Relations between red alder composition and understory vegetation in young mixed forests of southeast Alaska

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Abstract: Interest in mixed red alder (*Alnus rubra* Bong.) – conifer young-growth stands has grown in southeast Alaska, USA, because they appear to provide much more productive understory vegetation and wildlife habitat than do similar-aged pure conifer stands. We studied understory vegetation in nine even-aged young-growth stands (38–42 years old) comprising a gradient of red alder – conifer overstory composition, with red alder ranging from 0% to 86% of stand basal area. Conifers were Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). We measured understory biomass and net production (current annual growth) in each stand by species and plant part and estimated carrying capacity for black-tailed deer (*Odocoileus hemionus sitkensis* Cowan) with a food-based habitat model. Highly significant positive relations ($P < 0.002$) were found between red alder basal area and all of the following: total understory biomass ($r^2 = 0.743$), net production of shrubs ($r^2 = 0.758$) and herbs ($r^2 = 0.855$), and summer carrying capacity for deer ($r^2 = 0.846$). The high correlation between red alder and herbaceous production is especially important, because herbs are least abundant and most difficult to maintain in young-growth conifer forests of this region. Red alder offers prospects for increasing understory vegetation biomass and its food value for deer and other wildlife when included as a hardwood overstory species in mixed hardwood–conifer young-growth forests.

Résumé : L'intérêt pour les jeunes peuplements mixtes d'aulne rouge (*Alnus rubra* Bong.) et de conifères s'est accru dans le sud-est de l'Alaska, É.-U., parce qu'ils semblent fournir passablement plus de végétation de sous-bois et d'habitats fauniques que des peuplements purs de conifères du même âge. Les auteurs ont étudié la végétation de sous-bois dans neuf jeunes peuplements équiennes (âgés de 38–42 ans) dont la composition de l'étage dominant présentait un gradient d'aulne rouge et de conifères allant de 0 à 86 % de la surface terrière en aulne rouge. Les conifères étaient l'épinette de Sitka (*Picea sitchensis* (Bong.) Carr.), la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et le cèdre de l'Ouest (*Thuja plicata* Donn ex. D. Don). Dans chaque peuplement, ils ont mesuré la biomasse du sous-bois et la production nette (accroissement annuel courant) par espèce et pour différentes parties des plantes et ils ont estimé la capacité de support pour le cerf à queue noire (*Odocoileus hemionus sitkensis* Cowan) selon un modèle d'habitat basé sur la nourriture. Des relations positives très significatives ($P < 0{,}002$) ont été observées entre la surface terrière de l'aulne rouge et chacune des variables suivantes : la biomasse totale du sous-bois ($r^2 = 0{,}743$), la production nette d'arbustes ($r^2 = 0{,}758$) et d'herbes ($r^2 = 0{,}855$) et la capacité de support estivale pour le cerf ($r^2 = 0{,}846$). La forte corrélation entre l'aulne rouge et la production herbacée est particulièrement importante parce que les herbes sont moins abondantes et plus difficiles à maintenir dans les jeunes peuplements de conifères de cette région. L'aulne rouge offre la possibilité d'augmenter la biomasse du sous-bois et sa valeur nutritive pour le cerf et d'autres espèces quand il est inclus comme feuillu dans le couvert arborescent des jeunes forêts mixtes de feuillus et de conifères.

[Traduit par la Rédaction]

Introduction

Interest in mixed hardwood–conifer forests has grown worldwide in recent years as forestry has increasingly shifted emphasis from wood fiber production to forest management practices that enhance biodiversity and incorporate "ecosystem management" concepts (Wilson 1988; Salwasser 1994; Anglestam 1998). Ecological roles of hardwoods, mixed within coniferous forests, have become recognized for biodiversity (Humphrey et al. 1998; Ferris and Humphrey 1999; Diaci 2002; Boncina et al. 2003), nutrient cycling and long-term site productivity, wildlife habitat, and human aesthetic values (Woods 1984; Hansen et al. 1991; Webster and Lorimer 2002). In regions where dense, young conifer forest shades out understory food and cover for wildlife (e.g., habitat for deer), inclusion of hardwoods in the young-growth

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forest might mitigate the effects of even-aged timber management and facilitate the broad goals of ecosystem management in forestry (Hanley and Barnard 1998).

In southeast Alaska, USA, naturally regenerated forests are predominately multiaged (>300 years) "old-growth" forests dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) with species-rich and abundant understories (Harris and Farr 1974; Alaback and Juday 1989; Hanley and Brady 1997). Modern forestry in the region has favored clear-cut logging, and the regenerated young-growth stands are even-aged Sitka spruce and western hemlock, with Sitka spruce favored in commercial forestry (Harris 1974). Young-growth Sitka spruce and western hemlock forests have provided poor fish and wildlife habitat, however, because they typically regenerate (naturally) at such a high density of stocking that understory vegetation is severely reduced throughout the time of conifer canopy closure (~25–30 years stand age) until well past 100 years stand age (Alaback 1982, 1984*a*, 1984*b*). Precommercial silvicultural thinnings, thus far, have been unsuccessful in establishing a productive and diverse understory vegetation for longer than a few years (Doerr and Sandburg 1986; Hanley 2005), and widely spaced thinnings have resulted in a dense second layer of western hemlock regeneration (Deal and Farr 1994). The problem has been especially vexing for habitat for black-tailed deer (*Odocoileus hemionus sitkensis* Cowan), because the highly nutritious ground-layer herbs are the most difficult of all species to establish and maintain in understories of young-growth spruce–hemlock forests (Hanley et al. 1989; Hanley 1993). Black-tailed deer is the most important game and subsistence species in the region, and habitat quality for deer is usually an important consideration in multiple-use forest management.

Red alder (*Alnus rubra* Bong.) is the most common hardwood tree in southeast Alaska. It fixes nitrogen and is most common as a pioneer species on sites where mineral soil has been exposed to seedfall (Viereck and Little 1972; Harris and Farr 1974; Ruth and Harris 1979). Unlike Sitka alder (*Alnus crispa* (Ait.) Pursh), a common tall shrub on exposed mineral soils or avalanche areas, red alder is a tree, typically reaching heights of 10–15 m (Viereck and Little 1972). Although it is relatively uncommon in the upland old-growth forests of the region, it is very common along stream courses and upland areas where soil has been disturbed, such as in some of the early (1950–1960s) clear-cut logging operations (Harris and Farr 1974; Ruth and Harris 1979). Occurrence of red alder in clearcuts decreased sharply in the 1970s with the advent of high-lead logging systems that minimized soil disturbance (Ruth and Harris 1979). Red alder was long considered a "weed" species in commercial forestry because of its potential competition with conifers for light and space (Shainsky and Radosevich 1992; Newton and Cole 1994), but its value for mitigating some of the negative effects of clear-cut logging on wildlife and fish habitat have recently been noticed (McComb et al. 1993; Hanley and Barnard 1998; Piccolo and Wipfli 2002). Understories of young-growth mixed red alder – conifer forests in southeast Alaska have been found to be highly productive, species rich, and diverse, even when compared with old-growth forests (Hanley and Hoel 1996; Deal 1997; Hanley and Barnard 1998). Mixed red alder – conifer forests in the region appear to provide high-quality habitat for small mammals (Hanley 1996; Hanley and Barnard 1999*a*), birds (Willson and Comet 1996), and fish in freshwater streams (Wipfli 1997), because of relatively high production and diversity of plant seeds and foliage (Hanley and Barnard 1999*b*), terrestrial and arboreal insects and arthropods (Stiles 1980), and aquatic macroinvertebrates (Piccolo and Wipfli 2002). In older young-growth stands, red alder is likely important as a "snag" tree for cavity-nesting birds at a time when few conifers are of sufficient size and decay state. Thus, red alder is an important component of forests for a variety of reasons ranging from understory plant species richness and variety of growth forms, to invertebrate animal production and diversity, to wildlife habitat for a wide variety of vertebrate species. Scientific study of mixed red alder – conifer forests in southeast Alaska, however, has begun only recently (Hanley and Hoel 1996; Deal 1997; Wipfli 1997; Hanley and Barnard 1998; Piccolo and Wipfli 2002).

Studies thus far (cited previously) have contrasted "mixed alder – conifer" against "conifer" treatments. Although they have consistently shown greater understory biomass, production, cover, species richness, and habitat value for wildlife and fish in the "mixed" than in the "conifer", they have not been able to provide any quantitative relations between relative abundance of red alder and relative abundance or richness in the understory or habitat value. Quantitative analysis requires quantitative relations derived from a gradient of stands rather than a simple contrast of stand types.

The main objective of our study was to test and derive quantitative relations between the proportion of red alder in mixed alder – conifer stands and selected understory variables within a study area at the southern end of the Alexander Archipelago of southeast Alaska. We studied the understory of nine stands of similar age within the same general study area but differing greatly in their proportion of red alder as a percentage of total stand basal area. Although this was an observational study, and we cannot determine cause and effect relations between alder and the understory, the study does provide an empirical basis for evaluating relations between red alder and conifers and their associated understory in even-aged, young-growth, mixed red alder – Sitka spruce – western hemlock forests. On the basis of the comparative studies cited previously, we hypothesized that percent composition of red alder in the overstory would be a strong predictor of understory production and composition. We related the following measures of understory vegetation to the percent composition of red alder in the overstory: total aboveground biomass, aboveground net production (current annual growth) by plant species and major growth forms, and food value for black-tailed deer (as a surrogate measure for wildlife habitat that has direct importance to people; Hanley 1993).

Deal et al. (2004) and Orlikowska et al. (2004) studied the overstory structure and dynamics of these same stands in detail and reported the following: (1) variation in tree size distributions and canopy layers increased with increasing proportion of red alder in the stands; (2) red alder did not significantly reduce the size of the largest conifers within the stands; (3) few small-diameter conifers occurred within the stands with even mixtures of red alder and conifers; (4) red alder height growth had been greater than that of conifers during the first 18–25 years, but conifers had overtopped the

Table 1. Site characteristics of nine stands constituting a gradient in red alder composition within mixed red alder – conifer young-growth forests that are 38–42 years old.

Stand name	Elevation (m)	Slope (%)	Aspect (°)	Geomorphic position	Soil type
UGE	300	21	223	Mountain flank	Karta–Tolstoi
CED	250	42	48	Mountain flank	Tolstoi – rock outcrop
LM	250	16	196	Mountain flank	Tolstoi
LGE	250	7	198	Mountain base	Tolstoi–Karta
M22	350	25	185	Mountain flank	Tolstoi–Karta
BS	200	42	54	Mountain flank	Tolstoi – rock outcrop
GP	500	14	230	Mountain base	Tolstoi–Karta and Tonowek–Tuxekan
AF	200	9	198	Mountain base	Tolstoi–Karta
BR	200	41	46	Mountain flank	Tolstoi–Karta

Note: Stands are listed in increasing proportion of red alder.

red alder after that and were about 4–9 m taller than the red alder at 38–42 years stand age; and (5) the red alder was expected to decline with time and eventually drop out of these stands without self-replacement, possibly increasing overstory structural diversity further by creating gaps.

Methods

Study area

Our study took place in the Maybeso Creek (~46 km^2) and adjacent Harris River drainages (~108 km^2), Prince of Wales Island (55°49′N, 132°67′W), in the Tongass National Forest, southeast Alaska. Prince of Wales Island has a mild cool and moist maritime climate, typical of southeast Alaska, with an annual precipitation of approximately 2700 mm and an average annual temperature of 6 °C (Western Regional Climate Center 2002*a*, 2002*b*). The geology of the area is characterized by broad glacial valleys that contain volcanic bedrocks with some conglomerate and dioritic outcrops (Nowacki et al. 2001). Both watersheds are represented mostly by Tolstoi–Karta, Tolstoi–Rock outcrop and Tonowek–Tuxekan soil types that are well drained and moderately to highly productive for forest growth (Deal et al. 2004) and were logged at virtually the same time. They did not offer "replication" in a statistical sense. The Maybeso and Harris River watersheds were extensively logged beginning in 1953, when large clearcuts were used to produce wood for the first pulp mills in the region (Harris 1974). The young-growth stands that developed after clear-cutting were mostly Sitka spruce and western hemlock with some western redcedar (*Thuja plicata* Donn ex D. Don); they also contained considerable amounts of red alder resulting from exposed mineral soil caused by the logging methods of that time (Harris 1974; Harris and Farr 1974; Ruth and Harris 1979), which involved much soil scarification from logging machinery and dragging logs across the ground.

Site selection

During the summer of 2000, we sampled nine 38- to 42-year-old mixed red alder – conifer stands, with red alder composition ranging from 0% to 86% of the total stand basal area, to quantify relations between overstory stand composition and understory plant composition and biomass. That range (except for the highest value) in red alder composition is fairly common in this region, but only in stands regenerated with clear-cutting and significant soil disturbance (e.g., tractor logged) during the 1950s–1960s. All stands were on similar physical settings with no clear trend in relation to red alder composition (low elevation, lower hillside, moderate slope, well-drained Tolstoi and Karta soils; Table 1) but differed in the prevalence of exposed mineral soil. Red alder responds very strongly to exposed mineral soil in southeast Alaska (Viereck and Little 1972; Harris and Farr 1974; Ruth and Harris 1979), and virtually all the red alder in our stands appeared to have established on exposed mineral soil. Although we did not measure amounts of exposed mineral soil, the proportion of exposure in each stand's surface area appeared proportional to the relative abundance of red alder. Our stand selection criteria were the following: (1) the proportion of red alder basal area representing a continuum from pure conifer to predominantly red alder, (2) stands that were logged and naturally regenerated, (3) no intermediate management activities such as tree thinning or red alder girdling, (4) stand size of 5–10 ha (minimum size 2 ha), (5) elevation of less than 150 m, (6) slopes of 10%–40%, (7) no unusual site conditions within stands such as gravel borrow pits, logging roads, or beaver ponds, and (8) relative ease of access for logistical reasons and sampling efficiency (Wipfli et al. 2002). Although the stands were chosen subjectively, they were chosen entirely on the basis of overstory and site characteristics and not on any apparent understory relations. We emphasized finding a variety of stands that constituted a gradient in the proportion of red alder in the overstory while simultaneously meeting the other site criteria as well.

Data collection

We established a uniformly spaced, systematic grid of 20 sample points throughout each of the nine stands to determine overstory species composition and the biomass of understory vegetation. At five of those points, randomly selected in each stand, we installed fixed-area plots to estimate the red alder component as a percentage of the total stand basal area. Each fixed-area plot included four circular plots (Avery and Burkhart 1994): one large 0.05 ha plot (radius 12.62 m), and three small 0.0025 ha plots (radius 2.82 m). One small plot was located at the large-plot center, and the other two were 8 m from the plot center in randomly selected directions. We recorded tree species and measured the diameter at breast height (DBH, diameter at 1.3 m) for all live trees; within the 0.05 ha plot we measured trees with

Table 2. Stand density and tree species composition of nine stands listed in increasing percentage of red alder in total tree basal area (% BA).

	Basal area		Species composition			
Stand name	Total (m^2/ha)	Red alder (% BA)	Red alder	Sitka spruce	Western hemlock	Western redcedar
UGE	59.6	0	0	493	819	0
CED	50.6	3	24	705	2533	488
LM	48.0	16	348	601	753	468
LGE	60.8	18	451	843	689	27
M22	54.4	28	392	265	1415	0
BS	47.8	33	291	303	672	57
GP	45.5	39	560	519	801	0
AF	46.0	64	680	645	333	27
BR	38.0	86	708	275	389	240

Note: Tree density includes all live trees with DBH ≥3 cm.

DBH ≥20 cm, and within the three 0.0025 ha plots we measured trees with DBH ≥3 cm.

We measured understory biomass in thirty-five 1-m^2 quadrats (1 m × 1 m) in each of the nine stands during early August, when understory biomass is at its peak: four quadrats were located in each of the five fixed-area 0.05-ha overstory plots, 4 m from the plot center in each of the four cardinal directions. Additionally, one quadrat was located at each of the other 15 sample points, 4 m north or 4 m south of the point, with north or south determined randomly.

Species-specific biomass of shrubs, conifer seedlings (<0.5 m tall), ferns, and herbaceous plants rooted within each quadrat was determined by clipping the plants at their base and weighing them with Pesola spring scales with an accuracy of 0.1 g. We excluded plants that were more than 50% dead, with the exception of woody plants, where we removed dead branches and included the rest of the plant in the biomass sample. We measured total aboveground biomass for herbaceous plants, including ferns, horsetails, and *Lycopodium* spp. Each species of shrub was separated into three components: leaves (including flowers), twigs (growth of current year), and stems (growth of prior years), because these components differ greatly in their nutritional value as deer forage (see next section). Similarly, each species of conifer seedling was separated into new growth (current year) and old growth (prior years). We collected subsamples of all species and parts of plants at each stand at the time of sampling for dry mass determinations (variable number of samples, more if raining). Samples were weighed before and after oven-drying (24 h at 105 °C) for dry and fresh mass correction factors. Although we refer to our measures of current annual growth as "aboveground net production", they do not include incremental growth in stem diameters of shrubs and trees or losses to herbivory or mortality. Plant nomenclature follows Hultén (1968), except for devilsclub (*Oplopanax horridum* (Smith) Miq.) and red alder.

Analysis

We combined tree data from the fixed-area plots to calculate the mean percentage of red alder (as percentage of the total stand basal area) within each stand. The understory biomass data from all 35 quadrats were averaged to obtain estimates of dry mass biomass (kilograms per hectare) by species and plant part for each stand. We used linear regression analyses to test the relations between the proportion of red alder basal area and (1) understory biomass and (2) "carrying capacity" for deer (see next paragraph). We used the F test for regression and $\alpha = 0.05$ to test the statistical significance of the regression (Draper and Smith 1966). We were specifically interested in red alder as the predictor (independent) variable and did not analyze the effects of conifers directly. The understory is very sparse in young-growth conifer stands in the region (Alaback 1982), regardless of the conifer species composition (DeMars 2000).

We quantified understory food value for black-tailed deer (deer-days per hectare) with a food-based nutritional model for deer habitat (Hanley and Rogers 1989). The model was a linear programming model that maximized the combined biomass of all foods while meeting specified minimum constraints for digestible energy and digestible protein concentrations of the combined biomass. The maximum biomass (kg/ha) was then divided into the specified daily dry-matter intake of an adult female deer (g/day), yielding the number of deer days that the food base could support at that specified level of nutritional requirements. For simplicity, we termed that number "carrying capacity" (deer-days per hectare) while fully realizing that our value does not involve any consideration whatsoever of the dynamics of plant–herbivore interactions or the long-term sustainability of that level of use. Our estimates of food biomass in winter were the summer values minus all deciduous species or plant parts; we did not include any effect of snow. Our seasonal estimates of digestible energy and digestible protein concentrations in the food were specific to each species and plant part and came from an unpublished regional database (T.A. Hanley, unpublished data) based on the following studies plus other unpublished studies: Hanley and McKendrick (1983), Hanley et al. (1992), McArthur et al. (1993), and Parker et al. (1999).

Results

Total tree density ranged from 1312 to 3750 trees/ha across all stands, with composition being approximately 47% western hemlock, 26% Sitka spruce, 7% western redcedar, and 19% red alder (Table 2). Total stand basal area ranged from 38.0 to 60.8 m^2/ha, with the percentage of red alder ranging from 0% to 86%.

Total aboveground biomass of understory vegetation ranged from 10.24 to 616.76 kg/ha across the nine stands (Table 3)

Table 3. Aboveground biomass (mean ovendry mass, kg/ha) of understory vegetation in nine stands[a], listed by growth form, with stands listed in increasing order of their percentage of red alder basal area (BA).

	Stand name (% of red alder BA)								
Species	UGE (0%)	CED (3%)	LM (16%)	LGE (18%)	M22 (28%)	BS (33%)	GP (39%)	AF (64%)	BR (86%)
Forbs									
Actaea rubra	—	—	—	—	—	0.12	—	—	—
Coptis asplenifolia	—	0.48	0.03	—	—	0.03	—	—	—
Cornus canadensis	—	0.63	—	—	—	0.02	0.13	—	—
Lysichiton americanum	—	0.02	0.13	—	—	—	—	9.23	—
Maianthemum dilatatum	—	—	—	—	—	0.15	0.11	—	0.15
Monesis uniflora	—	—	—	0.03	—	0.12	—	—	—
Osmorhiza purpurea	—	—	—	0.42	—	—	—	—	—
Rubus pedatus	—	0.33	—	—	—	0.03	0.06	0.20	—
Streptopus amplexifolius	—	—	—	—	—	0.13	0.48	—	0.13
Stellaria crispa	—	—	—	—	—	—	—	1.19	—
Tiarella trifoliata	0.26	0.45	0.95	1.72	0.64	7.06	0.42	1.66	2.66
Tolmiea menziesii	—	—	—	—	0.02	2.35	2.22	7.39	14.72
Viola glabella	—	—	—	—	—	0.44	0.26	0.39	—
Total forbs	0.26	1.92	1.11	2.19	0.74	10.47	3.68	20.21	17.67
Ferns									
Adiantum aleuticum	—	—	0.25	—	—	0.07	—	—	—
Athyrium felix-femina	0.40	3.97	0.39	2.29	0.52	10.19	1.06	3.68	16.11
Blechnum spicant	0.03	3.18	0.03	0.02	1.76	0.79	1.38	—	0.84
Dryopteris expansa	1.29	0.84	2.85	0.96	4.60	6.02	9.36	5.14	5.98
Gymnocarpium dryopteris	1.38	1.68	0.80	3.53	0.63	2.92	2.64	8.17	7.83
Thelypteris phegopteris	—	—	0.78	0.59	0.19	0.81	1.39	—	—
Total ferns	3.10	9.66	5.10	7.39	7.70	20.80	15.84	16.99	30.76
Graminoids									
Carex deweyana	—	—	0.69	—	—	—	—	—	—
Luzula parvafolia	—	—	0.20	—	—	—	—	0.25	—
Trisetum spp.	—	—	0.09	—	—	—	0.09	1.72	—
Unknown grass	—	—	—	1.78	0.02	—	—	—	—
Total graminoids	—	—	0.98	1.78	0.02	—	0.09	1.97	—
Total herb	3.36	11.59	7.19	11.37	8.45	31.27	19.61	39.18	48.44
Shrubs									
Menziesia ferruginea									
Leaf	—	3.31	—	0.24	—	—	—	2.32	—
Twig	—	1.38	—	0.39	—	—	—	2.33	—
Stem	—	41.59	—	2.74	—	—	—	24.35	—
Oplopanax horridum									
Leaf	—	3.00	—	—	—	—	—	—	5.21
Twig	—	0.67	—	—	—	—	—	—	2.68
Stem	—	11.81	—	—	—	—	—	—	6.99
Ribes bracteosum									
Leaf	—	—	—	—	—	—	0.03	20.87	—
Twig	—	—	—	—	—	—	0.00	0.19	—
Stem	—	—	—	—	—	—	0.20	190.72	—
Ribes laxiflorum									
Leaf	—	—	0.09	20.15	—	—	—	14.53	15.60
Twig	—	—	0.01	11.88	—	—	—	4.68	3.85
Stem	—	—	0.31	18.29	—	—	—	42.00	43.81
Rubus spectabilis									
Leaf	0.05	1.35	3.84	1.11	17.09	6.88	34.34	15.05	77.12
Twig	0.02	0.66	0.89	0.36	5.10	2.04	18.04	2.69	33.78
Stem	0.06	4.64	13.91	7.60	54.48	20.52	108.65	88.88	261.78

Table 3 (*concluded*).

Species	Stand name (% of red alder BA)								
	UGE (0%)	CED (3%)	LM (16%)	LGE (18%)	M22 (28%)	BS (33%)	GP (39%)	AF (64%)	BR (86%)
Sambucus racemosa									
Leaf	—	—	—	—	—	—	0.12	—	9.25
Twig	—	—	—	—	—	—	0.14	—	23.85
Stem	—	—	—	—	—	—	0.00	—	45.25
Vaccinium ovalifolium[b]									
Leaf	0.13	5.13	0.53	0.09	0.01	1.03	1.41	0.08	—
Twig	0.31	10.88	0.89	0.38	0.01	1.63	1.71	0.10	—
Stem	5.50	118.81	5.46	0.00	0.19	29.92	14.65	0.16	—
Total shrubs	6.07	203.22	25.51	12.91	76.87	62.00	179.28	347.73	465.90
Tsuga heterophylla[c]									
New growth	0.06	0.55	—	—	—	—	—	—	1.18
Old growth	0.75	27.64	—	—	—	—	—	—	37.98
Total vascular plants	10.24	243.00	33.12	74.59	85.32	93.28	198.88	448.13	616.76

[a]Only species with a biomass of at least 0.10 kg/ha in one stand are listed in the table, but values for excluded species are included in totals. Species excluded from table listing were the following: *Aqualegia formosa, Circaea alpina, Claytonia siberica, Equisetum pratense, Galium* spp., *Prenanthes alata, Trisetum cernum.*

[b]Includes *Vaccinium alaskensis.*

[c]Western hemlock seedlings only.

Fig. 1. Total aboveground understory biomass (ovendry mass) of nine stands in relation to percentage of red alder in the total tree basal area of each stand.

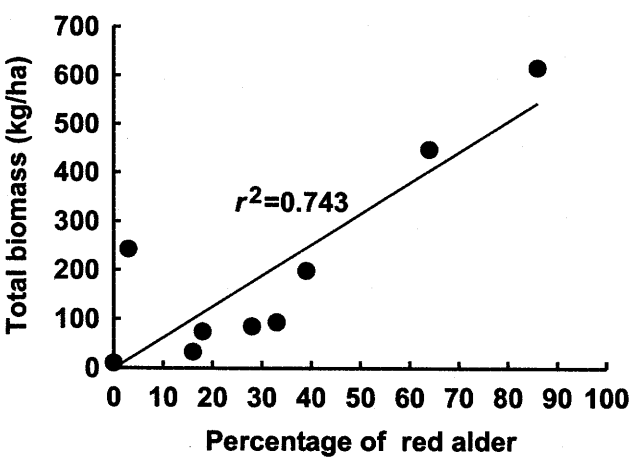
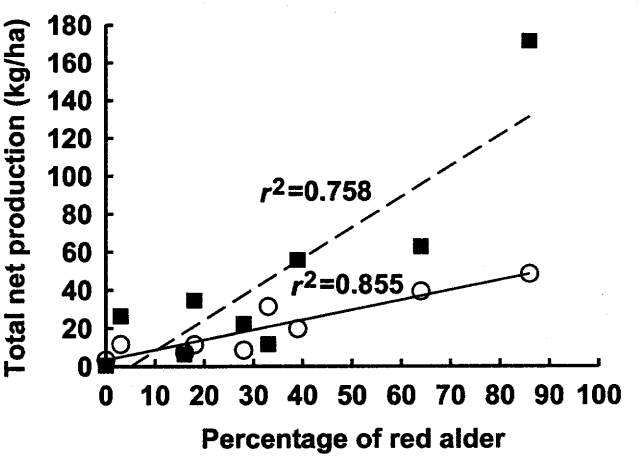


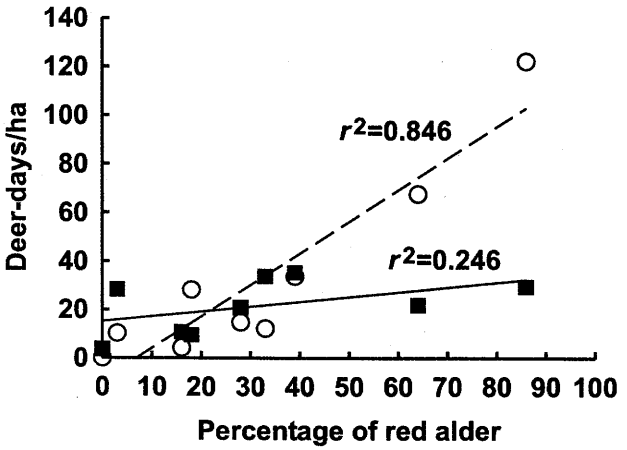
Fig. 2. Total aboveground net production (current annual growth, ovendry mass) of herbs (circles and solid line) and shrubs (squares and broken line) of nine stands in relation to percentage of red alder in the total tree basal area of each stand.



and was highly correlated with percentage of red alder basal area in the stand (Fig. 1, r^2 = 0.743, P < 0.001). Total aboveground net production (biomass of current annual growth) ranged from 3.92 to 220.95 kg/ha. The greatest increases in net production with increasing percentage of red alder were observed in shrubs (Fig. 2, r^2 = 0.758, P < 0.002), especially salmonberry (*Rubus spectabilis* Pursh) (Table 3). However, total herbaceous biomass also increased significantly with increasing percentage of red alder (Fig. 2, r^2 = 0.855, P < 0.001), especially foamflower (*Tiarella trifoliata* L.) and youth-on-age (*Tolmiea menziesii* (Pursh) Torr. & Gray) among the forbs and lady fern (*Athyrium filix-femina* (L.) Roth) and oakfern (*Gymnocarpium dryopteris* (L.) Newman) among the ferns (Table 3). Very few tree seedlings were found (Table 3). The sharp increase in shrub biomass with increasing red alder is a bit misleading in that much of the effect was in the most alder-dominated stand (Fig. 2; Table 3). Excluding that stand, however, the relation between percentage of red alder and total shrub biomass is still statistically significant (r^2 = 0.567, P < 0.02) but with a shallower slope.

Carrying capacity for deer in summer increased significantly (r^2 = 0.846, P < 0.001) and markedly (from 0.05 to 122.18 deer-days/ha) with increasing percentage of red alder, but there was no relation between carrying capacity and percentage of red alder in winter (r^2 = 0.246, P > 0.10, mean + SE = 21.51 + 3.78 deer-days/ha) (Fig. 3). In all cases, except for three stands in winter, digestible energy was the factor limiting the carrying capacity (Table 4). In the other three stands during winter, total available biomass was the limiting factor (quantity of food rather than quality of

Fig. 3. Carrying capacity (deer-days per hectare) of food resources for black-tailed deer during summer (circles and broken line) and winter (squares and solid line) of nine stands in relation to percentage of red alder in the total tree basal area of each stand. Calculations were based on the following values for summer (doe with fawn) and winter, respectively: metabolizable energy requirement of 12 970 and 4017 kJ/day; digestible protein requirement of 107.2 and 9.5 g/day; and daily dry matter intake of 1340 and 525 g/day (Sadleir 1980; Hanley et al. 1992; Robbins 1993; Parker et al. 1999).



food). In none of the cases, during either season, was digestible protein the limiting factor.

Discussion

Our results are from a retrospective study of nine stands within one general study area. More stands and more study areas would have strengthened our analysis, and our conclusions need experimental testing. However, our results are qualitatively similar to other results in other study areas in the northern region of southeast Alaska (Hanley and Hoel 1996; Deal 1997; Hanley and Barnard 1998) and provide the first quantitative relations between the relative abundance of red alder, its associated understory, and the food value of that understory for deer. As such, our study can be viewed as a first step toward a quantitative ecology of relations between mixed red alder forests and their understory in southeast Alaska.

Understory composition and biomass

The hypothesized relations between red alder composition of the forest overstory and understory biomass and production were strong and consistent throughout the 0%–86% range for red alder (Figs. 1 and 2). Although the regressions were strongly influenced by the two stands with the greatest proportion of red alder, there was no evidence of a threshold response, except perhaps for the high amount of salmonberry in the 86% red alder stand. This is important knowledge for designing silvicultural systems in the future. Perhaps of greater ecological significance, however, is the high positive correlation between herbaceous biomass and increasing percentage of red alder (Fig. 2). This relation, too, was consistent throughout the range of stands studied. It is important from both a wildlife habitat perspective and a forest management perspective, because it is the herb component that is most difficult to maintain through secondary succession of even-aged stands following clear-cutting in southeast Alaska (Alaback 1982; Hanley 1993), including precommercial thinning (Doerr and Sandburg 1986; Deal and Farr 1994; Hanley 2005). The herbaceous species showing the greatest affinity with red alder were species commonly associated with wet or riparian sites (i.e., foamflower, youth-on-age, lady fern, and oakfern), despite all of our sites being well-drained upland sites.

Among shrubs, salmonberry, red elderberry (*Sambucus racemosa* L. var. *racemosa*), devilsclub, and stink currant (*Ribes bracteosum* Dougl. ex Hook.) appeared to be associated with high proportions of red alder, while blueberry (*Vaccinium ovalifolium* Sm.) and fool's huckleberry (*Menziesia ferruginea* Sm.) were most abundant at intermediate proportions of red alder (Table 3). Salmonberry, red elderberry, devilsclub, and stink currant are common species in riparian forests, while blueberry and fool's huckleberry are most common in upland forests in southeast Alaska (Hanley and Hoel 1996). The predominance of "riparian" shrubs in the red alder dominated stands, along with the associated herbs (foamflower, youth-on-age, lady fern, and oakfern) is consistent with a common pattern reported for the region (Hanley 2005): red alder understories are dominated by species characteristic of wet or riparian sites rather than by species most characteristic of upland sites. Perhaps a more correct interpretation of site affinities for those species, however, is that they are associated with soil disturbance and

Table 4. Parameter values of optimal solutions to linear programming model for quantifying the value of understory vegetation as food for deer.

	Biomass (kg/ha)		Nutritional quality of optimal solution	
Stand name	Total available	Optimal solution	DDM (%)	DP (%)
UGE summer	3.9	0.1	**11.3**	10.7
CED summer	38.5	13.8	**11.3**	9.7
LM summer	13.4	5.7	**11.3**	10.5
LGE summer	46.0	37.8	**11.3**	8.6
M22 summer	30.7	19.8	**11.3**	10.9
BS summer	42.8	16.4	**11.3**	9.6
GP summer	75.4	45.2	**11.3**	10.7
AF summer	102.1	90.5	**11.3**	11.1
BR summer	221.0	163.7	**11.3**	10.7
UGE winter	**1.9**	1.9	10.2	7.4
CED winter	19.4	14.9	**9.0**	5.1
LM winter	**5.7**	5.7	9.7	6.6
LGE winter	15.8	5.0	**9.0**	5.0
M22 winter	12.1	11.0	**9.0**	6.0
BS winter	**17.7**	17.7	10.4	6.4
GP winter	31.3	18.6	**9.0**	6.2
AF winter	17.0	11.5	**9.0**	5.9
BR winter	72.1	15.5	**9.0**	5.7

Note: The linear programming goal was to maximize the quantity of understory biomass that could be combined while meeting specified minimum constraints for digestible energy (DE, kJ/g) and concentration of digestible protein (DP, percent dry matter). Summer nutritional constraints were 11.3 kJ/g DE and 8.0% DP. Winter nutritional constraints were 9.0 kJ/g DE and 1.8% DP. The limiting factor in each analysis is indicated in bold.

mineral soils, rather than "wet" or "riparian" conditions, whereas blueberry and fool's huckleberry are associated with undisturbed organic soils. Although we cannot rule out a microsite effect associated with variation in light availability, soil moisture, soil structure, and fertility, it is not unreasonable that some understory species are favored by exposed mineral soil resulting from soil disturbance in the same way that red alder is favored by exposed mineral soil. Cause and effect relations, however, require experimental study rather than retrospective study. We can conclude only that, whatever the cause, those species are characteristic of red alder understories in southeast Alaska, regardless of site location. While devilsclub appears to be more dominant in red alder understories in the northern end of southeast Alaska (Hanley and Hoel 1996; Hanley and Barnard 1998), the predominance of salmonberry in this more southern study area is consistent with a latitudinal trend in salmonberry–devilsclub under Pacific coastal red alder forests (Newton and Cole 1994).

Aboveground net production in all of our stands (maximum 221 kg/ha; Table 3) was less than that typical for old-growth forests of the region (272–915 kg/ha; Hanley and Brady 1997), but it was much greater than that of pure conifer even-aged stands (e.g., stands UGE and CED in our data set; Table 3). Total stand basal area tended to decrease with increasing basal area of red alder (Table 2; $r^2 = 0.61$, $P < 0.01$), and total understory production (Table 3) was inversely proportional to total stand basal area ($r^2 = 0.56$, $P < 0.02$). Thus, our understory results might be considered a basal area relation as well as a red alder relation. It would have been desirable to have had data from more red alder dominated stands, especially those with high basal areas.

More light penetrates canopies of red alder than of conifers, and red alder increases mineralizable nitrogen in the forest floor (Miller et al. 1993). The elevated levels of light and nitrogen may extend 5–10 m beyond the individual trees into the stand (Lavery et al. 2004). A mixture of red alder among conifers, therefore, likely increases both light and nitrogen for understory vegetation throughout a stand. When young conifers (especially western hemlock) cannot benefit from those conditions by establishing and growing (Deal et al. 2004), inclusion of red alder in the young-growth conifer stand may circumvent the problem reported by Deal and Farr (1994) of a second layer of western hemlock seedlings becoming established in precommercially thinned pure conifer stands. The combination of greater light penetration, increased soil fertility, and increasing canopy structural diversity through time (i.e., prolonging the increased light through the successional sequence) may provide a suitable environment for understory vegetation without the need for intensive precommercial silviculture of the stand. These relations between overstory structure and understory environment are consistent with the greater amounts of understory vegetation in mixed red alder – conifer than in pure conifer observed in young-growth forests throughout the region (Hanley and Hoel 1996; Deal 1997; Hanley and Barnard 1998).

Red alder occurs naturally in southeast Alaska in areas where disturbance has exposed mineral soil and opened the forest canopy (e.g., riparian gravel bars, landslide areas, clear-cut logging with tractor skidding, abandoned road beds, etc.) (Harris and Farr 1974; Ruth and Harris 1979). It also appears to grow well in young clearcuts when planted as rooted cuttings into undisturbed soils (J.M. Russell, unpublished data, Tongass National Forest, Sitka, Alaska). If forest managers want to include red alder in young-growth stands, they could either increase soil disturbance during logging or plant red alder cuttings. The understory response to planting, however, is currently unknown.

Food value for black-tailed deer

The increased understory biomass with increasing red alder composition resulted in greater carrying capacities for black-tailed deer as the percentage of red alder increased in the overstory (Fig. 3). However, the relation was not entirely that simple: carrying capacity for deer was highly correlated with percentage of red alder in summer, but there was no such relation in winter. The reason for the seasonal difference in response is directly attributable to the species composition of the understories of these stands. Summer food value increased with increasing red alder because the quantity of both forbs and shrubs increased with increasing red alder (Fig. 2) and the nutritional quality of forbs and shrubs (including salmonberry, red elderberry, and devilsclub) is high in summer (Parker et al. 1999). However, in winter, most of these red alder associated species are either senescent (forbs and ferns) or of very low nutritional quality (salmonberry, red elderberry, devilsclub, stink currant) (Hanley and McKendrick 1983; Parker et al. 1999). The only high-quality winter forage that occurred in any significant quantity in these stands was foamflower; it is an evergreen forb and remains highly nutritious in winter (Hanley and McKendrick 1983, 1985). The common, important winter forages for deer in southeast Alaska are other winter-evergreen forbs (bunchberry dogwood (*Cornus canadensis* L.), goldthread (*Coptis asplenifolia* Salisb.), and five-leaved bramble (*Rubus pedatus* Sm.)), arboreal lichens (*Usnea* spp. and *Alectoria* spp.), and blueberry twigs (Hanley and McKendrick 1983, 1985; Parker et al. 1999). Those species are relatively common in upland old-growth forests with undisturbed soils (Hanley and Brady 1997), but all of those species were relatively uncommon or did not occur in the red alder dominated stands in our study. Thus, the high-biomass, high-quality summer understory of the red alder dominated stands turns into a moderate-biomass (moderate in comparison to the very low biomass of pure conifer stands) and low-quality understory in winter. Furthermore, this analysis does not take snow accumulation into account, yet snow accumulation would be greater under the deciduous red alder than under the evergreen conifers. Therefore, while red alder mixed within young-growth stands might improve summer habitat for deer significantly, its potential benefits for winter habitat are probably few and quite limited. The 100% pure conifer stand, however, had such a low (near zero) amount of understory biomass that any increase in understory vegetation would likely be an improvement over that.

Effects for other wildlife species may differ from those for deer. For example, red alder stands with understories similar to those in the highest percentage of red alder stands of the present study (Hanley and Hoel 1996) provided year-round habitat for Keen's mouse (*Peromyscus keeni sitkensis* Merriam) that was of equal quality to that of both upland and riparian old-growth forests (Hanley and Barnard 1999*a*).

In that case, the plant species diversity and variety of fruits and seeds, including wind-borne Sitka spruce seed in winter, apparently were the determining factors (Hanley and Barnard 1999*b*). Wildlife habitat consequences of red alder in young-growth conifer stands, therefore, differ seasonally and for different wildlife species, depending on the wildlife species' habitat requirements.

We have studied and discussed the effects of red alder within mixed young-growth stands (at the stand scale). Another alternative might be the inclusion of red alder and mixed alder – conifer stands within a conifer mosaic at the landscape scale. This is the more common, naturally occurring pattern in the region, but with a relatively low abundance of red alder stands. Whether such a "coarse-grained" strategy of landscape management would yield similar benefits to the fine-grained (within stand) patterns that we have studied is an open question. However, pure conifer stands are known to yield very sparse understories in this region, and pure red alder stands would have virtually no effect on snow interception (with respect to winter deer habitat).

Conclusions and management implications

Mixed hardwood–conifer stands in young-growth forests of southeast Alaska offer a marked improvement in wildlife habitat over pure conifer even-aged stands in a region where forest management practices historically have been focused on pure-conifer stands. The pattern of overstory–understory relations observed in the present study is consistent with the patterns observed in similar studies further north in the Alexander Archipelago of southeast Alaska (Hanley and Hoel 1996; Deal 1997; Hanley and Barnard 1998), but this study provides insight into the relations between overstory and understory as a function of the relative abundance of red alder in the stand. As relative abundance of red alder (percentage of basal area) increased, understory production (including that of herbs) and summer food value for deer increased proportionately (present study) while having only minor consequences in diminishing conifer wood production and wood quality (Deal et al. 2004). From a summer deer habitat point of view, therefore, the more red alder in the stand, the better would be the habitat. However, intermediate levels of red alder might result in better winter habitat for deer and even greater understory diversity, because the conifers could provide some snow interception (Kirchhoff and Schoen 1987), which is very important for keeping forage available to deer (Parker et al. 1999), and conifers are more favorable for some important winter forage species (e.g., blueberry, bunchberry dogwood, five-leaved bramble) that are relatively uncommon under red alder (Hanley 2005). Intermediate levels of red alder would also be a great improvement over no red alder at all. Qualitatively, these findings in Alaska are similar to those discussed by Humphrey et al. (1998) for biodiversity in mixed birch (*Betula* spp.) – Sitka spruce plantations in Scotland.

From an optimal, multiple-use forest management point of view (conifer wood production, hardwood production, understory diversity, deer habitat), a balanced mix of red alder and conifers is probably most desirable — in our case, probably somewhere near 30%–60% basal area in stands of this age (38–42 years). Those stands captured most of the understory benefits associated with the red alder while having minimal consequences for conifer wood production (Deal et al. 2004; also see Lavery et al. 2004). It must be kept in mind, however, that our study is only a "snapshot" in the time sequence of secondary forest succession, and overstory–understory relations should be expected to vary with stand age. Although our observations are consistent with general patterns observed elsewhere in southeast Alaska for a variety of stand ages, we have no experience with clear-cut-regenerated mixed red alder stands that are greater than 50 years of age.

Red alder is not an abundant species in the upland predominantly old-growth forest landscapes of southeast Alaska, and under long rotations that exceed the life-span of red alder (perhaps 60–130 years; Smith 1968; Newton and Cole 1994) we would expect it to diminish and remain uncommon in old stands. However, red alder may play a very important role in the ecology of managed young-growth forests in this region, greatly increasing understory vegetation and improving wildlife and fish habitat over that of pure conifer young-growth stands, while simultaneously adding a hardwood component to the forest. Mixed hardwood – conifer stands could be of significant importance in the future managed forests in this region of strongly conifer dominated natural forests.

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