Effects of species mixtures on growth and stand development of Douglas-fir and red alder

Steven R. Radosevich, David E. Hibbs, and Claudio M. Ghersa

Abstract: In the Pacific Northwest, a mixture of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red alder (*Alnus rubra* Bong.) often results when red alder regenerates naturally in planted conifer stands. The relationships among stand structure, tree mortality, tree size, and understory development in the two species mixtures were explored at two sites for the first 16 years after planting. Treatments included a range of species proportions, and red alder was either planted simultaneously with Douglas-fir or planting was delayed for 5 years. Red alder was also removed from some simultaneously planted proportions. Both replacement effects (total stand density held constant) and additive effects (stand density doubled) of the interaction were considered. Red alder grew relatively better at Cascade Head Experimental Forest in the Coast Range, while Douglas-fir grew better at H.J. Andrews Experimental Forest in the less temperate Cascade Mountains. Possible production benefits from mixed plantings were examined using two methods of calculation. Potential production benefits from certain planted proportions of the two species occurred at H.J. Andrews Experimental Forest. No planting time or species proportion resulted in yield improvements over monoculture stands at Cascade Head Experimental Forest. Understory species also varied because of differences in site and stand characteristics that resulted from the differences in planting times and species proportions.

Résumé : Dans la région nord-ouest du Pacifique, des peuplements mixtes de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et d'aulne rouge (*Alnus rubra* Bong.) se constituent souvent lorsque l'aulne rouge se régénère naturellement dans des plantations de conifères. Les relations entre la structure du peuplement, la mortalité des arbres, les dimensions des arbres et le développement de la végétation sous un couvert composé de différentes proportions des deux espèces ont été étudiées dans deux stations au cours des 16 premières années suivant la plantation. Les traitements incluent plusieurs combinaisons des deux espèces dans différentes proportions et la plantation soit simultanée, soit décalée de 5 ans, de l'aulne rouge. L'aulne rouge a aussi été éliminé de certaines combinaisons où les deux espèces avaient été plantées simultanément. Tant les effets de remplacement (la densité totale du peuplement est maintenue constante) que les effets additifs (la densité du peuplement est doublée) de l'interaction entre les deux espèces ont été pris en compte. La croissance de l'aulne rouge était supérieure à la forêt expérimentale Cascade Head dans la chaîne côtière alors que celle du douglas de Menzies était meilleure à la forêt expérimentale H.J. Andrews soumise au climat plus rigoureux de la chaîne des Cascades. Les gains potentiels de production des plantations mixtes ont été étudiés selon deux méthodes de calcul. Des gains potentiels de production ont été réalisés à la forêt expérimentale H.J. Andrews avec certaines proportions des deux espèces. Ni le moment de la plantation, ni le mélange des espèces n'ont amélioré le rendement des plantations à la forêt expérimentale Cascade Head comparativement aux peuplements monospécifiques. La composition en espèces de sous-bois a aussi varié en raison des différences entre les stations et entre les peuplements engendrées par les différents traitements.

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Introduction

Associations of plant species are common in most habitats, and the importance of interactions among such species in forest systems is well recognized (Crawley 1997; Menalled et al. 1998; Callaway and Pennings 2000; Freckleton and Watkinson 2001). However, vast areas of land continue to be managed for single-species productivity (Cox and Atkins 1979; Menalled et al. 1998). Recent commitments to improve biological diversity, reduce human-caused disturbance, and increase productivity now provide management opportunities for taking advantage of more complex interactions within multispecies stands (Kohm and Franklin 1997).

Many studies have focused on the association of Douglas-fir (*Pseudotsuga menzesii* (Mirb.) Franco) and red alder (*Alnus rubra* Bong.) because both the species are highly valued (Newton et al. 1968; Hibbs et al. 1989; Puettmann et al. 1992; Knowe and Hibbs 1996) and the size and allometry of the trees are strongly affected by the intensity of intra- and inter-specific competition (Shainsky and Radosevich 1991;

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S.R. Radosevich[1] and D.E. Hibbs. Department of Forest Science, Oregon State University, Corvallis, OR 97331-5752, USA.
C.M. Ghersa. Instituto de Investigaciones Fisiologicas y Ecologicas Vinculadas a la Agricultura (IFEVA), Departamento Recursos Naturales y Ambiente, Facultad de Agronomia, Universidad de Buenos Aires, Argentina.

[1]Corresponding author (e-mail: steve.radosevich@oregonstate.edu).

Knowe and Hibbs 1996; Menalled et al. 1998). Studies also reveal that silvicultural practices such as tree planting, spacing, and thinning can alter tree height, stem diameter, and crown size (Assmann 1970; Shainsky and Radosevich 1991, 1992; Grotta et al. 2004) in these two species. Newton et al. (1968) and Shainsky and Radosevich (1991) observed that during early stages of succession, when red alder and Douglas-fir often co-exist as relatively dense stands, the species compete for environmental resources. In such cases, the presence of red alder usually has a negative effect on Douglas-fir growth; but if the species co-exist at lower densities and (or) for longer periods of time, the presence of red alder, especially on soils with poor to moderate fertility, can improve conifer growth (Shainsky and Radosevich 1991; Callaway and Pennings 2000). Lower densities of red alder can be achieved by thinning, but delayed planting of red alder relative to that of Douglas-fir also can reduce competition between the species. In mixed-species plantations, later planting of red alder relative to that of Douglas-fir compensates for the more limited ability of Douglas-fir to capture site resources early in stand development (Shainsky and Radosevich 1992).

Halpern (1988) studied early succession of forest communities in the western Cascade Mountains of Oregon and concluded that life-history characteristics, species' competitive relationships, and the timing, intensity, and frequency of disturbances are important factors determining alternative pathways of succession. This potential to influence plant succession is based on an assumption that the density and arrangement of the species cause changes in plant community composition and structure over time (Wilson et al. 1996; Crawley 1997; Kohm and Franklin 1997), which for planted stands implies improved understory development and performance of the planted species. We test this assumption using an experiment established in 1984–1986 at two forest sites in western Oregon where Douglas-fir and red alder were planted at specific densities and proportions. Red alder also was thinned or its planting delayed by 5 years in the experiment.

Material and methods

Site characteristics and planting methods

A long-term experiment was established in 1984–1986 at two forest sites, Cascade Head Experimental Forest in the Oregon Coast Range and H.J. Andrews Experimental Forest in the central Oregon Cascade Mountains. Tree seedlings used at both sites were 2–0 and 1–0 nursery stock from local seed sources for Douglas-fir and red alder, respectively.

Cascade Head Experimental Forest is located at T6S R10W S15 and S 22 within 2 mi (1 mi = 1.6093 km) of the Pacific Ocean at 330 m above sea level (Table 1) in the *Picea sitchensis* vegetation zone (Franklin and Dyrness 1971). Previous vegetation consisted of mature *Picea–Tsuga/Aplopanax horridum/Athyrium filix-femina* communities with abundant components of *Rubus* sp. and red alder. The site is considered fertile (Table 1); basalt is overlain with loam having local pockets of duff up to 1 m in depth. The growing season averages 180 frost-free days per year, with relatively high temperatures and a high percentage of cloudy days even during summer. Average minimum and maximum temperatures are 2.2 and 20.9 °C, respectively. Average annual precipitation is 250 cm, and occurs primarily between October and May, often as rain and fog drip. June through September are characterized by periodic rainfall events often separated by 3- to 4-week periods without precipitation.

In the summer of 1985, an approximately 120-year-old stand of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was clear-cut and the site broadcast-burned. The site was subsequently planted to specific plant densities, spacing, and species proportions (Table 2) the following spring (1986). Dead trees were replaced after each of the first three growing seasons (1986–1988). During the summer of 1987, shrubs and volunteer trees were hand-slashed or -pulled. Volunteer trees were cut again during the summer of 1990, when the red alder in one red alder/Douglas-fir proportion (Table 2) was also removed. All vegetative residue from these operations remained on the plots.

The H.J. Andrews Experimental Forest is located in the *Tsuga heterophylla* vegetation zone (Franklin and Dryness 1971) of the west slope of the Cascade Mountains (Table 1). Previous vegetation consisted of old-growth forest (approximately 500 years of age) dominated by *P. menziesii* and *T. heterophylla*. A dense *T. heterophylla* subcanopy, perhaps originating from a fire of moderate severity approximately 150 years ago, kept understory vegetation sparse. Soil is a deep, well-drained gravelly loam over a cobbly silt loam C horizon formed from basic igneous rock and volcanic ash. Summer drought and high temperatures from June through September characterize the climate. Average minimum and maximum temperatures, annual precipitation, and length of the growing season are shown in Table 1. Winter snowpack is often transient at this site, with temporary accumulations occasionally exceeding 1 m.

In the spring and summer of 1985, this experimental site was clear-cut. It was broadcast-burned the following fall, which reduced soil-surface organic matter significantly. Since soil organic matter is believed to be a substantial component of long-term site productivity, the site is now considered to be of moderate soil fertility (Table 1). The site was planted to Douglas-fir the following spring (1986) according to the densities, spacing, and species proportions listed in Table 2. However, red alder were not planted until the following growing season (spring 1987) because of a mistake in planting the previous year. Trees that died were replanted the next year (1988) but not thereafter. Some elk browsing was observed on the treatments for several years after planting.

Experimental design

A modified replacement series (Jolliffe et al. 1984) experiment, where total tree density in every treatment is constant, while proportion between the species (deWit 1960; Radosevich 1987) varies, was used to examine the association of red alder and Douglas-fir. The series includes six proportions of red alder and Douglas-fir and is repeated three times at each experimental site in a randomized complete-block design. Each replicated series was repeated twice at each site (Table 2), one with the species planted at the same time (simultaneous planting) and the other with the red alder planted 5 years later than the Douglas-fir (delayed planting). Red alder was also removed 5 years after planting in a

Table 1. Descriptions of the sites at two experimental forests used to study long-term interference between Douglas-fir and red alder.

	H.J. Andrews	Cascade Head
Longitude	122°10′W	124°00′W
Latitude	44°14′N	45°05′N
Elevation (m)	800	330
Soil parent material	Andesite	Basalt
Annual precipitation (cm)	230	250
Avg. minimum temperature (°C)	–8.5	2.2
Avg. maximum temperature (°C)	26.9	20.9
Growing season (days)	134	180
Soil nitrogen concentration at 0–15 cm (ppm)	1500	4200
Soil phosphorus concentration at 0–15 cm (ppm)	1800	1600

Table 2. Douglas-fir and red alder proportions, densities (trees/plot), planting times, and spacing at the two experimental sites.

	Tree density (no./plot)				
		Red alder			
Proportion (Douglas-fir/ red alder)	Simultaneous planting* (Douglas-fir)	Simultaneous planting*	Delayed planting†	Removed‡	Tree spacing (m × m)
1.0/0	81	0	—	—	3 × 3
0.9/0.1	73	8	—	—	3 × 3
0.9/0.1	73	—	8	—	3 × 3
0.7/0.3	57	24	—	—	3 × 3
0.7/0.3	57	—	24	—	3 × 3
0.5/0.5	41	40	—	—	3 × 3
0.5/0.5	41	—	40	—	3 × 3
0.5/0.5 (1.0/0)	41	40	—	40	4.2 × 4.2§
0.3/0.7	24	57	—	—	3 × 3
0.3/0.7	24	—	57	—	3 × 3
0/1.0	0	81	—	—	3 × 3
0/1.0	0	—	81	—	3 × 3
1.0/0	41	0	0	—	4.2 × 4.2
0/1.0	0	0	40	—	4.2 × 4.2

*Trees were planted on the same day at the beginning of the study at Cascade Head. Red alder were planted 1 year later than Douglas-fir at H.J. Andrews.

†Red alder were planted 5 years later than Douglas-fir.

‡Red alder were planted at the same time (see *) but removed 5 years later.

§Douglas-fir and red alder were initially planted at the same time as an equal mixture (0.5/0.5) at 3 m × 3 m spacing. After 5 years, red alder was removed, resulting in a proportion of 1.0 Douglas-fir and spacing of 4.2 m × 4.2 m.

0.5:0.5 proportion of the two species (Table 2). Plots are 27 m by 27 m and the trees are planted on a fixed 3 m × 3 m grid. In addition, one treatment each of pure Douglas-fir and pure red alder were planted at a 4.2 m × 4.2 m spacing. This wider spacing resulted in the same density of each species as the 0.5:0.5 species proportions for the mixed stands when planted on the 3 m × 3 m grid. Thus, the monoculture treatments at the widest spacing (4.2 m × 4.2 m) can be compared with 0.5:0.5 species proportions at 3 m × 3 m spacing and also allow an assessment of the effect of other densities on the outcome of the species association (Jolliffe et al. 1984; Firbank and Watkinson 1985; Roush et al. 1989).

Measurements

A 25-tree measurement plot was centered inside each treatment, creating a buffer two tree rows wide around every measurement area. All trees sampled were measured at the end of the growing season every year from 1990 through 1993, and then in 1995 and 1998. Tree density, total tree height, height to the base of the live crown, and stem diameter at breast height (DBH) were determined. Ratios of total height to DBH and height to live crown (hlc) to total height (th) were also calculated. Cover and height measurements of other tree, shrub, and herbaceous vegetation were obtained during the 1989 growing season and at the end of the 2000 growing season. In 1989, a line-intercept technique was used to estimate cover by species of intercepted vegetation along the diagonals of each measurement plot in each treatment. In 2000, a complete species list was compiled using a survey of the entire area of every treatment. Species constancy and frequency were calculated from these data. The canopy structure of the vegetation in 2000 in each treatment plot was also characterized by creating a diagram of the vertical canopy distribution of the most conspicuous species. Leaf stratification of the understory was determined by locating two points within a treatment and placing a pole at each point. Observations focused on two canopy heights (0–1.0 and 1.0–2.0 m of each pole), and we recorded the length (cm) of pole intercepted by leaves in each of the two layers. Visual cover for both heights was estimated at two additional locations, 5 m from each pole, giving eight understory cover values for every treatment.

Data analysis

All data are expressed according to the originally planted proportions (Table 2). Analysis of variance was used to determine the effects of the independent variable initial species proportion, planting time (simultaneous or delayed), and red alder removal on tree mortality, height, height to live crown, and DBH of Douglas-fir and red alder and overall plant species richness and cover using a General Linear Model (SAS Institute Inc., Cary, North Carolina, 1997). Proportions were arcsine-transformed. Tree height and DBH were fit to proportion by a non-linear least squares procedure to obtain regression coefficients. Stem volume index per tree (SVI) was calculated as the product of $(DBH)^2$ and height. Wood produced by trees in each species mixture, using SVI as an estimator, was used to calculate average production relative to that produced in pure stands at the 3 m × 3 m spacing, i.e., relative yield (RY) (deWit 1960; Harper 1977). Relative yield total (RYT) was obtained as the sum of RY for both species (RYT = yield of Douglas-fir in mixture + yield of red alder in mixture/yield of Douglas-fir in pure stand + yield of red alder in pure stand). Relative land output (RLO) was also used to compare productivity of species mixes versus pure stands. RLO was calculated according to Jolliffe (1997) and is an assessment of mixed stand productivity when equivalent amounts of land are allocated to pure stands and to each species in the mixture (RLO = yield of Douglas-fir in mixture + yield of red alder in mixture/equivalent fraction of Douglas-fir in pure stand + equivalent fraction of red alder in pure stand).

Results and discussion: overstory

Vegetation structure

The establishment phase of a forest stand is characterized by relatively rapid changes in species dominance, level of competition, and plant mortality (Halpern 1988). During the first 5 years of this experiment, considerable effort was expended to reduce the effects of mortality of planted trees and the spontaneous occurrence of other species at each site. In addition, herbivore damage, primarily by elk, was sometimes significant on planted trees and on spontaneously arrived vegetation during this period (Fuentez-Rodriguez 1994). Thus, tree mortality and the stand structure that resulted in each treatment (Figs. 1 and 2) were caused by the interaction of these factors and by the species–density–proportion interactions that were implemented (Table 2).

Tree mortality

Tree mortality was mainly attributed to the death of Douglas-fir at Cascade Head Experimental Forest and red alder at H.J. Andrews Experimental Forest (Table 3). Overall mortality was lowest at Cascade Head, and most tree death occurred after the 6th year from planting (1990). The highest Douglas-fir mortality at Cascade Head was observed when the two tree species were planted at the same time and the proportion of red alder was 0.3 or greater (Table 3). Douglas-fir mortality began at the highest proportion of red alder and increased progressively through time and proportions as the surviving trees grew. The greatest mortality of Douglas-fir occurred between 1993 and 1998. Delaying red alder planting did not affect the mortality of Douglas-fir at any proportion, although some significant red alder mortality occurred at Cascade Head as a result of delayed planting of that species (Table 3).

At H.J. Andrews, mortality of red alder was significant (Table 3). However, much of the variation in mortality occurred in a single block, ranging from 10% to 100%, and occurred shortly after planting (data not shown). The percentage of red alder mortality generally increased as the proportion of red alder decreased. High red alder mortality occurred in the monocultures of that species (Table 3).

The differential tree species mortality that occurred caused a shift in actual versus planted densities and proportions (Tables 2 and 3). However, mortality was 15% or less in most planted tree densities (108 of 132 total plots in 1998) when examined on a plot-by-plot basis. Less than 10% mortality was found in 92 of the total 132 plots. Thus, most proportions were similar in 2000 to those originally planted. When tree species mortality was greater than 15% (24 of 132 total plots), the new proportions that resulted likely differ from those planted, 7 and 13 plots for Cascade Head and H.J. Andrews, respectively. Three of the proportions at Cascade Head are similar to the original proportion, 0.5:0.5, although now at wider spacing and unknown arrangement. The other four new proportions at Cascade Head result in proportions similar to those previously planted as other treatments. At H.J. Andrews, 12 of the 13 different plot proportions resulting from tree mortality are similar to an originally planted proportion, but are now also at unknown arrangements and spacing. The remaining new plot proportion is a pure stand of Douglas-fir at low density.

The original planted proportions were used for all analyses. The effects of interference between red alder and Douglas-fir have been discussed by Shainsky and Radosevich (1991, 1992) and focus on ecological–physiological mechanisms to explain how specific allocation of resources by individual trees can account for differences in growth rate and wood production of the two species. The stem-exclusion process in tree stands caused by closing canopies is also well known (Oliver and Larson 1990). Multiple stems of red alder also resulted when the density of that species was low. Many studies address natural thinning and attribute tree mortality to a single factor. In our experiment, however, tree mortality appeared to be a consequence of multifactor interactions, some occurring shortly after the experiment began (Fuentez-Rodriquez 1994) and some later (Table 3). Site, planting time, red alder removal, and species proportion interacted as the experiment progressed, causing different levels of tree mortality. The effects of environmental factors other than species proportion and red alder planting time on tree mortality diminished as the experiment progressed.

The tree mortality observed in the experiment led to differences in actual versus planted species densities and proportions by 1998. However, mortality is a normal consequence of growth suppression from tree–tree competition, and it is

Fig. 1. Representations of vertical structure in 2000 of tree and understory vegetation in treatments at Cascade Head Experimental Forest planted at different proportions of Douglas-fir (DF) and red alder (RA). The two species were planted simultaneously in a 3 m × 3 m grid (*a*), red alder planting was delayed or they were removed after 5 years (*b*) or planted at low density, separating trees by 4.2 m × 4.2 m (*c*). The numbers at the bottom denote mean vertical cover (%) of the understory in the first and second metres of the vegetative canopy for each treatment, with 1 standard deviation of the mean for each height in parentheses.

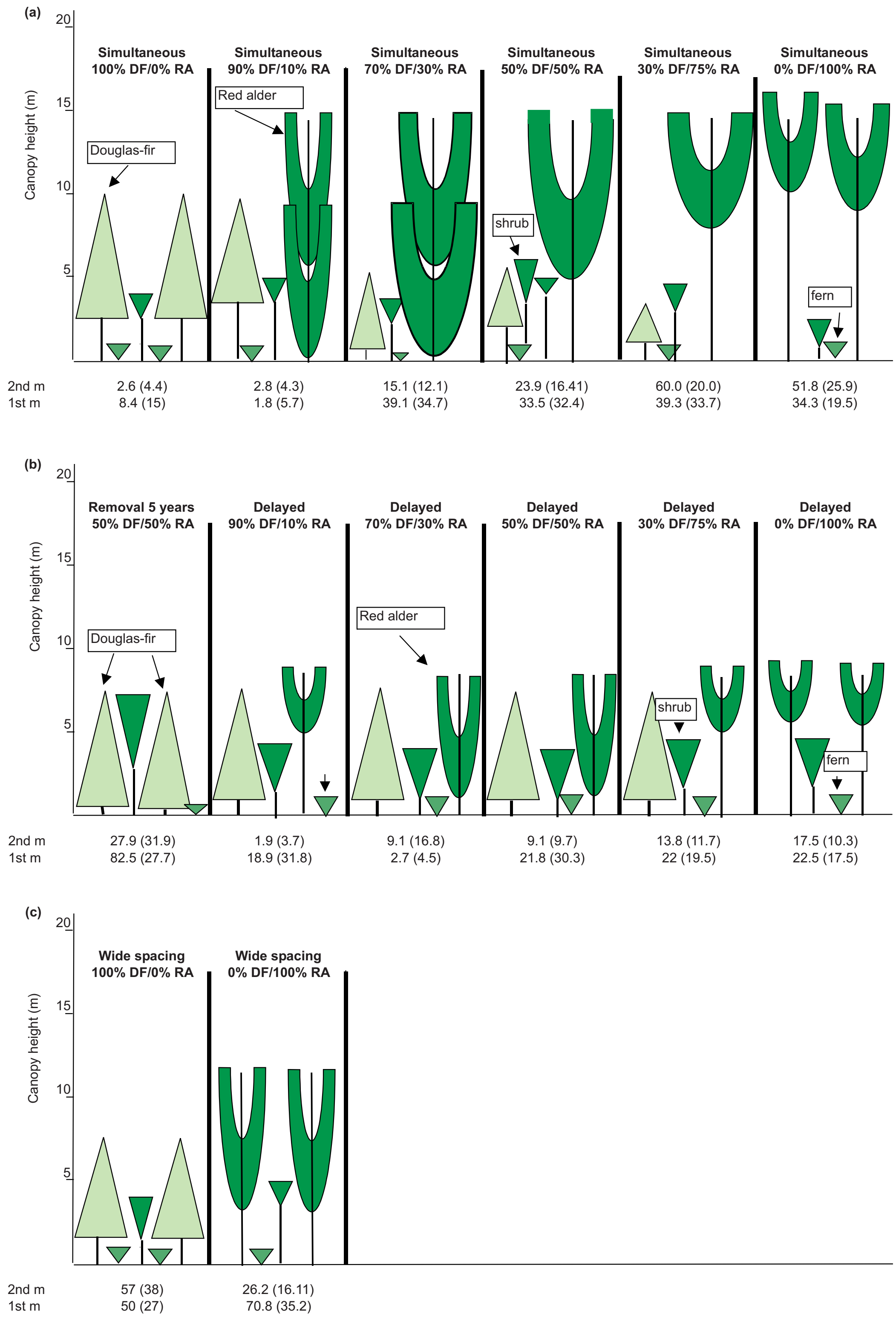


Fig. 2. Representations of vertical structure in 2000 of tree and understory vegetation treatments at H.J. Andrews Experimental Forest planted at different proportions of Douglas-fir (DF) and red alder (RA). The two species were planted simultaneously in a 3 m × 3 m grid (*a*), red alder planting was delayed or they were removed after 5 years (*b*), and (or) planted at low density, separating trees by 4.2 m × 4.2 m (*c*). The numbers at the bottom denote mean vertical cover (%) of the understory in the first and second metres of vegetative canopy for each treatment, with 1 standard deviation of the mean for each height in parentheses.

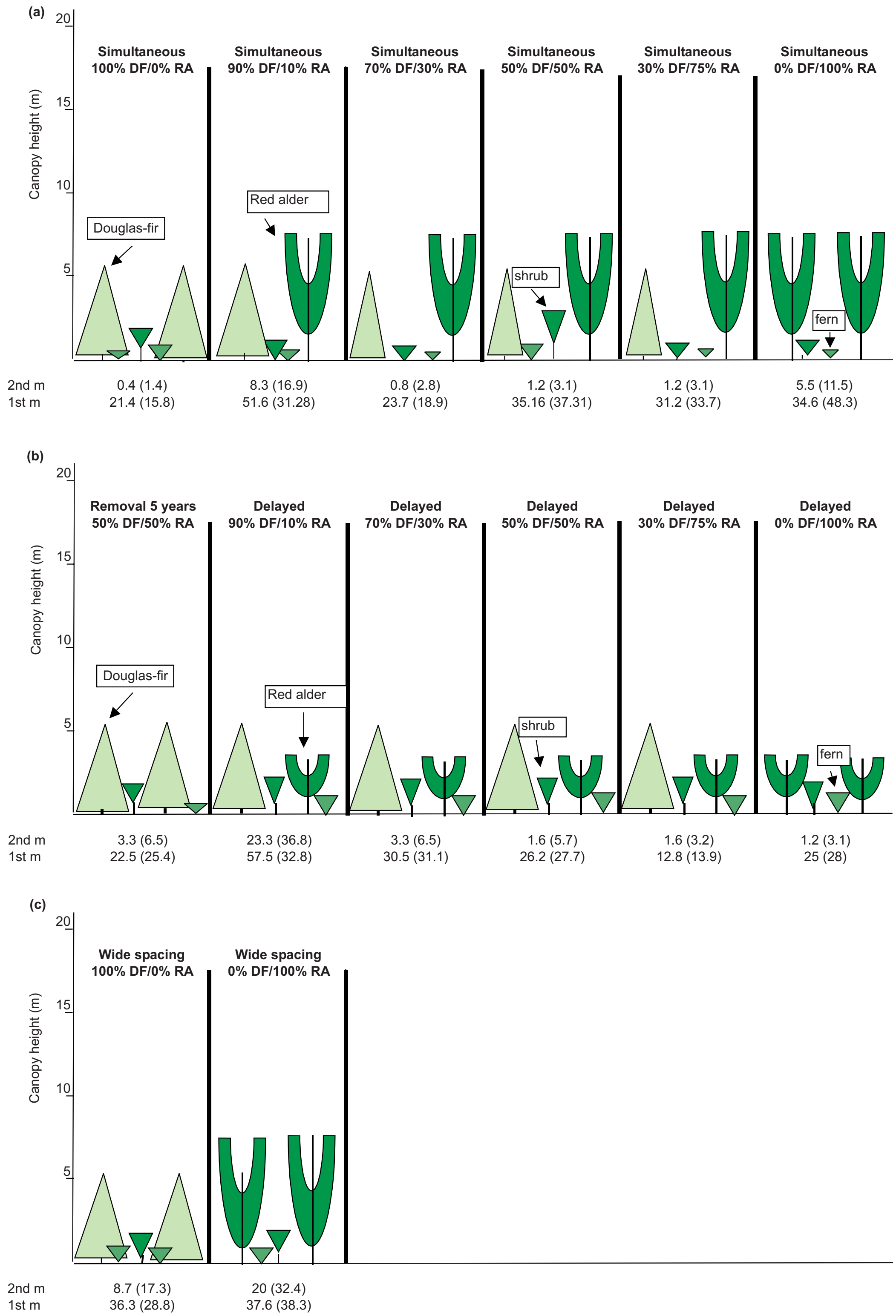


Table 3. Mean cumulative mortality of Douglas-fir and red alder planted as pure stands and mixtures.

		Proportion (Douglas-fir / red alder)											
		Simultaneous planting						Delayed red alder planting					
Site	Year	1.0/0	0.9/0.1	0.7/0.3	0.5/0.5	0.3/0.7	0/1.0	1.0/0	0.9/0.1	0.7/0.3	0.5/0.5	0.3/0.7	0/1.0
Cascade Head	1990	0/—	0/0	0/0	5/0	0/0	—/0	0/—	0/0	3/0		3/0	5/0
	1991	0/—	0/0	0/0	5/0	0/0	—/0	0/—	0/0	3/0		3/0	5/0
	1992	0/—	0/0	2/0	5/0	5/0	—/0	0/—	0/0	6/0	3/0		5/0
	1993	3/—	2/0	4/2	8/0	33/0	—/0	3/—	7/8	6/5		3/0	
	1995	3/—	2/7	12/5	14/0	55/0	—/0	5/—	11/15	6/5		3/0	
	1998	4/—	7/7	31/5	33/0	61/0	—/0	4/—	11/17	8/9	3/30	5/18	—/0
		c/—	c/ns	b/ns	b/ns	a/ns	—/ns	ns/—	ns/d	ns/e	ns/ef	ns/d	—/f
Andrews	1990	0/—	2/16	2/24	3/8	0/4	—/5	2/—	7/0	2/0		0/0	
	1991	0/—	2/16	2/24	3/8	0/4	—/5	2/—	7/0	2/0	0/0		5/0
	1992	0/—	2/20	2/26	3/8	0/7	—/11	2/—	9/0	4/0		0/0	
	1993	0/—	3/31	3/32	5/13	5/29	—/16	3/—	9/0	4/0	3/0	5/0	—/0
	1995	0/—	3/36	3/42	8/15	5/33	—/16	3/—	19/42	8/46	5/21	5/26	—/27
	1998	1/—	3/49	3/42	11/28	5/33	—/22	4/—	19/42	10/58	11/21		5/29
		0/—	ns/g	ns/gh	ns/h	ns/h	—/h	j/—	i/k	i/k	i/l	j/l	—/jl

Note: Tree mortality began in 1990 and is expressed as a percentage of the total number of trees in each treatment each year. Different letters in a column indicate significant differences (p = 0.05) before 1998 and other years for a species according to site planting time and planted proportion (rows; 3 m × 3 m spacing only). Where no value is given, no trees of that species were planted (i.e., in pure stands). No mortality of the trees in the 4.2 m × 4.2 m spacing had occurred by 2000.

likely that this response will continue as the experiment continues. Analyses in subsequent years should take the alteration in densities, species proportion, and spatial management into account, since all can influence plant–plant interactions (Harper 1977; Radosevich et al. 1997).

Tree height

Regardless of species proportion, planting time, or red alder removal, the greatest heights of either species occurred at Cascade Head (Fig. 3). However, red alder only overtopped Douglas-fir when the species were planted at the same time. In the delayed-planting red alder series at both sites, Douglas-fir performance was unaffected by red alder (Fig. 3). Average red alder height at H.J. Andrews was 1.8 times greater than that of Douglas-fir in 1990 in simultaneously planted mixed stands (Fig. 3). Eight years later (1998), height differences between the species decreased, but red alder trees were still 1.4 times taller than Douglas-fir (Fig. 3). At Cascade Head, the height ratio between the species was much greater than that observed at H.J. Andrews. In 1990, red alder was 4.4 times taller than Douglas-fir, but in 1998 the height ratio was 2.7 (Fig. 3).

The effect of the increasing red alder proportion in the simultaneously planted mixtures was apparent by 1998 at Cascade Head but not at H.J. Andrews. At that time, the ratios of specific tree heights at Cascade Head were 1.8, 2.1, 4.3, and 5.0 as the proportion of Douglas-fir decreased from 0.9 to 0.3 (Fig. 3). The 5-year delay in planting red alder resulted in about a 40% reduction of average height of red alder at both sites. This effect from delayed red alder planting eliminated the proportional effect of red alder on Douglas-fir height at Cascade Head (Fig. 3).

In 1998 at H.J. Andrews, there were no differences in the average heights of Douglas-fir growing in either pure stands at narrow or wide spacing (Fig. 3) or any proportion in the simultaneous or delayed planting. Removal of red alder after 5 years at H.J. Andrews resulted in an increase in the height of Douglas-fir, which were about 1 m taller in 1998 than those in either monoculture of Douglas-fir (Fig. 4). At Cascade Head and H.J. Andrews, trees growing as pure stands at the narrow spacing were statistically equal in height to trees grown at the wider spacing. Trees in these pure stands were also similar in height to those in the delayed-planting series. Trees growing in either monoculture stand type at Cascade Head were also taller than those in the simultaneously planted mixture (Figs. 3 and 4). Douglas-fir treatments with simultaneous planting and 0.5 (Figs. 3 and 4) or 0.3 (Fig. 3) proportions of Douglas-fir were shortest and never exceeded 4 m average height. When red alder were removed or their planting was delayed, taller Douglas-fir trees resulted compared with the same proportion under simultaneous planting (Figs. 3 and 4). Therefore, both delayed planting and removal of red alder reduced interspecific competition of that species with Douglas-fir. Although Douglas-fir in pure stands were either as tall as or taller than those found in the species mixtures (Figs. 3 and 4), only delayed planting resulted in decreased red alder height in both the wide and the narrow monoculture plantings of that species (Fig. 4).

Diameter (DBH)

At H.J. Andrews, Douglas-fir DBH was similar to (simul-

Fig. 3. Average Douglas-fir (DF) and red alder (RA) height measured in 1990, and height, diameter at breast height (DBH), and height to live crown / total height (crown/height) in 1998, after they were planted as pure stands and at different proportions of the two species. Pure Douglas-fir stands are the same for both simultaneous and delayed red alder plantings. Different upper- and lower-case letters indicate significant differences ($p < 0.01$) among treatments for red alder and Douglas-fir, respectively.

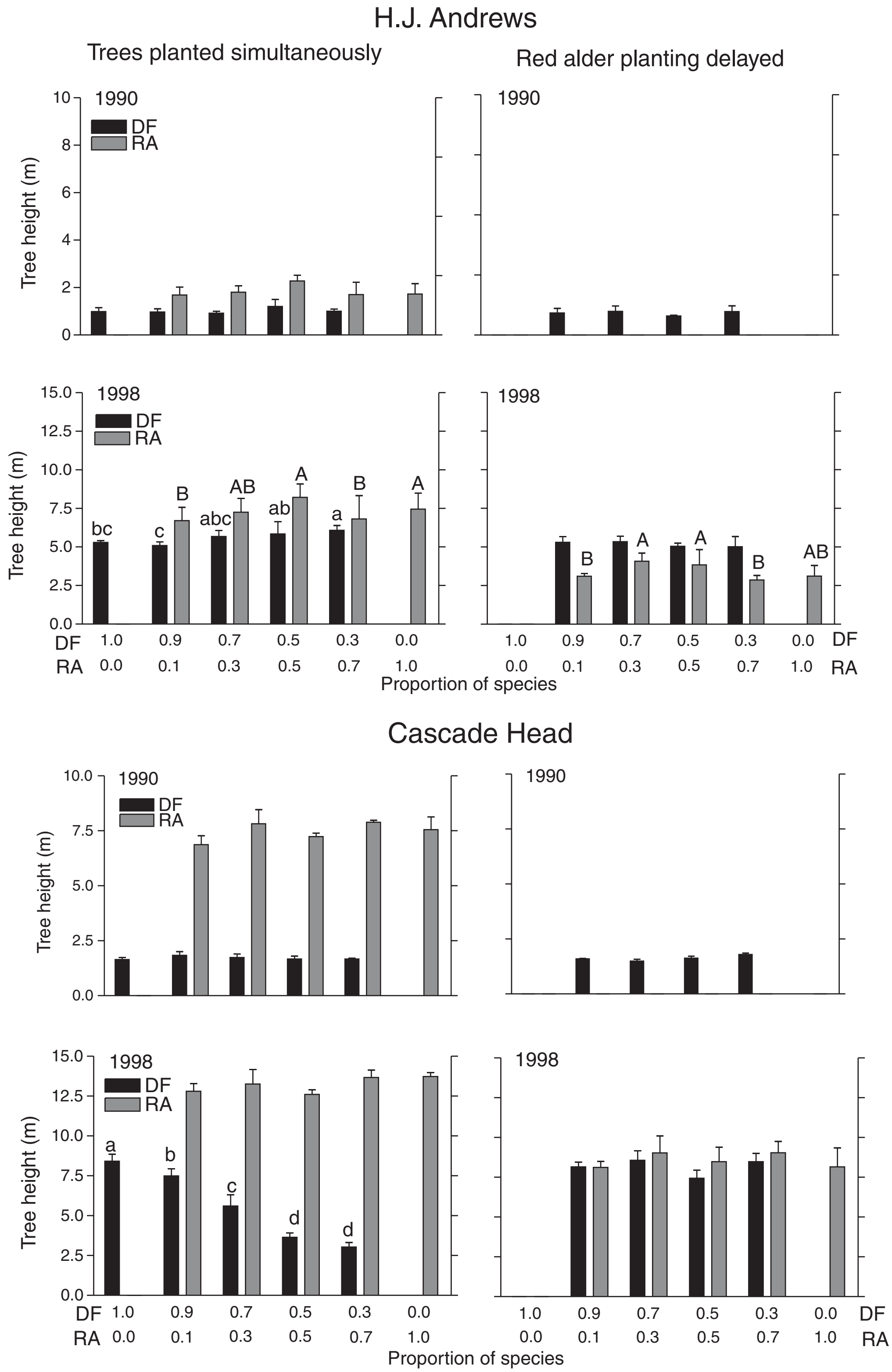


Fig. 3 (*concluded*).

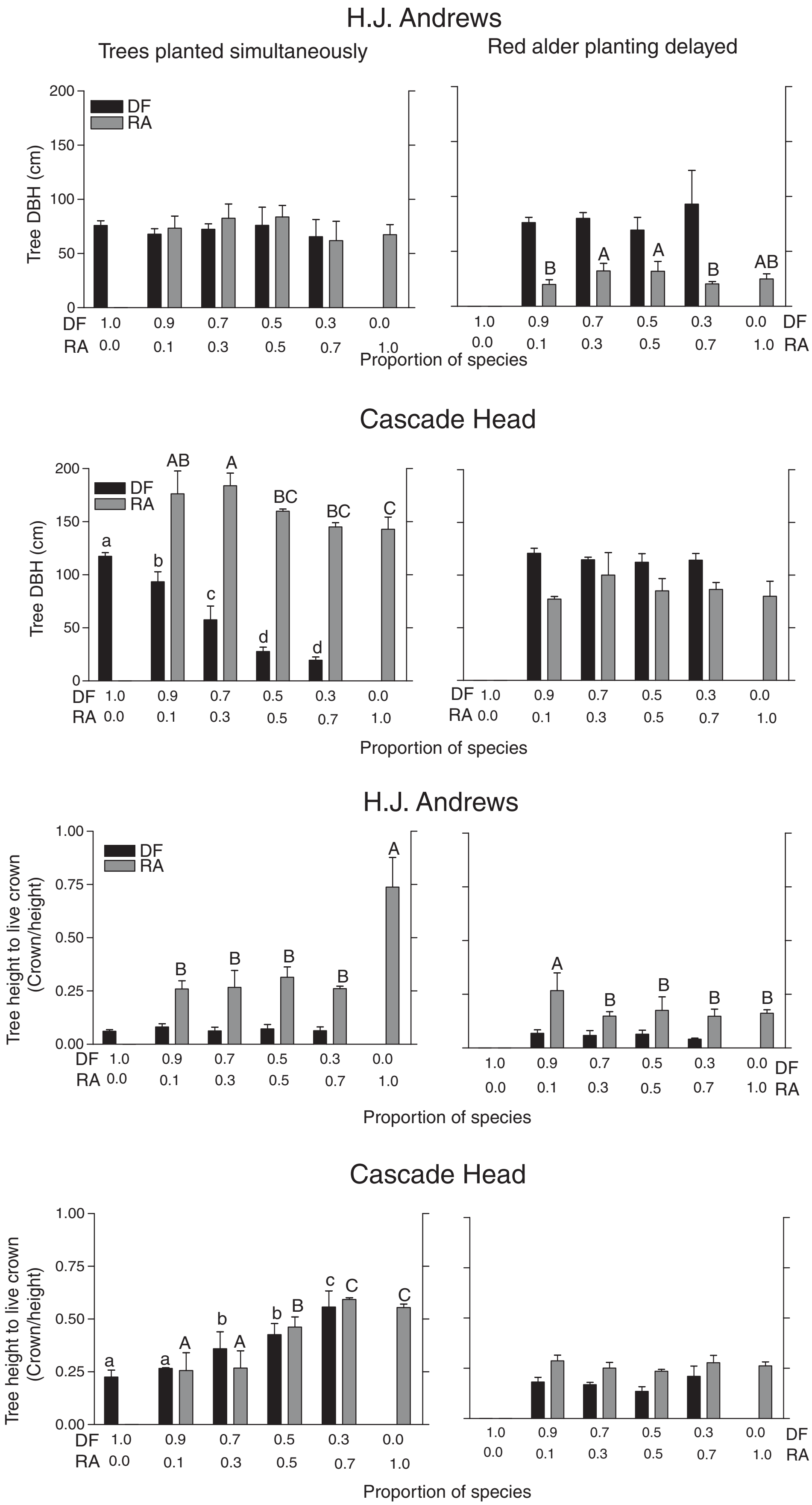
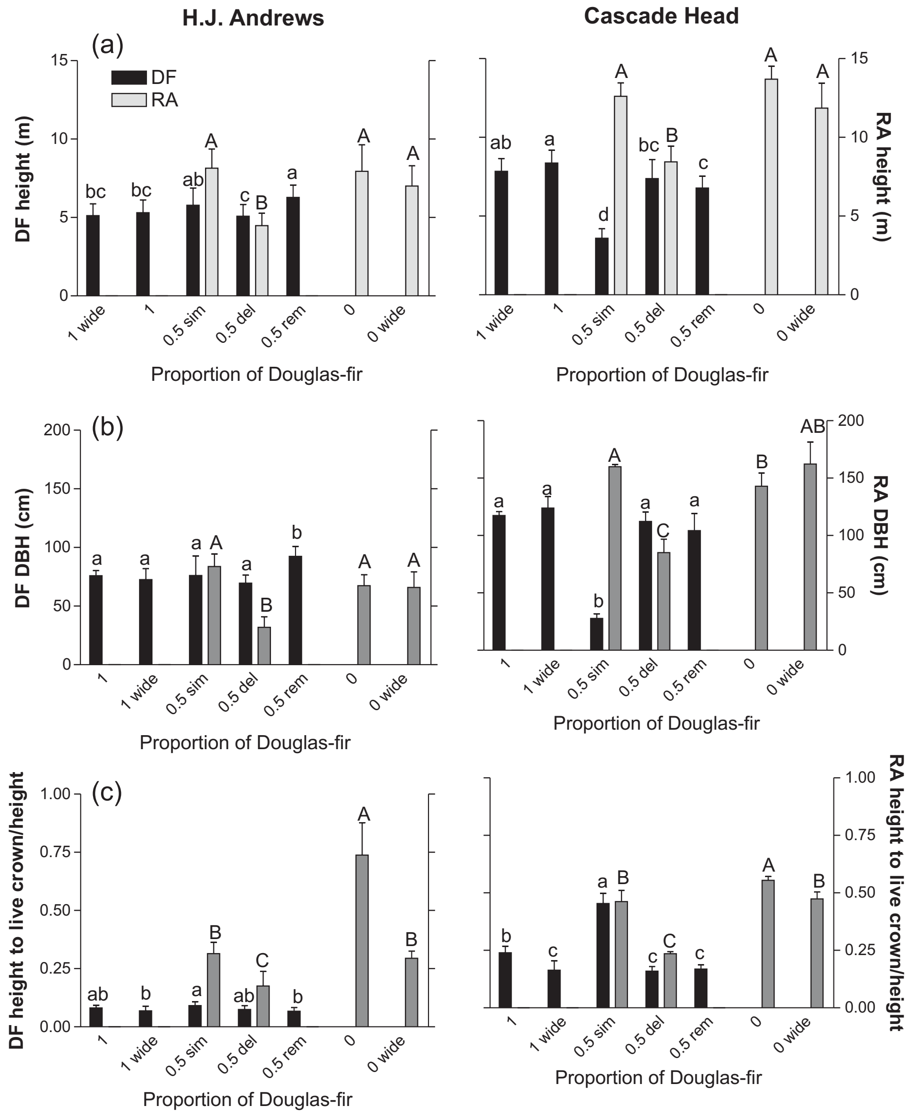


Fig. 4. Average Douglas-fir (DF) and red alder (RA) height (*a*), DBH (*b*), and the ratio of height to live crown / total height (lc/th ratio) (*c*) measured in 1998, 13 years after trees were planted in pure stands and species mixtures ("sim", simultaneous planting; "del", delayed planting of red alder; "rem", red alder removed after 5 years). The numbers along the *x* axis indicate the proportion of Douglas-fir in the mixture. In pure stands, species were planted at 3 m × 3 m (1 and 0) and 4.2 m × 4.2 m spacing (proportion 1 wide and 0 wide). Of the species mixtures, only the 0.5 species proportion is shown. Different upper- and lower-case letters indicate significant differences ($p < 0.01$) among treatments for red alder and Douglas-fir, respectively.



taneous planting) or greater than (delayed planting) red alder DBH (Fig. 3). Delaying red alder planting by 5 years, regardless of species proportion, reduced red alder DBH to one-third relative to trees in similar treatments with simultaneous planting. Red alder with the largest diameter were found when 0.3 and 0.5 proportions of red alder were in the mixture (Fig. 3). In contrast, boles of red alder were 2-, 3-, 5-, and 5-fold larger than those of Douglas-fir in the 0.1, 0.3, 0.5, and 0.7 proportions of red alder, respectively (Fig. 3), at Cascade Head. Delayed alder planting at this site resulted in larger diameter Douglas-fir trees (Fig. 3) than simultaneous planting regardless of the proportion of red alder. The simultaneously planted red alder trees in the 0.7 proportion of Douglas-fir were similar in diameter to those in the 0.9 proportion of Douglas-fir, and larger than trees growing in all other treatments (Fig. 3). DBH results for both species growing at wide versus narrow spacing in pure stands and red alder removed at the 0.5 proportion were similar to those found for tree height (Fig. 4).

Allometry: height–DBH relationship

As expected (Shainsky and Radosevich 1992), red alder always overtopped Douglas-fir except when red alder planting was delayed. This species difference in height growth was best expressed at Cascade Head (Figs. 1 and 2). Other studies have shown red alder to have a strong negative effect on Douglas-fir growth (Newton et al. 1968; Cole and Newton 1986, 1987), which increases as red alder density increases, especially if Douglas-fir densities are low (Shainsky and Radosevich 1991). Shainsky and Radosevich (1991) also found that red alder stem volume could increase in some proportions of mixed red alder and Douglas-fir stands in comparison with red alder monocultures. This response was also evident in our experiment, where the 0.3 and 0.1 proportions of red alder to Douglas-fir resulted in larger red alder DBH (Fig. 4) without appreciably changing tree height (Figs. 3 and 4). Delaying red alder planting at both sites dramatically altered the competitive relationship between the species, favoring Douglas-fir.

As for most plants, changes in allometry were expected in Douglas-fir and red alder in response to intra- or inter-specific density stress (Knowe and Hibbs 1996; Shainsky and Radosevich 1992). Linear regressions indicated that trees of both species grew taller per unit of diameter of red alder at the H.J. Andrews site, especially when planting of red alder was delayed. This effect was also observed in simultaneous plantings and a high proportion of red alder (Figs. 3 and 4). This response in plant allometry is most often associated with reduced radiation caused by shading of an overstory canopy (Smith 1962). At Cascade Head, where red alder grew tallest and thus captured most of the light resource, severe intraspecific competition for the resource apparently caused red alder to be shorter per unit of diameter than expected.

Allometric changes in individual Douglas-fir only appeared at Cascade Head when the red alder proportion exceeded 0.1, but this response was not evident when planting of red alder was delayed. This response once again demonstrates the ability of red alder to overtop Douglas-fir in fertile environments (Newton et al. 1968). In proportions at Cascade Head that were simultaneously planted, the relationship between height and diameter was generally lower for red alder than for Douglas-fir, a response also noted by Shainsky and Radosevich (1991, 1992), suggesting that Douglas-fir is less sensitive to environmental heterogeneity than red alder (Chan et al. 2003). The relatively greater tolerance of Douglas-fir to shade allows it to better persist in an understory and respond positively at some combined densities of the two species.

Ratio of height to live crown / total height

Easter and Spies (1994) indicate that the lc/th ratio is correlated with the light extinction caused by canopy closure: the larger the ratio, the greater the extinction that is believed to occur. In our experiment, site had a strong effect on the lc/th ratio, an effect especially apparent with Douglas-fir if both species were planted simultaneously (Fig. 3). At H.J. Andrews, the lc/th ratio for Douglas-fir did not change in response to any treatment. However, this ratio for red alder differed statistically between pure stands and all proportions that were simultaneously planted. With delayed planting, only the 0.9 proportion of Douglas-fir was statistically different from the other treatments at H.J. Andrews. For Douglas-fir at Cascade Head, the average lc/th ratio was about 5-fold larger than for the trees in similar treatments at H.J. Andrews (Fig. 3). Moreover, at Cascade Head, the lc/th ratio for both species increased as the proportion of red alder in the mixtures increased, and for tree height, delaying red alder planting eased the negative effect of red alder on Douglas-fir (Fig. 3). Also at Cascade Head, delayed red alder planting (Fig. 3) and the 0.5 species proportion with red alder removed (Fig. 4) resulted in a twofold reduction of the Douglas-fir lc/th ratio, which reached only about 0.15. This effect of red alder removal and delayed planting on the lc/th ratio was less apparent at H.J. Andrews than at Cascade Head.

Branch mortality caused by canopy closure only occurred at Cascade Head, where red alder was best able to express its growth potential (Fig. 1). At this site and in the mixed simultaneously planted stands, the lc/th ratio for both species increased as the red alder proportion in the mixture increased. The lc/th ratio for red alder growing in monoculture was the same as for the 0.7/0.3 mixture of alder and Douglas-fir (Fig. 3). This response demonstrates, in accordance with Shainsky and Radosevich (1991, 1992), that the effects of red alder density stress on the performance of both species, and of individual red alder on themselves, are greater than the effects on Douglas-fir or those caused by Douglas-fir density (Grotta et al. 2004). The similar and low values of this ratio when red alder was removed, delayed in planting, or widely spaced indicate that the capacity of red alder to overtop and produce an overstory leaf area can be reduced to increase light availability for Douglas-fir growth.

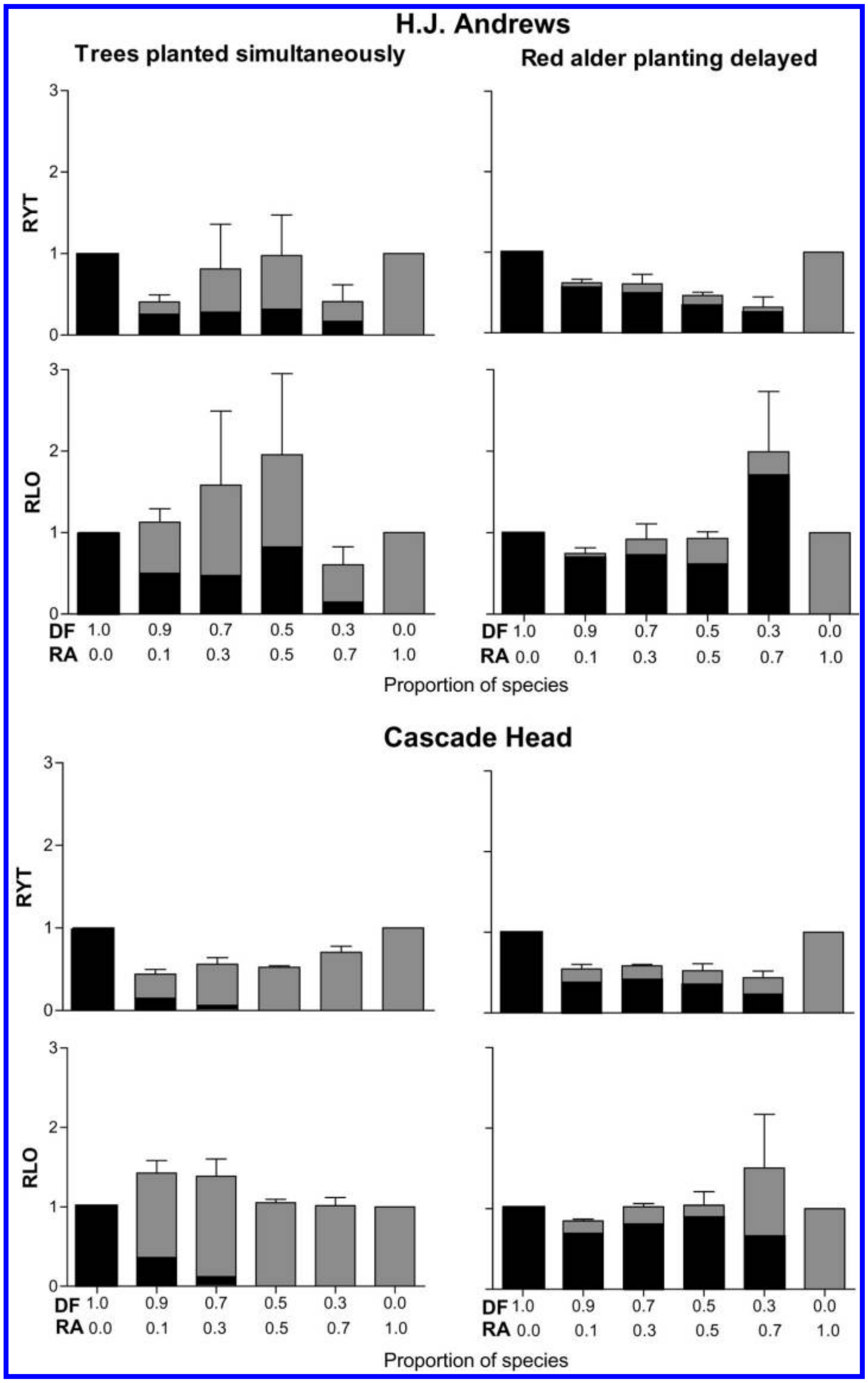
Relative yield and land output of species mixes

Interference among species growing in mixtures is believed to be a combination of two processes, facilitation and competition (Goldberg 1990; Vandermeer 1989; Radosevich et al. 1997). Both processes are possible between Douglas-fir and red alder (Tarrant 1961; Cole and Newton 1986, 1987; Shainsky and Radosevich 1991, 1992; D'Amato and Puetmann 2004). The key hypothesis in all such studies is that gradients of resource availability can be created by gradients of species densities. These relative densities (proportions) contribute to both intra- and inter-specific interactions (Chan et al. 2002), and result in changes in tree size and structure over time (Grotta et al. 2004).

RYT and RLO were calculated from SVI values derived in this experiment. These calculations are indicators of production enhancement (>1) or penalty (<1) when species are planted in mixtures. RYT is the composite of RY values of each species, and is compared with the yields of both species when planted separately. RLO is similar to RYT except that the proportion of land devoted to each species in mixtures is compared with an equivalent amount of land growing a pure stand of each species (Jolliffe 1997).

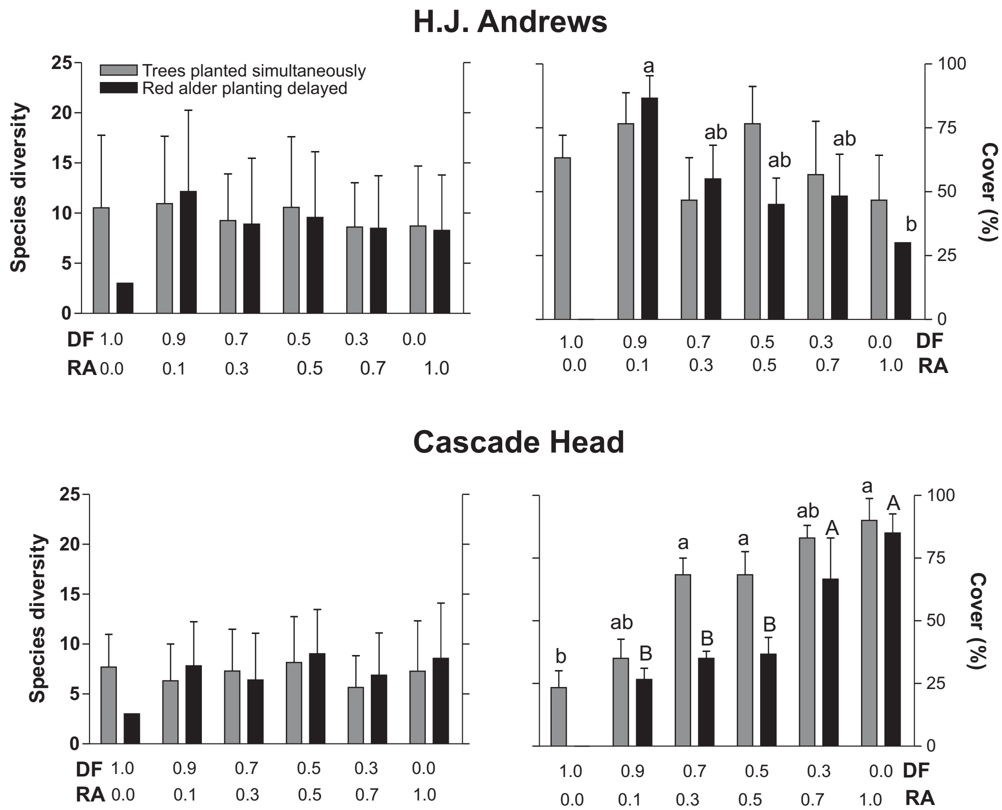
No positive mixture effect was observed at either site or with simultaneous or delayed tree planting when RYT values were calculated for the proportions of the two species (Fig. 5). However, positive mixture effects were observed when RLO was calculated, although results varied by site, planting time, and proportion of the planted mixture. Variation among treatment blocks, probably due to tree mortality (Table 3) or site variability, also made interpretation of these effects difficult. A positive mixture effect (RLO) with simultaneously planted red alder and Douglas-fir was observed at H.J. Andrews at 0.9, 0.7, and 0.5 proportions of Douglas-fir and the 0.3 proportion of Douglas-fir when red alder planting was delayed. Over-yields at these proportions resulted from improved growth of red alder with simultaneous plantings and from Douglas-fir when planting of red alder was delayed (Fig. 5). At Cascade Head, delayed planting of red alder improved the competitive relationship between the two species, favoring Douglas-fir (Fig. 5), regardless of the

Fig. 5. Relative yield total (RYT) and relative land output (RLO), 13 years after planting, in treatments with different mixtures of Douglas-fir (DF) and red alder (RA) at the two experimental sites. The species were either planted simultaneously or RA planting was delayed for 5 years. A tree volume index (SVI) was calculated as the product of height and $(DBH)^2$. Relative yield (RY) was then determined as the yield of each species in a particular proportion relative to the yield of that species in pure stand. RYT is the sum of the RY values for the two species. RLO was determined as the summed yields of the two species grown in mixtures divided by the summed yields of the two species grown on the same land area in pure stands.



method of calculation. These observations, which culminate in Fig. 5, indicate the influence of the method of calculation when assessing intra- and inter-specific effects among mixtures and monocultures of species (Jolliffe 1997; Radosevich et al. 1997), but also suggest that appropriate silvicultural practices can result in production advantages from planting

Fig. 6. Average number of plant species (left-hand side) and percent understory cover (right-hand side) for pure stands and proportions of Douglas-fir (DF) and red alder (RA) at H.J. Andrew (top) and Cascade Head (bottom) in 2000, 14 and 16 years after planting at each site, respectively. Douglas-fir and red alder were planted simultaneously or alder planting was delayed by 5 years. The numbers along the *x* axis indicate the proportion of Douglas-fir to red alder (DF/RA). Different upper- and lower-case letters indicate differences in the simultaneous- and delayed-planting treatment, respectively.



mixtures of red alder and Douglas-fir (Kohm and Franklin 1997).

Because the species in this study differ in phenological, physiological, and architectural characteristics, whether a tree has one species or the other as its neighbor has an effect on its growth. Douglas-fir is less sensitive to water stress than red alder (Shainsky and Radosevich 1991, 1992; Chan et al. 2003). Red alder, unlike Douglas-fir, has a nitrogen (N)-fixing root associate, has faster early height growth, is deciduous, and has more transparent foliage (Grotta et al. 2004). Therefore, the resources available to any given plant in a mixture or pure stand depend on the species, its size, and the proximity of its neighbors. These results also indicate the importance of site, with the occurrence of a positive effect from any particular species proportion being most likely at H.J. Andrews. In this experiment H.J. Andrews represents sites with relatively low resource levels compared with Cascade Head (Table 1). Delayed planting of red alder at H.J. Andrews did not provide a production advantage, as determined using RLO, as did simultaneous planting. This observation may be due to the smaller size of delayed-planted red alder and therefore greater distances for the species to interact. Other studies indicate that the relative size advantage gained by Douglas-fir in mixtures when planting of red alder is delayed allows that species to acquire more resources than when it is in pure stands (Shainsky and Radosevich 1992; Chan et al. 2003, Grotta et al. 2004).

Understory richness and cover

In 1989, gamma diversity (total number of species found) was greater at H.J. Andrews than at Cascade Head (70 and 64 species, respectively). Despite the lower overall richness at Cascade Head, alpha diversity was much higher at Cascade Head in 1989 (15 and 10 species per plot, respectively; data not shown). In 2000, gamma diversity reached 112 species at H.J. Andrews and 89 species at Cascade Head. Alpha diversity dropped at Cascade Head to eight species and held constant at H.J. Andrews. Because variation among plots was high and the richness in sampling systems differed between the two dates presented, only comparisons between gamma diversity values at one date and alpha diversity values within sites at that date are meaningful. In 2000, we found that tree species proportion did not affect alpha diversity. Species richness for proportions with simultaneous planting at both sites was statistically equal. Similarly, species richness resulting from tree proportions with delayed planting or removal of red alder did not vary (Fig. 6).

Site differences in gamma diversity are to be expected (Waring et al. 2002; Sarr et al. 2005) and are generally attributed to the greater intensity of the competitive environment of the Coast Range (Sarr et al. 2005). The lack of treatment effect is less expected, especially at H.J. Andrews, where initial soil N levels were not high. Fertilizer studies have shown that increased fertility can decrease diversity (Tilman 1987, 1994; Goldberg 1990), so there is an unrealized potential for N-fixation by red alder to increase soil N as the proportion of red alder increases, which results in a decrease in species diversity.

Understory cover in 2000 was generally high but ranged between 25% and 90% (Fig. 6). At Cascade Head, understory cover increased with red alder proportion in both simultaneous and delayed red alder planting plots. At H.J. Andrews, a surprising and significant reduction in understory cover was found with increased red alder proportion in the simultaneous planting treatments but no effect in the delayed-planting plots. In this region, most studies have shown lower understory cover under evergreen canopies than under deciduous canopies (Franklin and Dyrness 1988).

Conclusion

Early forest stand development is characterized by rapid changes in species dominance (Halpern 1988). The most pronounced improvement of mixed plantings of red alder and Douglas-fir in this experiment was evident at the site with lowest relative fertility (H.J. Andrews). At Cascade Head, the more fertile site, delaying red alder planting or removing it entirely from the mixture after 5 years improved Douglas-fir growth and the species' response to red alder proportion. However, delaying red alder planting or removing it from the species mixture did not improve the performance of individual Douglas-fir trees at H.J. Andrews, since it is likely that spontaneously occurring understory vegetation utilized the released resources and space (Figs. 1 and 2), so red alder remained too small to be an effective competitor.

In this experiment, species dominance was affected by tree mortality, especially during the first 5 years of the study. The mortality (Table 3) occurred in response to site variables (Table 1) and the presence of spontaneously occurring vegetation and animal browsing, as well as to planting times and densities and proportions of the two species that were implemented (Table 2). In general, Douglas-fir was favored at H.J. Andrews, while red alder was favored at Cascade Head (Figs. 3 and 4). At Cascade Head, endogenous patch dynamics driven by the rapid growth of red alder controlled and reduced the growth of Douglas-fir.

The proportion of the planted species in the Douglas-fir/red alder mixtures played a role in individual tree performance at both sites (Figs. 3 and 4), together with the understory species cover that resulted after disturbance (Figs. 1, 2 and 6). Tree architecture and stand (treatment) structure could also be manipulated by using particular tree proportions and delayed red alder planting to increase or reduce tree canopy layers (Fig. 3), affecting SVI and subsequently RYT and RLO (Fig. 5). The changes in community and tree canopy structure and understory development were created by the different treatments as the planted trees grew through time. While these changes suggest that mixtures of trees can be used to manipulate or direct succession in a new forest, the determination of possible positive yield benefits from species mixtures may depend on the method of calculation and experimentation (Jolliffe 1997; Radosevich et al. 1997). Defining the proportions of Douglas-fir and red alder in managed forest stands could be used to improve the performance of one or both planted species as well as overall forest productivity (Chan et al. 2003), wood quality (Grotta et al. 2004), and plant species diversity (Figs. 1, 2, and 6).

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