Ryvarden 1986) or not decayed) for all dead trees. Type of wood decay was based solely on visual observation and the presence of fungal fruiting bodies, because there is no reliable field test to distinguish decays. On each fixed-area plot, tree increment cores were taken from two randomly selected live trees from each species and crown class to determine stand cutting date and tree age and to perform tree ring analyses with a total of 50–60 trees sampled in each stand. In addition, one dominant alder and one dominant conifer tree were randomly chosen from each 0.05-ha plot for tree age and height growth analysis. Not all plots had dominant alders and conifers, and a total of 35 red alders and 31 conifers (26 spruce and 5 hemlock trees) were destructively sampled to reconstruct height growth patterns of overstory trees. Selected trees were felled and intensively

Table 1. Stand density, species composition, and soil characteristics of nine sites listed with an increasing proportion of red alder basal area.

		Basal area		Species composition				Soil characteristics		
Site	Cutting date	Stand (m^2/ha)	Alder (% BA)*	Alder (trees/ha)	Spruce (trees/ha)	Hemlock (trees/ha)	Cedar (trees/ha)	Geomorphic position	Geomorphic deposit	Soil type
UGE	1958	59.6	0	0	493	819	0	Mountain flank	Colluvial–Alluvial	Karta–Tolstoi
CED	1960	50.6	3	24	705	2533	488	Mountain flank	Colluvial	Tolstoi–Rock outcrop
LM	1958	48.0	16	348	601	753	468	Mountain flank	Colluvial–Alluvial	Tolstoi
LGE	1958	60.8	18	451	843	689	27	Mountain base	Colluvial–Alluvial	Tolstoi–Karta
M22	1960	54.4	28	392	265	1415	0	Mountain flank	Alluvial	Tolstoi–Karta
BS	1960	47.8	33	291	303	672	57	Mountain flank	Colluvial–Alluvial	Tolstoi–Rock outcrop
GP	1962	45.5	39	560	519	801	0	Mountain base	Alluvial	Tolstoi–Karta and Tonowek–Tuxekan
AF	1958	46.0	64	680	645	333	27	Mountain base	Alluvial	Tolstoi–Karta
BR	1960	38.0	86	708	275	389	240	Mountain flank	Colluvial–Alluvial	Tolstoi–Karta

*BA, basal area.

sampled, with stem sections collected at the base of root collar, 1.3 m, 3 m, and at every subsequent 2 m up the bole to the top of the tree. The presence and extent of any wood decay present in these sections from live trees were also recorded as an indication of heart rot. Two soil pits within each of the 0.05-ha fixed-area plots were used to assess the relationship between soil particle size and water content with the abundance of alders and conifers. These soil pits were excavated to a depth of 50 cm and described according to the Soil Survey Manual (Soil Survey Division Staff 1993). All of the material from the pits was passed through a 75- and 20-mm sieve for particle size analysis. A subsample of particles passing the 20-mm sieve was oven-dried (105 °C for 24 h) to determine field moisture content.

Data analyses

Tree data for the fixed-area plots were combined by stand to determine species composition, tree density, basal area, tree height and diameter distribution, and stand and tree growth. Alder and conifer height growth was reconstructed for each destructively sampled tree based on tree height and age data from stem sections. Alder and conifer height growth patterns were plotted and averaged for each stand, and a species height growth curve was developed from data on all sampled trees. Tree data from the fixed-area plots were combined and averaged by stand to determine the effect of increasing amounts of alder (percent of alder as a proportion of total live stand basal area) on stand density and tree size. The proportion of alder basal area was regressed with total stand basal area, tree density (live and dead, separately), mean diameter of all conifers, and mean diameter of the 100 largest conifers per hectare (SAS Institute Inc. 1990). Using a similar model, we also regressed the proportion of alder basal area with soil moisture and soil particle size class (<20, 20–75, and >75 mm). We also evaluated potential differences in wood production (total basal area) as a function of increasing proportions of alder by regressing the proportion of alder basal area for our 45 plots with total basal area.

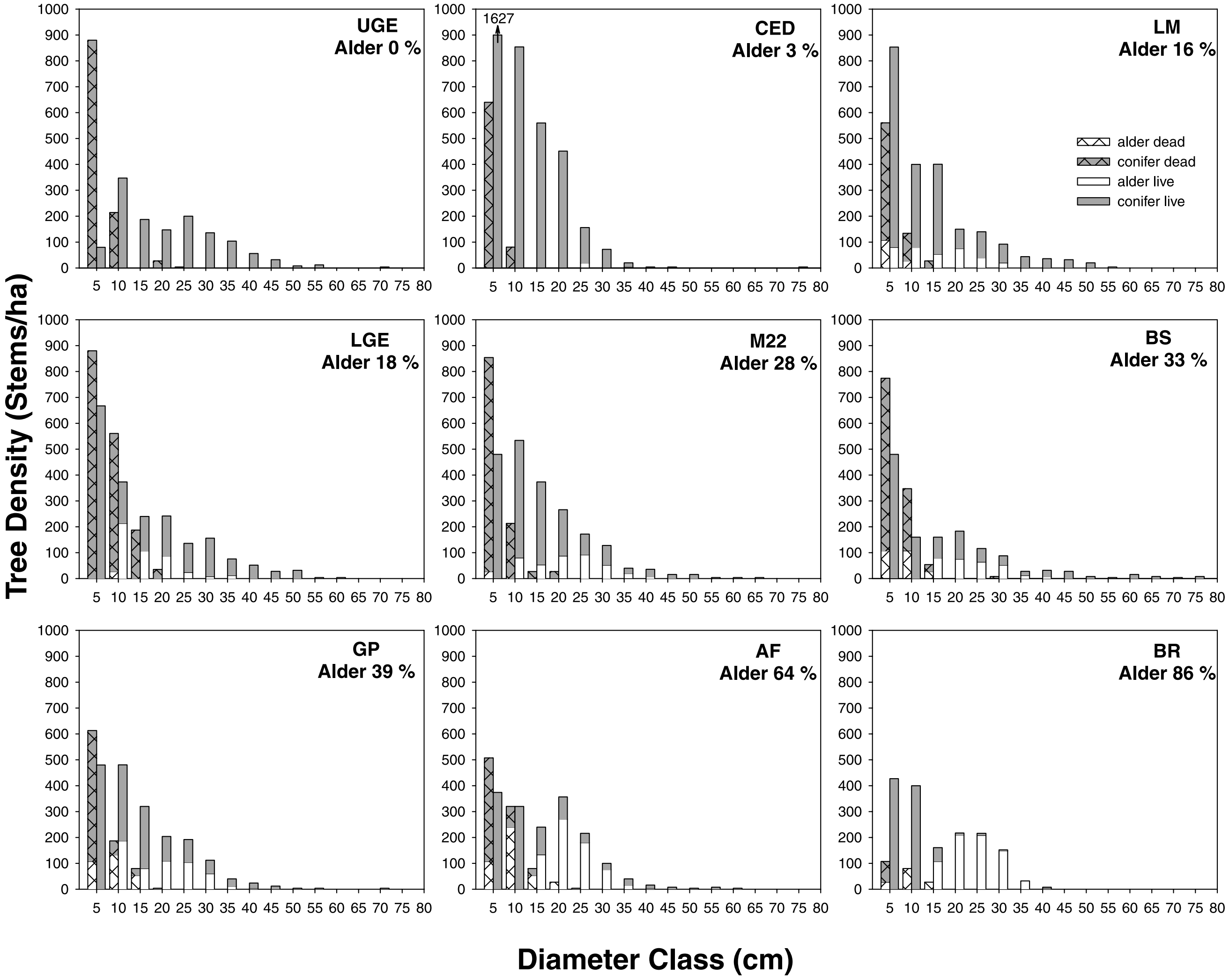
We segregated data on dead trees into two diameter classes (3.0–9.9 and ≥10.0 cm) and calculated the number of dead stems per hectare and the proportion of trees by type of tree mortality for each diameter class. These diameter classes were chosen because they were used to classify small and large woody debris, respectively, in a concurrent study (Gomi et al. 2001). Pearson's χ^2 test (SAS Institute Inc. 1990) was used to test for variability among types of dead trees (i.e., uprooted, standing, broken bole, broken at root collar) by species and size classes.

Results

Current stand density, composition, and size distribution of live and dead trees

Stem section and increment core age data indicate that the nine sites were harvested 38–42 years ago (Table 1). Following harvesting, all stands naturally regenerated with variable mixtures of red alder, western hemlock, Sitka spruce, and western redcedar. Most trees were new regeneration, although several small residual conifers remained from the former stand. All red alder were new trees established after

Fig. 2. Tree diameter distribution of live and dead red alders and conifers in nine young-growth forests. Conifers include combined total of Sitka spruce, western hemlock, and western redcedar. The percent alder for each stand is the alder proportion of total stand basal area.



logging. Tree composition in the current stands ranged from 0%–86% alder as a proportion of total live stand basal area. Tree density (all live stems ≥3 cm DBH) ranged from a maximum of 3750 trees/ha at a predominantly conifer stand (CED, 3% alder) to approximately 1300 trees/ha at two stands with different compositions (BS, 33% alder; UGE, 0% alder; Table 1).

Diameter distributions of live trees differed between red alders and conifers. All of the conifers in this study (Sitka spruce, western hemlock, and western redcedar) had similar diameter distributions and were combined as conifer. Live conifers had many more trees in the smallest size classes, with decreasing numbers of trees in progressively larger size classes following a reverse J-shaped diameter distribution (Figs. 2 and 3*a*). The diameter distribution of dead conifers followed the same pattern, with even greater confinement to the smallest diameters (i.e., 5-cm class) and no appreciable mortality in overstory trees >20 cm (Fig. 2). In contrast with the conifers, the diameter distribution of live alders had a bell-shaped distribution, with the greatest number of alders in the 20- to 30-cm diameter classes and fewer smaller and larger diameter trees (Fig. 3*a*). Most alders that died were also small diameter trees, but unlike dead conifers that were restricted to the smallest size class, most dead alders were in the 10-cm class (Fig. 2). The number of dead conifer stems generally exceeded that of dead alder even in stands of relatively balanced composition. We recorded 293 dead alders and 591 dead conifers/ha at the GP site (39% alder) and 427 dead alders and 511 dead conifers/ha at AF (64% alder). Sixty percent or more of all dead trees were found standing, with small percentages each with broken boles, down with broken roots, and uprooted (Fig. 4). This pattern of dead tree structures was similar for both conifers and alders and for small (3 cm ≤ DBH < 10 cm) and for larger trees (DBH ≥ 10 cm). Small dead conifer stems were by far the most abundant on a stems/ha basis (Fig. 4). The only other groups of dead trees that exceeded 20% were small alders on the ground with broken roots and large uprooted alders.

Mixed alder–conifer stands had more complex diameter distributions than pure or conifer-dominated stands. The conifer-dominated stands (UGE, 0% alder; CED, 3% alder; LM, 16% alder) had several hundred trees in the smallest di-

Fig. 3. (*a*) Average tree diameter distribution and (*b*) average tree height distribution of all alder and conifer trees at nine sites.

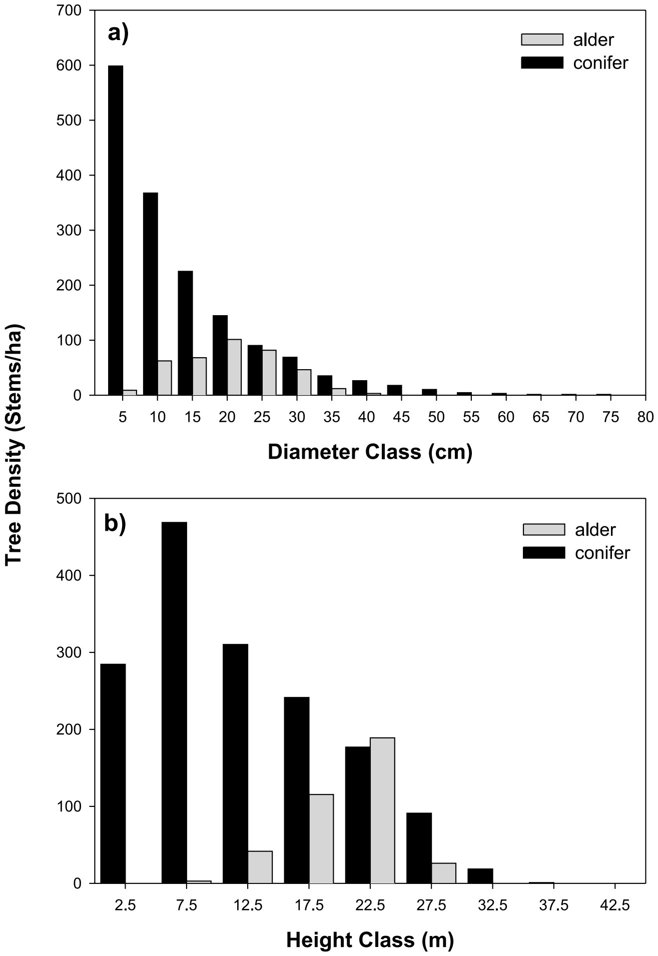
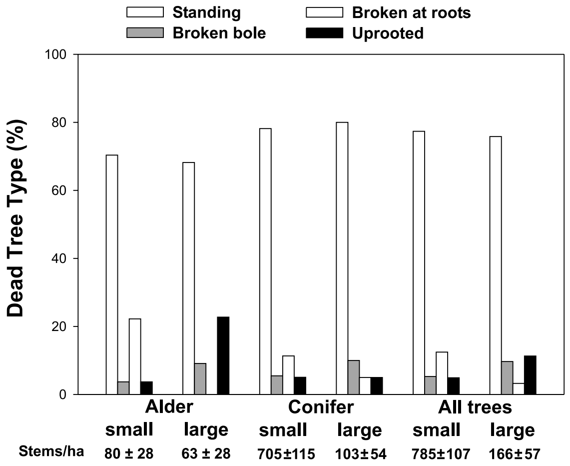


Fig. 4. Dead tree structures for alder and conifer. Small and large sizes refer to diameters of 3–9.9 and ≥10 cm, respectively, which are small and large classes of woody debris (Gomi et al. 2001). Stems/ha values refer to mean and standard error from the nine stands.



ameter classes, with fewer large or mid-sized diameter trees (Fig. 2). Stands with increasing proportions of alder (M22, 28% alder; BS, 33% alder) had fewer small diameter live trees but more mid-sized diameter alders and a few large diameter conifers. The alder-dominated stands (AF, 64% alder; BR, 86% alder) had fewer small diameter trees but many more 20- to 30-cm diameter alders. The alder in these stands provided a different diameter size cohort than the conifer-dominated stands that contained numerous small diameter trees. Live red alders were evenly distributed, with most trees in a narrow diameter (20–30 cm) and overstory height (20–25 m) range (Figs. 2 and 3). In contrast, all live conifers, including Sitka spruces, western hemlocks, and western redcedars, were unevenly distributed, with a few taller and larger-diameter trees and numerous smaller-diameter trees. These mixed alder–conifer stands created a multi-layered forest canopy with a few dominant overstory conifers, a midcanopy level of red alder, and a lower canopy level of small diameter conifers (Fig. 3*b*).

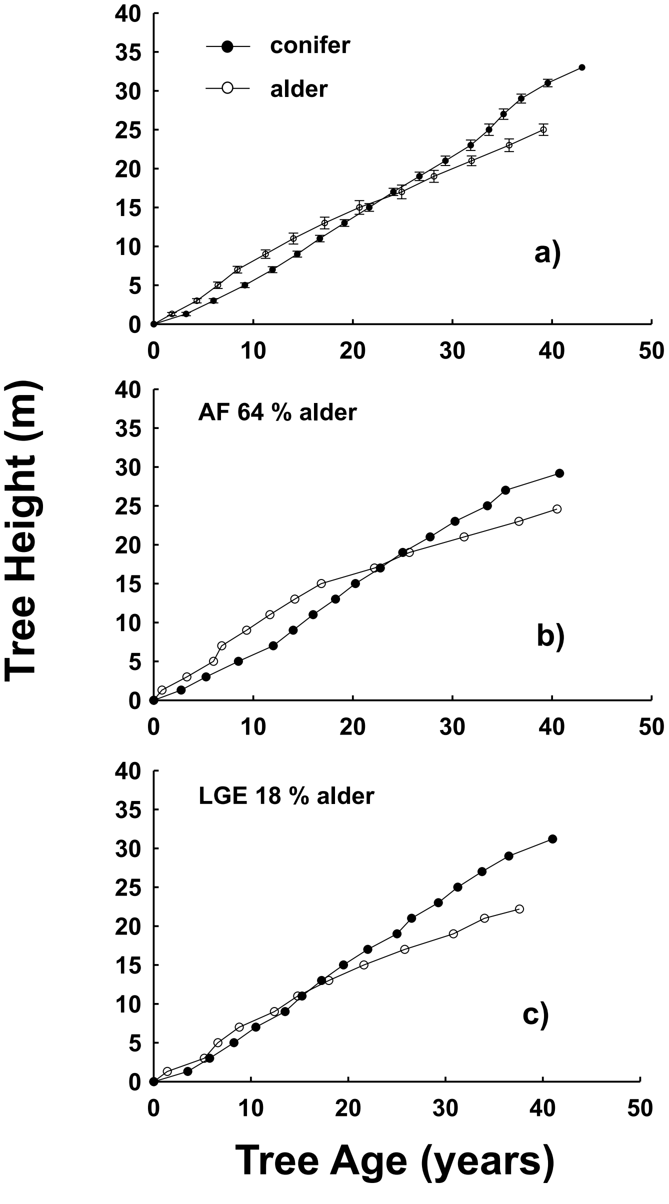
Development of mixed red alder – conifer stands

The combined height growth of all trees revealed different growth patterns for alders and conifers (Fig. 5*a*). Growth analysis showed that alders exhibited rapid early height growth but then slowed. Initially, conifers grew more slowly, but during the last 20–30 years they consistently had greater height growth than the associated alders. The combined data for all destructively sampled trees in the nine stands indicate that by age 22 years, conifer and alder heights were equal. In the current stands at age 40 years, however, conifers were an average of 6 m taller than associated alders. The height growth and development of alders and conifers varied considerably among sites. At an alder-dominated site (AF, 64% alder; Fig. 5*b*), the alders at the ages of 10, 20, and 30 years averaged a difference in height of +4.0, +1.5, and –2.0 m, respectively, compared with conifers of the same age. Height of dominant conifers was equal to the tallest alders at about 25 years after cutting (Fig. 5*b*), and in the current stand (year 2000), conifers averaged about 4.6 m taller than the associated alders. At the AF site, height growth of alders was uniform, with all of the alder heights slightly greater than 24 m. In recent years, conifers continued to grow rapidly while the alders consistently slowed in height growth. At a conifer-dominated site (LGE, 18% alder; Fig. 5*c*), this same general height growth pattern for alders was apparent with rapid early height growth followed by declining growth. The decline in height growth for alder at the LGE site, however, was more pronounced than that at the AF site. Alders at this site at the age of 10, 20, and 30 years averaged a difference in height of +2.1, –0.5, and –4.6 m, respectively, compared with conifers of the same age. Height of dominant conifers was equal to the tallest alders at about 18 years after cutting (Fig. 5*c*), and in the current stand (year 2000), conifers are now 9 m taller than the associated alders.

Relationship of alder composition with stand density and tree size

Tree species composition was related to differences in stand basal area and density of live and dead trees. Analysis of alder composition among the nine stands showed a significant decrease in total stand basal area with increasing proportion of alder basal area ($r^2 = 0.607$, $p = 0.013$; Fig. 6*a*). Tree density (e.g., stems >3 cm DBH), however, was not closely associated with alder composition: a slight and

Fig. 5. Height growth of dominant red alders and conifers (Sitka spruce and western hemlock) at research sites, including (*a*) average of all 35 alders and 31 conifers for the nine sites, (*b*) average height growth for six alder and four spruce trees for an alder-dominated site at AF, and (*c*) five alder and four spruce trees for a conifer-dominated site at LGE. Vertical lines in (*a*) represent standard errors.



nonsignificant decline in live trees/ha occurred with increasing proportion of alder basal area (Fig. 6*c*, $r^2 = 0.153$, $p = 0.298$). Whereas alder diameters were relatively similar among all of the sites, we found that the average diameter of all live conifers significantly decreased with increasing proportion of alder basal area ($r^2 = 0.518$, $p = 0.029$; Fig. 6*e*). This decrease in average tree size of conifers may explain why total basal area of stands declined with increasing alder composition (Fig. 6*a*) while tree stocking remained essentially unchanged (Fig. 6*c*). We also did not find a significant difference in mean diameter of the 100 largest trees/ha with increasing proportion of alder basal area in the stand ($r^2 = 0.209$, $p = 0.216$; Fig. 6*f*). Generally, the largest diameter conifers appeared to be relatively independent of alder composition, and we found large diameter trees across a wide range of alder–conifer mixtures. For dead trees, we did not find a significant correlation between increasing proportion of alder basal area and basal area of all dead trees (Fig. 6*b*, $r^2 = 0.009$, $p = 0.804$) or number of dead trees/ha (Fig. 6*d*, $r^2 = 0.266$, $p = 0.155$).

Stand composition and the distribution of alder were related to soil properties from both natural and anthropogenic disturbances. Alder is easily established on most types of soil, but is most competitive in disturbed, open areas with exposed, well-drained mineral soils that are not subject to seed desiccation (Haeussler 1988). Coarser soils generally appear to provide a more suitable substrate for alder colonization. Skid roads and landings, in particular, increased alder establishment in several of the sites, and coarse-textured alluvial soils supported more alder than colluvial sites. However, we found no significant correlation in the proportion of alder basal area with increasing proportion of coarse gravel (soil particle sizes 20–75 mm) ($r^2 = 0.067$, $p = 0.502$) on a stand area average. These stands also showed no significant relationship in the proportion of alder basal area with increasing field soil water content ($r^2 = 0.004$, $p = 0.876$). There was an apparent stratification of alder on the landscape, but the variability among soils within stands was large and we could not detect any significant influence of the soils on the relative composition of alder or conifer basal area.

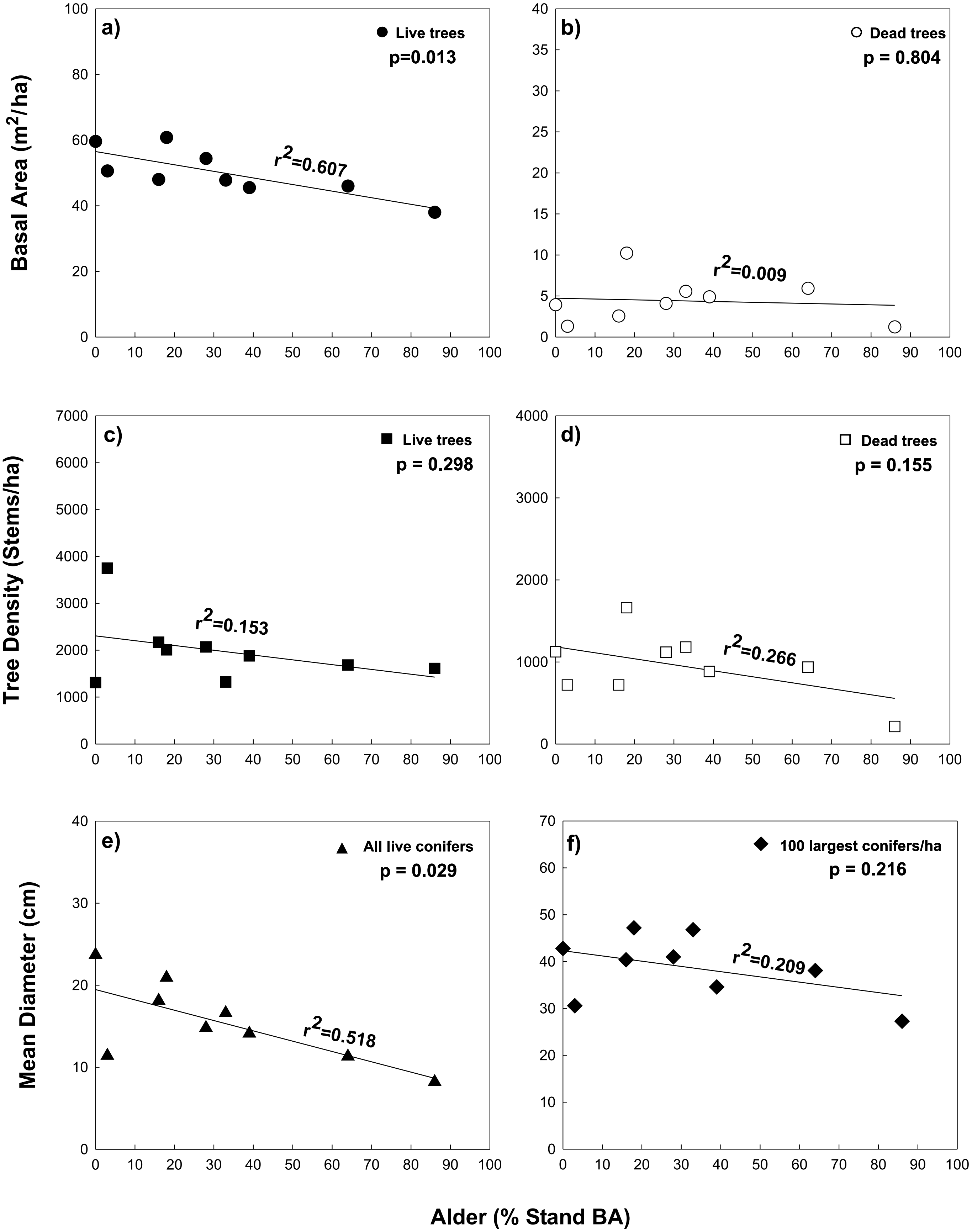
Discussion

Stand structure of mixed alder–conifer forests

Overall, mixed alder–conifer stands provided different tree size distributions and more complex forest structures than is typically found in pure conifer stands of the same age. Pure conifer young-growth stands in this region are typically very densely stocked (DeMars 2000) and have relatively uniform tree height and diameter distributions. Our results suggest that alder trees in these mixed alder–conifer stands can provide different tree size distributions with multiple canopy layers (Fig. 3*b*). We also found that the presence of alder did not significantly reduce the size of the largest trees in our stands (Fig. 6*f*). The largest trees in stands of this age are usually conifers, and these large trees could provide both a valuable future timber resource and an important source of large wood for instream fish habitat (Bisson et al. 1987).

The more complex structures found in these mixed alder–conifer stands have important management implications for forest wildlife resources. Researchers have reported broadly negative effects of clear-cut logging on wildlife habitat in southeast Alaska (Samson et al. 1989; Schoen et al. 1981, 1988; Wallmo and Schoen 1980; Hanley 1993). The principal problem is that dense conifer regeneration and canopy closure result in an understory with few herbs, few shrubs, and little forage for as long as 150 years after initial canopy closure (Alaback 1982*b*, 1984; Tappeiner and Alaback 1989). Attempts to reestablish understory plants through thinning young-growth stands have had limited success because of establishment and growth of additional conifer re-

Fig. 6. Total basal area (BA) of (*a*) live and (*b*) dead trees, tree density of (*c*) live and (*d*) dead trees, and the average diameter of (*e*) all live conifers and (*f*) the 100 largest conifers/ha as a function of the alder proportion of total stand BA.

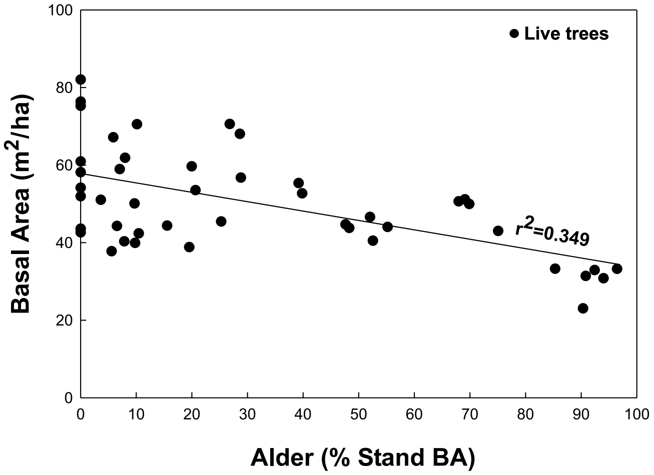


generation and little new herbaceous colonization (Deal and Farr 1994). A key finding of this study is the reduced number of small diameter conifers found in the more evenly mixed alder–conifer stands (e.g., BS, 33% alder; GP, 39% alder; and AF, 64% alder; Fig. 2). The lower stocking of these small diameter trees may allow more light to reach the forest floor that could help maintain understory plants. Previously reported studies from these same stands have shown a significant increase in herbaceous vegetation in mixed alder–conifer stands compared with pure conifer stands (Deal and Orlikowska 2002). Other studies in the Pacific Northwest and Alaska have also reported increases in species richness and understory vegetation in mixed alder–conifer stands (Franklin and Pechanec 1968; Deal 1997; Hanley and Barnard 1998).

Some forest structures were not closely associated with the presence of alder. Larger dead trees and internal wood decay of live trees (e.g., heart rot creating hollows) were not found in our young growth stands regardless of the alder component. Nearly all tree mortality in our young stands was confined to small, suppressed trees that died standing. In contrast, tree death in old-growth forests of southeast Alaska includes some overstory trees, and the common modes of death leave more variable woody debris structures (broken and uprooted as well as standing dead trees) (Hennon and McClellan 2003). White rot was the predominant type of wood decay in dead alder for both small and larger trees (96% and 100%, respectively). White rot was also more common than brown rot for both small and large dead conifers (87% and 77%, respectively). Edmonds and Isaacson (1999) made a similar finding in young-growth forests of western Washington. These results differ with old-growth conifer forests, where most wood decomposition is through the brown rot process (Hennon and McClellan 2003) that produces a relatively stable lignin structure. The distinction in decay type is important for soil development and nutrient cycling, because white rot results in the degradation of cellulose and lignin, but modified lignin remains as a stable structure with brown rot (Gilbertson and Ryvarden 1986).

This is a retrospective, primarily descriptive study and we caution drawing cause and effect relationships of alder with stand structure without further testing these results with experimental studies. Possibly some underlying factors unrelated to alder composition may be the driving force for the observed changes in forest stand structure. Red alder is common in disturbed, open areas with exposed, well-drained mineral soils, and disturbance certainly has played a large role in the establishment of alder. Some alternative explanations for the decrease in stand basal area with increasing amounts of alder may be site degradation from disturbance, lower tree stocking levels, or differences in soil nutrient levels. We did not detect any obvious signs of degraded sites such as very shallow soils that would influence growth, and we purposely avoided sampling in atypical locations such as rock quarries or gravel pits, where sites would be degraded. Tree density, however, was not closely associated with alder composition. For our nine sites, we found a slight and nonsignificant decline in tree density with increasing proportion of alder basal area (Fig. 6*c*). We also assessed whether the same pattern of declining basal area with increasing proportions of alder for our nine stands was evident within individual plots. We found a similar decline in total basal area for individual plots as the decline pattern for stands (Figs. 7 and 6*a*). Decline in plot basal area, however, was not linear, and basal area showed little change between 0% and 40% alder. Plots with more than 50% alder had a pronounced decline in total basal area compared with conifer-dominated plots. Plots with more than 80% alder had an even stronger decline in total basal area. These results suggest that the inclusion of small to moderate amounts of alder in predominantly conifer stands may have little effect on total stand basal area. However, these findings and our results in general need to be tested with experimental studies (e.g., planting different alder–conifer compositions), where possible confounding soil and disturbance factors can be controlled.

Fig. 7. Basal area (BA) of live trees in the 45 fixed-area plots as a function of the alder proportion of total BA.



Stand dynamics of red alder – conifer forests

Stand development in these 40-year-old mixed alder–conifer forests is highly dynamic, and the composition of the current forest overstory is different than it was at earlier stages. Alder height growth is initially rapid but then slows. Conifers eventually catch up in height with alders at about 18–25 years after logging, and overstory conifers are now 4–9 m taller than associated alders (Fig. 5). In the Pacific Northwest, this adjustment in red alder height growth has also been reported in mixed red alder and Douglas-fir stands (Newton et al. 1968; Miller and Murray 1978; Stubblefield and Oliver 1978). In our sites in southeast Alaska, Sitka spruce height growth increased earlier and trees grew more rapidly than for Douglas-fir. In Oregon, Newton et al. (1968) reported that under all environmental conditions, the initial growth of red alder was substantially better than that for Douglas-fir, and on wet sites it would take 38–42 years for Douglas-fir to emerge from the alder overstory. They suggested that Douglas-fir could not be expected to reach the overstory on some sites unless it was established 3–8 years before the alder. In Washington, Miller and Murray (1978) reported that emergence of Douglas-fir from alder overstory would take about 30 years, and they suggested limiting alder density to about 50–100 trees/ha. Other conifer species such as western hemlock and western redcedar in the Pacific Northwest survived as lower strata trees below the alder overstory and eventually grew above the alders, but it took several decades for these conifers to release (Stubblefield and Oliver 1978). In our mixed alder–conifer stands in southeast Alaska, the conifer height growth responded more quickly (particularly for Sitka spruce) and in some sites emerged from the alder overstory in as little as 18 years.

Long-term stand dynamics of mixed alder–conifer forests in southeast Alaska are uncertain. Red alder is expected eventually to die in these stands, but it is unclear how long this will take. Red alder is a relatively short-lived species and some researchers have reported considerable mortality of overstory alder by 50 years, and few stands remain intact beyond 100 years (Smith 1968). Newton and Cole (1994) report for stands in Oregon that the last alder will succumb in fewer than 130 years. In another site in southeast Alaska, 115-year-old red alder has been observed (P.E. Hennon, unpublished data); some red alder trees were still alive, but numerous large alders had died and were decaying on the ground. These stands in southeast Alaska will probably not be replaced by shrubs, as has been observed in some sites in the Oregon Coast Range (Newton et al. 1968; Hibbs and Bower 2001). The abundance of shade-tolerant conifers such as Sitka spruce and western hemlock suggests that a treeless shrub succession is improbable. The presence of alders makes the intense stage of stem exclusion less pronounced in mixed alder–conifer stands than that in pure conifer stands with more light available for understory plants. Also, when alders die out they may create more gaps in the canopy and lead to a condition that is either more open (Newton and Cole 1994) or favors regeneration of new trees or shrubs. Thus, red alder may have a legacy in these forests even long after it has died and decayed. Longer-term stand development is unclear, but without additional soil disturbances and large openings, red alder will likely not be able to colonize these openings and will probably be replaced by more shade-tolerant western hemlock or other conifers.

Sitka spruce may be a good candidate species to be grown with mixtures of red alder. Western hemlock, western redcedar, and Sitka spruce are all more shade tolerant than Douglas-fir (Minore 1979), and both hemlock and spruce respond well to release (Deal and Tappeiner 2002). Also, Sitka spruces have stiff terminals and maintain strong epinastic control of their leaders (Oliver and Larson 1990) and may tolerate abrasion from alder branches better than hemlocks or cedars. Both red alder and Sitka spruce frequently regenerate and become established on mixed mineral soils (Deal et al. 1991). Newton et al. (1993) also report that spruce can survive and grow in mixed alder–conifer stands under competitive conditions lethal to western hemlock and eventually emerge as alder matures. In the Pacific Northwest, a major timber management concern for Sitka spruce is stem deformity due to the spruce tip weevil (*Pissodes strobi*). These spruces are attacked by the spruce weevil when grown in full sunlight, and their stems become distorted. Spruces are reportedly less readily attacked when grown under shade (Gara et al. 1980), and the emergence pattern of spruce may have advantages for managing Sitka spruce. The spruce tip weevil does not occur in southeast Alaska, but the crown architecture and emergence growth pattern of spruce makes it a good candidate for forest management in mixtures with red alder.

There is increasing interest worldwide in the stand dynamics of mixed hardwood–conifer forests and their effects on forest productivity, biodiversity, wildlife, and other forest resources (Woods 1984; Webster and Lorimer 2002; Boncina et al. 2003). Our results suggest that mixed red alder – conifer forests of southeast Alaska can provide more complex forest structures than pure conifer stands with more even diameter distributions and multiple forest canopy layers. Although these results are from research conducted in the temperate rainforests of southeast Alaska, they may have broader geographic implications. Red alder is widely distributed throughout the west coast of North America (Harrington 1990) and other species of alder occur throughout the world. These alder species have biological properties similar to red alder in southeast Alaska and presumably similar effects in other ecoregions. Development of mixed hardwood–conifer stands beyond the young regenerating forest as demonstrated here will likely affect associated plant and animal species and ecosystem structure and function.

Conclusion

Mixed red alder – conifer stands contain different species' growth patterns, shade tolerance, and longevity, resulting in more complex stand dynamics than found in pure conifer forests. Alders exhibited rapid early height growth but then slowed, whereas conifer height growth was initially slow then rapidly increased, with dominant conifers now averaging 6 m taller than associated alders. Mixed red alder – conifer stands provided more heterogeneous structures than the pure conifer stands that typically develop in the region after clear-cutting. These mixed alder–conifer stands created a multi-layered forest canopy with a few large overstory conifers, a mid-canopy level of red alder trees, and a lower canopy level of small diameter conifers. Larger dead trees and internal wood decay of live trees were not found in these 40-year-old stands regardless of the alder component and most dead trees died standing. Basal area and wood production significantly decreased with increasing proportions of alder. The inclusion of alder in young-growth forests, however, did not significantly effect the production of the largest trees, and we found large diameter conifers across a wide range of alder–conifer mixtures. Altering the composition of young-growth conifer forests with the inclusion of red alder may improve habitat and food resources for deer and other wildlife and thereby offset some of the negative consequences of clear-cutting. Opportunities for increasing red alder in forests involve encouraging its reproduction by planting or regeneration through soil disturbance in newly harvested areas and favoring red alder when thinning forests where the tree species already occurs. Planting or maintaining red alder in clumps where competition with conifers is minimized will likely extend its presence through time in the stand. Well-planned silvicultural systems that include a mixture of red alder – conifer compositions could provide trees for timber production and also improve other forest resources that are often compromised in pure conifer young-growth forests in the region.

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