The effects of partial cutting on forest plant communities of western hemlock – Sitka spruce stands in southeast Alaska

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Abstract: The effects of partial cutting on plant species richness, community structure, and several understory species that are important for deer forage were evaluated on 73 plots in 18 stands throughout southeast Alaska. These partially cut stands were harvested 12–96 years ago when 16–96% of the former stand basal area was removed. The species richness and community structure of understory plants were similar in uncut and partially cut plots. However, plots where more than 50% of the basal area was cut had a significantly different plant community structure. Species composition and abundance also appeared to be distinctly different between hemlock-dominated and spruce-dominated stands. Partial cutting did not significantly change abundance for most of the important forage species for deer. The similarity in plant community structure between partially cut and uncut old-growth stands may be related to forest stand structures. The heterogeneous stand structures that develop after partial cutting are more similar to old-growth stands than to the uniform young-growth stands that develop after stand replacing disturbances such as clear-cutting.

Résumé : Les effets d'une coupe partielle sur la richesse en espèces végétales, sur la structure de la communauté et sur plusieurs espèces de sous-bois qui constituent une source importante de fourrage pour le chevreuil ont été évalués dans 73 parcelles réparties dans 18 peuplements situés dans le sud-est de l'Alaska. Ces peuplements partiellement coupés ont été récoltés il y a 12–96 ans alors que 16–96% de la surface terrière du peuplement original a été enlevée. La richesse en espèces et la structure de la communauté des plantes de sous-bois étaient semblables dans les parcelles non coupées et partiellement coupées. Cependant, dans les parcelles où plus de 50% de la surface terrière avait été coupée, la structure de la communauté végétale était significativement différente. La composition et l'abondance des espèces semblaient également nettement différentes entre les peuplements dominés par la pruche et les peuplements dominés par l'épinette. La coupe partielle n'a pas significativement changé l'abondance de la plupart des espèces qui constituent une source importante de fourrage pour le chevreuil. La similitude dans la structure de la communauté végétale entre les peuplements de vieille forêt partiellement coupés et non coupés est peut-être reliée à la structure des peuplements forestiers. Les peuplements à structure hétérogène qui se développent suite à une coupe partielle sont plus semblables aux peuplements de vieille forêt qu'aux jeunes peuplements uniformes qui se développent après des perturbations, comme la coupe à blanc, qui entraîne la régénération du peuplement.

[Traduit par la Rédaction]

Introduction

Disturbance has been widely recognized as a major force in the development, structure, and function of forests (Bormann and Likens 1979; Oliver and Larson 1990; Attiwill 1994). The importance of disturbance on plant succession has also been well documented (Whittaker 1953; Egler 1954; Connell and Slatyer 1977; Pickett and White 1985), and there has been recent interest in the role of disturbance in affecting forest community structure and composition (White 1979; Christensen 1989; Halpern 1989; Angelstam 1998). There may be important differences in scale and intensity between natural and human disturbances, but in many cases, the effects of human disturbance on ecosystem structure and function are not significantly different than those of natural disturbances (Attiwill 1994).

The natural disturbance regime in southeast Alaska is characterized by high-frequency, low-magnitude disturbance events (Brady and Hanley 1984) and gap-phase replacement (Alaback and Juday 1989; Lertzman et al. 1996), resulting in complex multiaged or uneven-aged stands (Deal et al. 1991; Nowacki and Kramer 1998). Proximity to the North Pacific Ocean results in cool summers and mild winters with abundant precipitation occurring throughout the year. Much of the precipitation occurs in the autumn season along with occasional hurricane force winds. The significance of this climate for the forest is that moisture is generally not a limiting factor for tree regeneration, wildfire is rare, and windthrow and wind-caused damage of trees are common. (Harris et al. 1974; Harris 1989; Deal et al. 1991; Nowacki and Kramer 1998).

There is increasing interest in devising new forest management strategies that accelerate the development of late-succession and old-growth stand characteristics and maintain biodiversity in managed forests (Franklin et al. 1981, 1997; Harmon et al. 1986; Franklin 1989; Larsen 1995). Several

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studies are underway in the Pacific Northwest region to evaluate the effects of different silvicultural prescriptions designed to accelerate the development of late successional forest characteristics (Arnott and Beese 1997; Coates and Burton 1997; Aubry et al. 1999; Curtis et al. 1999[2]). Recent forest management plans in Alaska have prescribed forest practices using a variety of silvicultural systems, including even-aged, two-aged, and uneven-aged management (USDA Forest Service 1997). However, even-aged silvicultural systems using clear-cutting have been almost exclusively used in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) – Sitka spruce (*Picea sitchensis* (Bong.) Carrière) forests of southeast Alaska since the establishment of large-scale timber operations in the early 1950s (Harris and Farr 1974). Little is known about forest management practices in this region, other than even-aged silvicultural systems, and the effects of proposed partial cutting on forest stand development and understory plant diversity and abundance are unknown. Research on alternatives to clear-cutting is currently being conducted in southeast Alaska using large experimental studies, but long-term results of this research will not be available for many years (McClellan et al. 2000). There is a need to retrospectively evaluate the effects of previous partial cutting on stand structure, forest overstory–understory interactions, and plant communities to assess the effects of partial cutting and to develop interim management guidelines for new silvicultural systems.

In southeast Alaska, forest stand development after stand-replacing disturbances such as clear-cutting is very different from the natural gap-phase disturbance regime common in the region. Stand development after clear-cutting follows a clearly defined pattern with the establishment and development of a new cohort of western hemlock and Sitka spruce trees (Alaback 1982*a*; Deal et al. 1991). Conifer regeneration, shrubs, and herbaceous plants are rapidly established (stand initiation), and understory plant biomass peaks around 15 to 25 years after clear-cutting (Alaback 1982*a*). Canopy closure occurs about 25 to 35 years after cutting followed by an intense period of intertree competition that prevents new tree regeneration (stem exclusion). The developing young-growth stands are extremely dense, and stands have relatively uniform tree height and diameter distributions. This stage of stem exclusion is long lasting in southeast Alaska and can persist for 50 to 100 years or longer (Alaback 1984). During the stem exclusion stage, stands notably lack the multilayered, diverse structure and shrub–herb layers found in old-growth or multiaged stands common in the region. Over time, disease, insect, and wind disturbances in these stands (Kimmey 1956; Hard 1974; Harris 1989) create gaps in the canopy, resulting in reestablishment of new tree cohorts (understory reinitiation) and other understory vegetation.

Forest development after stand-replacing disturbances such as clear-cutting has significant and long-term effects on understory plant development. Canopy closure eliminates most herbs and shrubs (Alaback 1982*a*), and attempts to reestablish understory plants through thinning dense young-growth stands have led to mostly conifer regeneration (Deal and Farr 1994) with little success in herbaceous plant colonization (Tappeiner and Alaback 1989). This intense stage of stem exclusion eliminates or significantly reduces the growth rate of understory vegetation for up to 100 years (Alaback 1982*b*, 1984; Tappeiner and Alaback 1989). The effect of a much reduced herb and shrub community for a long period of the stand rotation (100+ years) means that plant diversity and abundance are greatly reduced for over 70% of the stand rotation time period.

This long-lasting stage of stem exclusion has significant implications for wildlife such as Sitka black-tailed deer, which depend on these plants as forage (Wallmo and Schoen 1980; Schoen et al. 1988; Hanley 1993). For the first 15 to 25 years after clear-cutting, these young-growth stands provide greater understory plant biomass than old-growth stands (Alaback 1982*a*); however, snow accumulation makes them much less useful for deer habitat in the winter (Rose 1984; Kirchhoff and Schoen 1987; Schoen and Kirchhoff 1990). The dense, uniform canopy of young-growth hemlock–spruce stands and the abundant conifer regeneration established after thinning significantly reduce understory plant diversity and abundance. The establishment of these dense stands is recognized as having broadly negative consequences for wildlife habitat (Wallmo and Schoen 1980; Hanley 1993; Dellasalla et al. 1996). The use of partial cutting rather than clear-cutting in old-growth stands needs to be evaluated to determine if partial cutting can provide the critical stand structure for winter deer habitat, greater plant diversity and abundance, and important plant species for wildlife forage.

The effects of management practices such as partial cutting on forest plant communities in hemlock–spruce stands of southeast Alaska are unknown. Before undertaking a widespread shift to partial cutting, it is essential to understand stand development and to assess the potential role of partial cutting on understory plant diversity and abundance. The major objectives of this study were to analyze plant species diversity and abundance in partially cut and uncut stands, and to determine the changes in forest plant communities occurring after different intensities of partial cutting. I also evaluated several plant species that are important for deer forage and determined if either partial cutting or the intensity of cutting led to significant changes in their abundance.

Material and methods

Study areas

Southeast Alaska is a temperate rainforest region and part of the hemlock–spruce forest type that occupies a narrow 3000 km long band along the Pacific Coast from Coos Bay, Oregon, to Prince William Sound, Alaska (Barrett 1995). The region of southeast Alaska is characterized by rugged steeply rising coastal mountains and numerous densely forested islands (Harris et al. 1974). Partial cutting of forests was a common practice in southeast Alaska in the early 1900s until about 1950 when pulp mills were established in the region. Logging practices varied from hand logging at the turn of the century to A-frame, high-lead, and other cable-logging systems since the 1920s (Rakestraw 1981). Usually, individual Sitka

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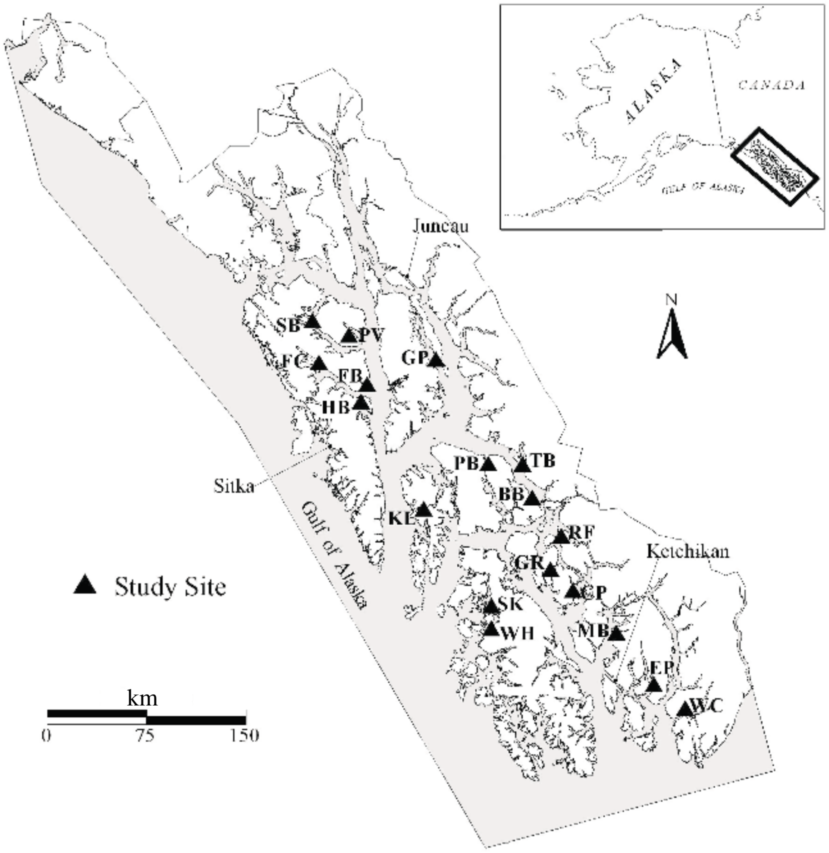
[2] Curtis, R.O., Clendenen, G.W., DeBell, D.S., et al. 1999. Study plan: silvicultural options for harvesting young-growth production forests. On file at Olympia Forestry Sciences Laboratory, PNW Research Station, Olympia, Wash.

Fig. 1. The 18 study sites in southeast Alaska. See Table 1 for definition of site codes.



spruce trees were cut for sawtimber, or western hemlocks were harvested for piling, leaving stands of variable density, species composition, and size.

Eighteen sites were selected to sample a range of "time since cutting", intensity of cutting, and geographic distribution throughout southeast Alaska (Fig. 1, Table 1). Potential study sites were selected from 200+ sites identified from a variety of sources, including USDA Forest Service district files, historical records, and maps. Study sites were selected under the following criteria: (*i*) a range of time since cutting from 10 to100 years; (*ii*) stands with only one cutting entry; (*iii*) a partial-cut area of at least 10 ha, with a wide range of cutting intensities at each site, including an uncut area; (*iv*) relatively uniform topography, soils, forest type, and plant associations within each site; and (*v*) geographical distribution throughout southeast Alaska. All study sites were within 2 km of the nearest shoreline and less than 100 m in elevation.

At each study site stand, surveys were conducted to assess and find a range of current stand densities and cutting intensities, and the number and size of cut stumps and overstory trees were noted. An uncut control and generally three partially cut areas (light, medium, heavy) were located at each site in 1995 and 1996. Overstory stand plots, centrally located within each partially cut area, were used to evaluate stand structure. A total of seventy-three 0.2-ha overstory plots were installed at the 18 study sites.

Stand reconstruction

Stands were reconstructed back to the date of cutting using cut stumps, current live trees, and snag information (Deal 1999). The date of cutting was determined by using tree radial-growth analyses (Henry and Swan 1974; Oliver 1982; Lorimer 1985) and verified by historical data if available. Patterns of tree release indicating an abrupt and sustained increase in growth for at least 10 consecutive years averaging at least 50–100% greater than the previous 10 years (Lorimer et al. 1988) were used to determine the date of partial cutting. These partially cut stands were harvested 12–96 years ago (Table 1).

I developed stump-to-breast-height equations (Deal 1999) to predict tree diameter at breast height (DBH) from the stump diameter, by using forward stepwise regression analysis (Snedecor and Cochran 1980). The basal area of each stump was multiplied by the appropriate overstory plot expansion factor to determine basal area cut per hectare for each plot. The diameter at time of cutting of current live trees was determined by using increment cores and stem sections from 986 western hemlock, Sitka spruce, western redcedar (*Thuja plicata* Donn ex D. Don), and yellow-cedar trees (*Chamaecyparis nootkatensis* (D. Don) Spach). I developed site-specific regression equations to predict DBH at time of cutting for all trees by relating DBH at time of cutting to current tree DBH, basal area, species, and plot cutting intensity (Deal 1999). The basal area of all trees at time of cutting was multiplied by the overstory plot expansion factor to determine stand basal area per hectare for each plot at time of cutting. Snag class and snag age data were used to determine snag DBH at cutting date, and then I estimated stand mortality since cutting. Each snag was assigned to a decay class, and a mean age for each decay class was determined (Hennon et al. 1990; P. Palkovic, unpublished data). The live-tree regression equations were used for snags, and snag DBH was predicted at the date of cutting. Periodic basal-area mortality per hectare was estimated for each plot. Data on the basal area that was cut, current live tree basal area at cutting date, and stand mortality since cutting were then combined to determine the proportion of basal area cut for each stand cutting treatment (Deal 1999). Cutting intensity ranged from 16 to 96% of the former stand basal area (Table 1).

Table 1. Descriptions of research sites listed chronologically by cutting date.

		Cutting intensity			Current stand composition[a]					
Research site (no. of 0.2-ha plots/site)	Cutting date	BA cut (%)	BA cut ($m^2 \cdot ha^{-1}$)	BA uncut ($m^2 \cdot ha^{-1}$)	BA ($m^2 \cdot ha^{-1}$)	All trees (trees/ha)	Spruce (%)	Hemlock (%)	Other[b] (%)	Forest type
TB, Thomas Bay (3)	1984	20–29	18–19	42–77	49–70	237–766	1–17	83–99	0	Western hemlock
GR, Granite (4)	1983	18–86	9–51	9–50	13–70	368–1440	0–7	93–100	0	Western hemlock
PV, Pavlof River (6)	1977	36–58	21–43	31–47	37–69	288–823	4–29	42–96	0–46	Sitka spruce
BB, Big Bear Creek (4)	1958	17–36	9–27	47–63	53–79	270–754	15–47	53–85	0	Sitka spruce
MB, Margarita Bay (4)	1958	23–83	9–48	10–30	41–63	694–2695	4–24	76–96	0	Western hemlock
RF, Rainbow Falls (4)	1942	34–61	15–25	16–29	44–66	348–1108	0–28	63–100	0–10	Sitka spruce
FC, Finger Creek (4)	1941	18–41	11–33	44–51	58–75	331–522	5–60	40–95	0	Western hemlock
WH, Winter Harbor (4)	1932	24–38	19–39	56–70	73–95	785–1311	2–33	67–98	0	Sitka spruce
SB, Salt Lake Bay (4)	1928	48–55	28–35	29–31	63–87	158-642	17–73	27–83	0	Sitka spruce
CP, Canoe Passage (4)	1927	16–75	9–57	19–46	44–66	815–2452	2–13	74–92	6–19	Western hemlock
EP, Elf Point (4)	1927	17–73	12–36	13–57	42–116	453–1443	2–4	72–96	0–24	Western hemlock
SK, Sarkar (4)	1925	27–59	14–28	19–37	57–76	467-1163	0–11	89–100	0	Western hemlock
HB, Hanus Bay (4)	1922	49–96	24–85	3–25	56–83	413–1180	6–62	38–94	0	Sitka spruce
KL, Kutlaku Lake (4)	1920	31–63	17–31	18–37	58–139	305–525	5–49	35–95	0–16	Sitka spruce
PB, Portage Bay (4)	1918	26–65	7–28	14–25	47–56	459–1202	5–33	67–95	0	Western hemlock
FB, Florence Bay (4)	1914	50–57	33–38	26–38	56–83	120–360	18–75	25–82	0	Sitka spruce
GP, Glass Peninsula (4)	1911	23–69	15–41	17–47	60–84	147–397	11–34	28–83	0–49	Sitka spruce
WC, Weasel Cove (4)	1900	17–51	9–23	22–45	53–75	450–1220	0–24	67–100	0–17	Sitka spruce

Note: The cutting intensity data refer to the range for the partially cut plots at each site. The current stand data include the range of both uncut and cut plots at each site. The forest type is the major overstory tree species at each site. BA, basal area.

[a] Stand data for trees and basal area includes all trees that are at least 2.5 cm DBH.

[b] The other minor species include western redcedar (*Thuja plicata*), yellow-cedar (*Chamaecyparis nootkatensis*), red alder (*Alnus rubra* Bong.), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière).

Stand data

For each overstory plot, tree species, DBH, tree height, and crown position were measured for all live trees greater than 2.5 cm DBH (1.3 m) to provide current stand structural information. Stand reconstruction provided data on the date and the intensity of cutting. The overstory plot data included time since cutting and stand structural data on the total stand basal area cut, residual basal area retained, proportion of stand basal area cut, stand density, and the proportion of spruce and hemlock in the stand (Table 1). Environmental data included elevation, slope, aspect, plant association, and forest type.

Vegetation data

Understory vegetation was sampled with ten 1 × 1 m vegetation quadrats (1.0 m^2), and ten 2 m radius shrub plots (12.57 m^2) systematically distributed within each of the seventy-three 0.2-ha overstory plots. Canopy cover classes by species for all herbs, mosses, lichens, liverworts, and tree seedlings less than 0.1 m tall were estimated within each vegetation quadrat. The canopy cover classes were estimated for shrub and understory tree species, and shrub and tree seedlings greater than 0.1 m tall were measured for height within the shrub plots. Canopy cover classes were as follows: <1, 1–5, >5–25, >25–50, >50–75, >75–95, and >95–100% (Daubenmire 1959).

Construction of data sets

The canopy cover data for the 10 vegetation quadrats and shrub plots were combined and averaged within each overstory plot to estimate mean abundance for each plant species found on the 0.2-ha overstory plots. The percent vegetation cover for each species was calculated using the midpoints of each canopy cover class. A plot-by-species matrix was constructed where species abundance data consisted of mean cover. Separate data sets were constructed and used to assess species diversity and plant community structure. One data set used the full set of 73 plots and 146 species. Another data set contained only vascular plants and included 73 plots and 56 species; this data set was used to assess species diversity and richness of vascular plants and to analyze the structure of the vascular plant community. Finally, a reduced data set was developed where species occurring in fewer than three plots were removed from the data set. No plots were removed, but 36 species occurring on only one plot and nine species occurring on only two plots were removed, creating a reduced data matrix of 73 plots and 101 species. The reduced data set was developed to determine if the elimination of rare species reduced the variability of species abundance and strengthened the relationship between plots and species composition. This reduced data set was later used for all additional analyses of plant community structure.

An environmental matrix comprising both quantitative and categorical variables was constructed using the stand structural and environmental data from the overstory plots. A class variable for cutting intensity was created using the proportion of basal area cut: uncut plots (0), plots with 1–25% of basal area cut (1), plots with 26–50% basal area cut (2), and plots with greater than 50% of the basal area cut (3).

Data analysis

Species richness and diversity measures for the full, reduced, and vascular plant (including separate subsets for herbs and shrubs) data sets were calculated using PC-ORD (McCune and Mefford 1997). Diversity measures for species (gamma diversity, the total number of plant species in the study; alpha diversity, the mean number of species in the overstory 0.2-ha plots; and beta diversity, the amount of species compositional change in plots) and data distribution (skewness and coefficient of variation) for both plots and species were determined. The data were tested for outliers. Diversity measures calculated included Shannon's diversity index, H', (Shannon and Weaver 1949) and Pielou's evenness index, E, (Pielou 1975) from

$$[1] \qquad H' = -\Sigma[p_i \ln(p_i)]$$

where p_i is the importance probability in element i, and

$$[2] \qquad E = \frac{H'}{\ln(\text{richness})}$$

To determine the effect of partial cutting on plant species richness, I blocked plots by site and then tested for differences in species richness between cut and uncut plots for all plants and for vascular plants separately, using contrast analysis (SAS Institute Inc. 1989). I then blocked plots by site and determined the effect of cutting intensity (% basal area (BA) cut) on species richness for all plants and for vascular plants.

Following construction of the reduced data set, I used multi-response permutation procedures (MRPP) and non-metric multidimensional scaling ordination (NMS) in PC-ORD (McCune and Mefford 1997) to analyze species composition and abundance (plant community structure). For the MRPP analysis, I pooled all of the partially cut plots and tested for differences in plant community structure between uncut and partially cut plots. I separated the recently harvested sites (cut 12–38 years ago; pre-canopy closure) from the older sites (cut 53–96 years ago; post-canopy closure) and compared plant community structure in four cutting intensity classes (uncut, 1–25% BA cut, 26–50% BA cut, and >50% BA cut). I used MRPP to test for differences in community structure between the uncut plots and the three plot cutting intensities. For ordination analysis, I initially used a Bray–Curtis ordination with Sorenson distance measure and variance–regression endpoint selection. This generally provided a good spread of points in the ordination, and I saved the ordination scores as an input configuration for NMS. I then used NMS ordination with Sorenson distance measure for two and three axes with 100 iterations. I also ran Monte Carlo tests on a series from six axes to one axis and compared the stress obtained from the randomized data with my data set (Kruskal 1964; Clarke 1993). All ordinations were rotated to align the variable forest type with axis 1. Forest type is the major overstory tree species based on plant association, and this was used to relate overstory tree composition with understory plant community structure. The final ordination model was selected as the one that explained the greatest amount of variation in the original distance matrix on the fewest number of axes. I then analyzed overlays of variables from the environmental matrix and reported the relation of NMS axes to plant species composition and abundance and key environmental variables associated with each axis.

The effects of partial cutting on wildlife habitat were examined by analyzing changes in the abundance of eight plant species important for deer forage (Hanley and McKendrick 1985; Kirchhoff and Hanley 1992). These plant species included five herbs (*Coptis asplenifolia*, *Cornus canadensis*, *Lysichiton americanum*, *Rubus pedatus*, and *Tiarella trifoliata*), one fern (*Dryopteris expansa*), and two shrubs (*Vaccinium ovalifolium* and *Vaccinium parvifolium*) (Pojar and MacKinnon 1994). Canopy cover for each species was averaged for each of the four plot cutting intensities. To determine the general effects of partial cutting on the abundance of these plant species, I blocked plots by site and tested for differences in abundance (mean cover) between cut and uncut plots for each species using contrast analysis (SAS Institute Inc. 1989). For a more detailed assessment of partial cutting effects, I then blocked plots by site and determined the effect of cutting intensity on the abundance for each plant species.

Table 2. Species diversity measures and data distribution for the full data set (146 plant species), reduced data set (101 plant species), vascular plants, herbaceous plants, and shrubs.

	Species diversity measures[a]					Data distribution			
						Coefficient of variation (%)		Skewness	
Data set	Gamma	Alpha	Beta	E	H'	Total of plots	Total of species	Plot mean	Species mean
Full	146	31.3	4.67	0.66	2.27	33.10	314.51	6.67	5.60
Reduced[b]	101	30.6	3.30	0.82	2.80	31.95	75.46	3.51	4.42
Vascular	56	14.7	3.81	0.66	1.77	50.83	221.75	4.56	5.40
Herb[c]	41	9.2	4.46	0.70	1.48	65.30	188.25	4.01	5.37
Shrub[d]	15	5.5	2.73	0.53	0.90	70.05	191.93	2.92	5.47

[a] Gamma diversity is the total number of plant species in the study; alpha diversity is the mean number of species in the overstory 0.2-ha plots; beta diversity is the amount of species compositional change in plots; evenness (E) = $H'/\ln(\text{richness})$, from Pielou (1975); diversity (H') = $-\Sigma(p_i \ln(p_i))$, where p_i is the importance probability in element i, from Shannon and Weaver (1949).

[b] The reduced data set included only species found on three or more plots.

[c] The herb data set included herbaceous plants and ferns.

[d] The shrub data set included woody shrubs and tree seedlings.

Results

Species diversity

The full data set had high species richness with 146 plant species found on the 73 partially cut and uncut plots (Table 2). Species richness was highly variable among stands, ranging from 19 to 48 species in cut plots at recently harvested sites (Margarita Bay and Thomas Bay, respectively) and from 18 to 42 species in cut plots at older sites (Sarkar and Weasel Cove, respectively). The vascular plant data set also was species rich, particularly for the relatively species-poor forest plant communities of southeast Alaska; it contained 56 species of shrubs, ferns, tree seedlings, and herbaceous plants (Table 2).

The removal of species occurring in fewer than three plots resulted in a reduced data set of 101 species. Overall, the reduced data set had substantially reduced variability in species abundance (E and H' measures), with only slightly reduced plot species richness (alpha diversity, Table 2). The data distribution for the full data set had highly variable species abundance with an average skewness of 6.67 and 5.60 for plots and species, respectively (Table 2). The coefficient of variation for plots was relatively low (33%), but very high for species (314%) reflecting the high variability in species abundance. The herb and shrub data sets (vascular plants) also had high variation in species abundance (high coefficient of variation and skewness). The reduced data reduced the variability of species abundance and strengthened the relationship between plots and species composition. This reduced data set was therefore used for all additional analyses of plant community structure.

Species richness was highly variable among stands, but after accounting for differences in species composition by blocking by site, I found no significant difference in species richness between the uncut and partially cut plots (p = 0.295). I also found no significant difference (p = 0.263) in the species richness of vascular plants between the uncut and partially cut plots. Species richness of all plants decreased with increasing cutting intensity (Fig. 2*a*), but the relationship was weak ($R^2 = 0.111$, $p = 0.137$). Species richness of vascular plants alone also decreased slightly with increasing cutting intensity (Fig. 2*b*) but the relationship was not significant ($R^2 = 0.020$, $p = 0.362$). The species richness of all plants and vascular plants was similar among the uncut and partially cut plots, and neither partial cutting nor the inten-

Fig. 2. The species richness of all plants (*a*) and vascular plants only (*b*) as a function of cutting intensity. The reported R^2 and p values are for the 55 partially cut plots only.

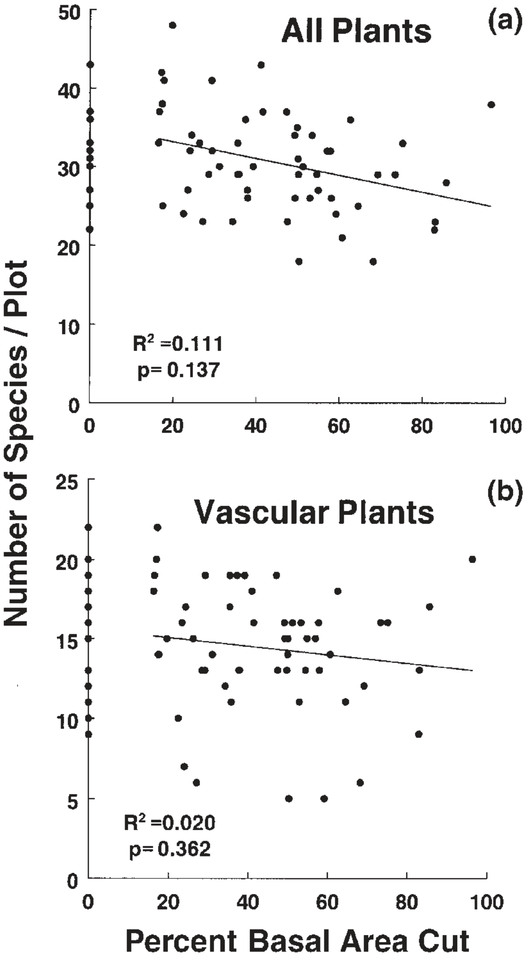
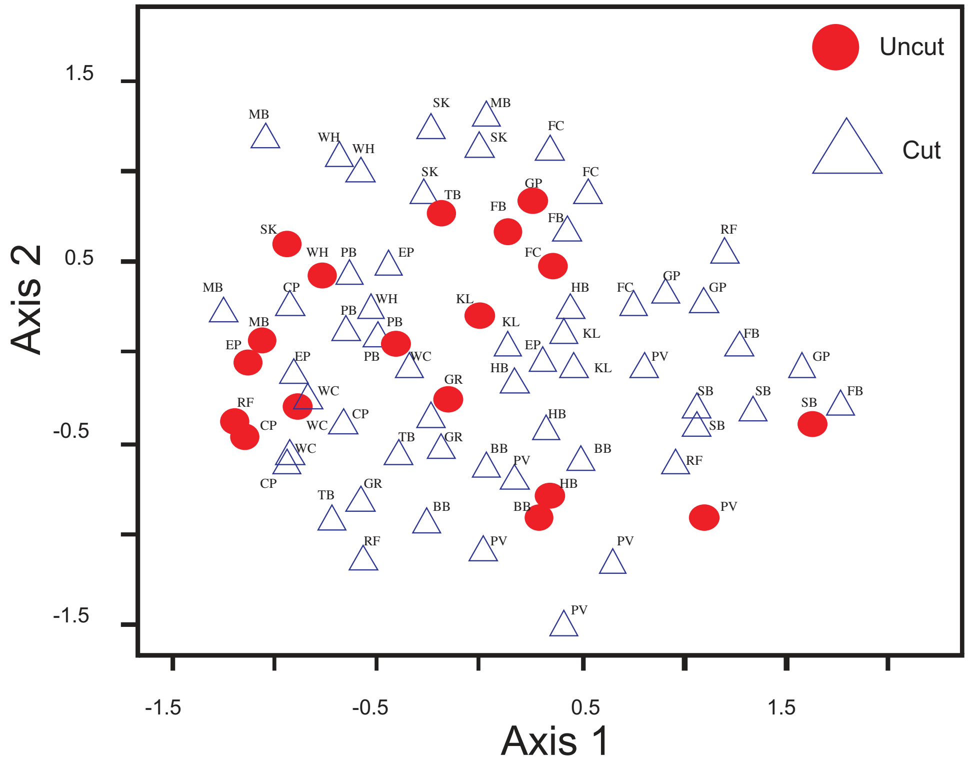


Fig. 3. The plant community structure in species space from non-metric multidimensional scaling for the 73 uncut and partially cut plots. See Table 1 for definition of site codes.



sity of cutting led to significant changes in plant species richness.

Plant community structure

The NMS ordination of plots showed that species composition and abundance (plant community structure) was similar in the uncut and partially cut plots (Fig. 3). The cut and uncut plots frequently grouped together by stand, and in some stands all plots formed tight clusters (e.g., SB, PB, KL, and WC; Fig. 3) indicating that plant communities were often more similar within stands than among stands. MRPP analysis also showed no significant differences in plant community structure between the partially cut and uncut plots ($p = 0.110$; Table 3).

Recently cut plots harvested 12–38 years ago, and not yet in the canopy closure – stem exclusion stage, did not significantly differ in community structure from the uncut plots ($p = 0.965$; Table 3). In contrast, plots harvested 53–96 years ago, and past the normal onset of canopy closure, appeared to have somewhat different plant community structure than the uncut plots ($p = 0.066$; Table 3). However, the apparently different response in recently harvested versus older sites was largely explained by the effect of cutting intensity. The light (1–25% BA) and medium (26–50% BA) cutting intensity plots were similar to the uncut plots for both the recently harvested and older sites, and they did not differ significantly in community structure from the uncut plots (p = 0.995, 0.559, 0.761, and 0.120, respectively; Table 3). However, the heavy cutting intensity plots (>50% BA) had a significantly different plant community structure than the uncut plots for both the recently harvested and older sites (p = 0.039 and 0.029, respectively; Table 3). Overall, plant communities were similar between the uncut and partially cut plots but the intensity of cutting appeared to cause significant changes in plant community structure.

Table 3. The effect of cutting intensity on plant community structure.

Cutting treatment comparisons (*n*)	MRPP probabilities
All uncut plots (18) vs. all partially cut plots (55)	0.110
Recent[a] uncut plots (5) vs. recent cut plots (16)	0.965
Older[a] uncut plots (13) vs. older cut plots (39)	0.066
Recent uncut plots (5) vs. recent cut plots with 1–25% of stand BA cut (6)	0.995
Older uncut plots (13) vs. older cut plots with 1–25% of stand BA cut (5)	0.559
Recent uncut plots (5) vs. recent cut plots with 26–50% of stand BA cut (6)	0.761
Older uncut plots (13) vs. older cut plots with 26–50% of stand BA cut (16)	0.120
Recent uncut plots (5) vs. recent cut plots with 51–99% of stand BA cut (4)	0.039
Older uncut plots (13) vs. older cut plots with 51–99% of stand BA cut (18)	0.029

Note: The multi-response permutation procedure (MRPP) probabilities are the probability of no difference in plant community structure between the respective groups of uncut and partially cut plots. BA, basal area.

[a] Recent sites include sites harvested 12–38 years ago; older sites include sites harvested 53–96 years ago.

Most stand and environmental variables, including stand density measures such as basal area and crown competition

Table 4. The correlation coefficient (r) and cumulative coefficient of determination (R^2) of stand and environmental variables and species variables with NMS ordination axes.

	r, axis 1	r, axis 2	R^2, both axes
Stand and environmental variables			
Time since cutting	0.043	0.361	0.132
Elevation	–0.432	0.022	0.187
Current stand BA	0.131	0.158	0.042
CCF[a]	–0.285	0.292	0.166
Total stems	–0.567	0.125	0.337
% spruce	0.551	–0.145	0.325
% hemlock	–0.517	0.212	0.312
% other species	0.038	–0.177	0.033
Stand BA cut	0.193	0.076	0.043
Stand BA uncut	–0.130	–0.037	0.018
% of stand cut	0.174	0.127	0.046
Species variables			
Athyrium filix-femina (fern)	0.649	–0.135	0.439
Coptis asplenifolia (herb)	–0.058	–0.357	0.131
Cornus canadensis (herb)	–0.208	–0.484	0.278
Dryopteris expansa (fern)	0.250	–0.161	0.089
Gymnocarpium dryopteris (fern)	0.645	–0.191	0.453
Lysichiton americanum (herb)	–0.035	–0.339	0.116
Oplopanax horridus (shrub)	0.638	–0.324	0.512
Rhytidiadelphus loreus (moss)	–0.603	0.019	0.364
Rubus pedatus (herb)	–0.100	–0.324	0.115
Tiarella trifoliata (herb)	0.519	–0.210	0.314
Vaccinium ovalifolium (shrub)	–0.525	–0.306	0.369
Vaccinium parvifolium (shrub)	–0.336	–0.051	0.116

Note: The ordination was rotated to align the variable "forest type" (major overstory tree species based on plant association) with the first axis. Species selected were either important species for deer forage or were species highly correlated with ordination axes. BA, basal area.

[a] CCF, crown competition factor = π(maximum crown width^2) × 100/(4 × 10 000) (Krajicek et al. 1961), where maximum crown width = 1.07 + 0.334($D^{0.8263}$) for southeast Alaska (Farr et al. 1989), and D is tree diameter.

factor, were poorly correlated with the first two axes of the NMS ordination (Table 4). However, stem density was negatively associated with axis 1 and explained the greatest amount of variation for both ordination axes ($R^2 = 0.337$; Table 4). Stem density was closely related to the proportion of hemlock in the stand, and species composition and abundance appeared to differ among densely stocked hemlock-dominated stands and lighter stocked spruce-dominated stands. Canopy coverage of a few dominant understory species (e.g., *Oplopanax horridus* and *Vaccinium ovalifolium*) was closely associated with overstory tree composition (forest type). *Oplopanax* was a frequent associate with Sitka spruce, and *Vaccinium* was a common associate with western hemlock. Two ferns (*Athyrium filix-femina* and *Gymnocarpium dryopteris*) also showed strong associations with Sitka spruce.

Abundance of important plant species for deer forage

I did not find any significant difference in four of the five most important herbs for deer forage (*Coptis asplenifolia*, *Cornus canadensis*, *Rubus pedatus*, and *Tiarella trifoliata*) between the uncut and partially cut plots (p = 0.085, 0.187, 0.345, and 0.780, respectively). Herbaceous cover varied greatly among stands and within different plot cutting intensities, and significant relationships with plant abundance and cutting intensity were generally not apparent (Fig. 4). However, the herb *Lysichiton americanum* (skunk cabbage) and the fern *Dryopteris expansa* (shield fern) showed different responses to cutting. The cover of skunk cabbage was significantly lower in the partially cut plots than in the uncut plots ($p < 0.001$). Skunk cabbage was uncommon and was found only on 18 plots (about 25% of plots in the study). Skunk cabbage is a recognized indicator of wet soil conditions (Klinka et al. 1989), and its presence and abundance are probably more related to wet microsites than cutting treatment. Cover for shield fern was significantly higher (p = 0.010) in the partially cut plots compared with the uncut plots, and cover significantly increased with increasing cutting intensity (p = 0.005; Fig. 4).

The shrub *Vaccinium ovalifolium* (blueberry) occurred in 70 of the 73 plots and showed a significant decrease (p = 0.008) in mean cover in the partially cut plots compared with the uncut plots. After accounting for differences in abundance by blocking by site, I found that blueberry cover also significantly decreased with increasing cutting intensity (p = 0.020; Fig. 4). There was no significant difference (p = 0.426) in cover of the shrub *Vaccinium parvifolium* between the uncut and partially cut plots.

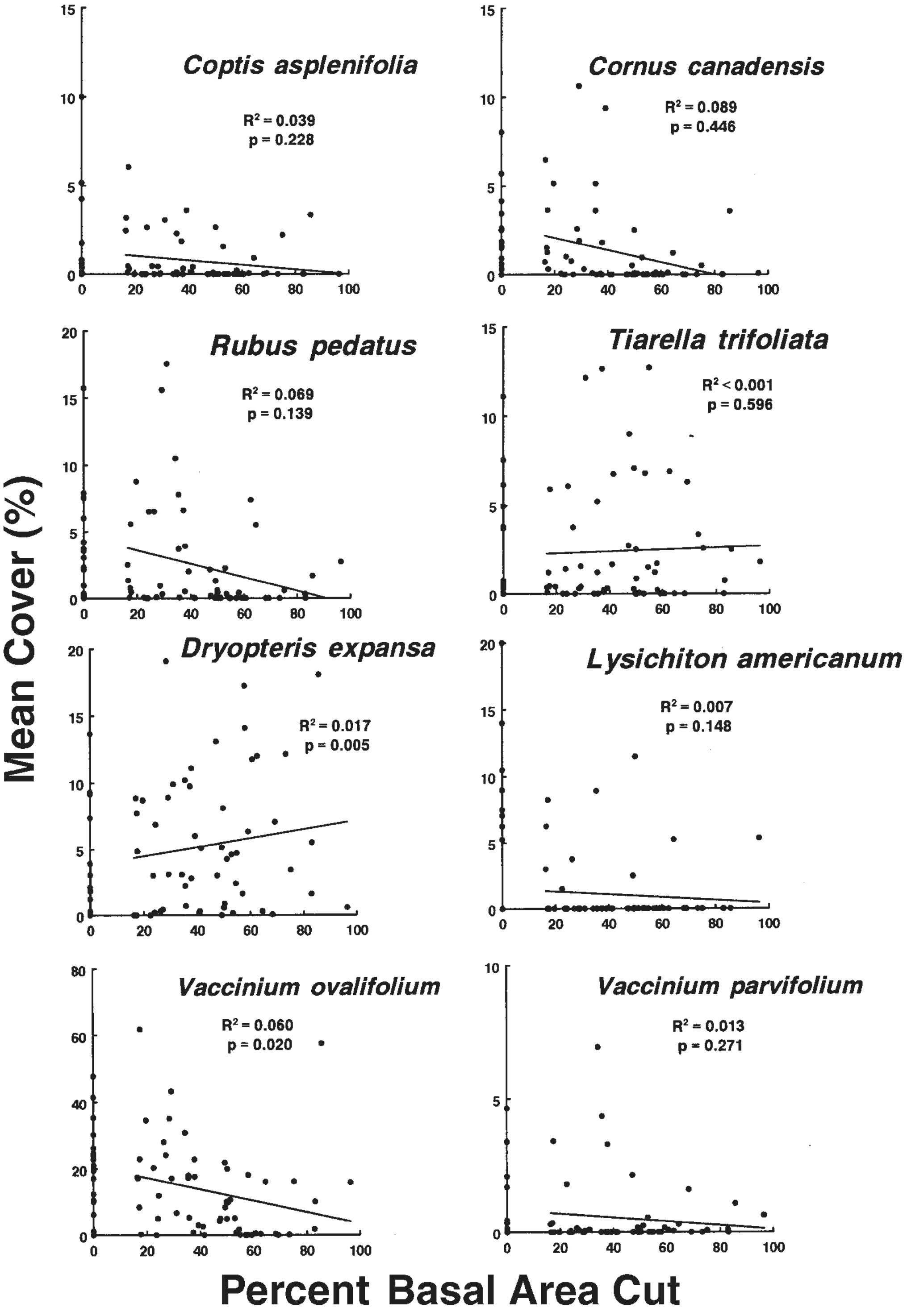
Discussion

Community composition and structure

The species richness of these partially cut stands is relatively high and comparable to levels reported for other old-growth stands in the region (Alaback 1982*a*, 1982*b*; Alaback and Juday 1989; Hanley and Hoel 1996; Hanley and Brady 1997). I found no significant differences in species richness between the uncut and partially cut plots in this study. The high species richness and abundance of understory plants in partially cut stands is very different from the typical plant understories found in stands developing after clear-cutting. The loss of biodiversity following clear-cutting is well documented in southeast Alaska (Wallmo and Schoen 1980; Schoen et al. 1988; Yeo and Peek 1992; Hanley 1993) and is closely associated with the rapid development of conifers (Alaback 1982*b*, 1984; Deal and Farr 1994). Canopy closure and the decline in plant abundance during the ensuing stem exclusion stage of stand development (Oliver and Larson 1990) is extremely intense and can last for over 100 years in southeast Alaska. Alaback (1982*a*) found that stands had very species-poor plant understories 40–90 years after clear-cutting. I also found significant differences in plant community structure between the uncut plots and the heavy cutting intensity plots. However, these differences in community structure after partial cutting were relatively small compared with the virtual elimination of shrubs and herbaceous plants that occurs after clear-cutting.

Some of the important plant species for deer forage showed slight reductions in cover following partial cutting. However, five of the eight most important species had no significant changes in abundance, two species decreased and one species increased in abundance following partial cutting.

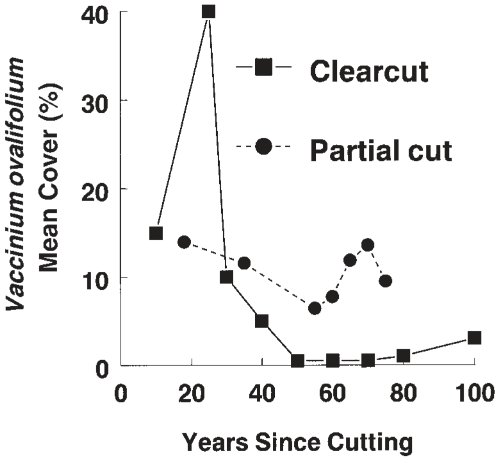
Fig. 4. The mean cover for eight plant species important for deer forage as a function of cutting intensity. The reported R^2 and p values are for the partially cut plots only.



Blueberry is a common shrub and an important food source for Sitka black-tailed deer in southeast Alaska, and the significant decrease in blueberry abundance with increasing cutting intensity may reduce available deer forage. However, the decrease in blueberry abundance after partial cutting is relatively small compared with the near elimination of understory shrubs and herbs that commonly occurs after clear-cutting. Comparison of partially cut and clear-cut stands shows the rapid peak and dramatic drop of blueberry abundance in stands 20–80 years after clear-cutting (clear-cutting data are from Alaback 1982*b*; Fig. 5). In contrast, the mean cover of blueberry in these partially cut plots was relatively constant over time and did not show the pronounced decrease in blueberry abundance during this stage of stand development.

Plant community structure appears resilient to partial cutting within a moderate range of cutting intensity. Ordination and MRPP analyses showed that similar plant communities

Fig. 5. Comparison of the abundance of *Vaccinium ovalifolium* in partially cut stands and in stands developing after clear-cutting (clear-cutting data from Alaback 1982*b*).



develop for different cutting intensities within individual stands. Thus, the differences in plant communities among stands do not appear to be attributable to cutting intensity. In this study, species composition remained relatively unchanged as stands developed after partial cutting. Species composition may be related to overstory tree composition (Hanley and Hoel 1996; Deal 1997), site differences in soil drainage (Hanley and Brady 1997; Bormann et al. 1995; Ver Hoef et al. 1988), or stand structures and other site-specific factors (Alaback 1984; Deal and Tappeiner 2001). Overall, partial cutting maintained diverse and abundant plant understories comparable to the plant communities typically found in old-growth stands.

The time since cutting did not have a significant effect on plant community structure, as older and more recently harvested stands had similar understories following partial cutting. This was a surprising result considering the changes in understories that normally occur following canopy closure in older stands and the differences in harvesting methods between the older and more recently harvested sites. At the turn of the century most stands were cut with individual-tree selection using hand-logging operations, which, since the 1920s, have been replaced by cable-logging systems (Rakestraw 1981; Deal 1999). Clear-cutting has led to marked changes in forest stand development but patterns of understory plant development following clear-cutting are similar with different harvesting systems. Alaback (1982*a*) reported "no clear differences in understory development after harvesting with various cable-logging systems" (e.g., A-frame, high-lead, and skyline). Thus, the controlling factor for understory plant development appears to be the intensity of cutting, and the time since cutting and specific harvesting systems appear less important.

Overstory–understory interactions

The reasons for differences in species composition and abundance in these partially cut stands appear complex and may be related to several factors, including tree species composition, stand density, and other site and environmental factors. Plant community structure appears to be closely associated with overstory tree composition and stand structure, especially as related to tree density and proportion of western hemlock. The nine plots with the fewest plant species averaged more than 1300 trees/ha, almost twice the average for all partially cut plots. In these species-poor understory plots, almost 90% of the trees were hemlock, and all nine plots were well above the cut plot average (79% hemlock). Furthermore, the six plots with the fewest vascular plants averaged almost 95% hemlock. It appears that these hemlock-dominated stands with large numbers of trees have severely suppressed understory development. These species-poor understory plots had numerous, small-diameter trees established soon after cutting. New tree regeneration was generally abundant on cut plots, and heavy cutting intensity favored establishment of both hemlock and spruce trees. The establishment of new-tree cohorts was positively related to the proportion of basal area cut, and new trees were always established in plots with at least 50% or more of the basal area cut (Deal and Tappeiner 2001). Plots with more than 50% of the basal area removed had significantly different plant community structure than uncut plots, and this cutting intensity level may be an important threshold for maintaining understory plant communities. The stands with large numbers of young-growth trees formed a dense new cohort that suppressed shrubs and herbs. The development of a new cohort that suppresses understory vegetation has been reported in other studies. In a coastal spruce–hemlock stand in Oregon, Alaback and Herman (1988) found that the establishment of a second cohort of trees below the overstory severely suppressed the understory vegetation. Deal and Farr (1994) also found that thinning young hemlock–spruce stands promoted dense germination of understory conifers and prevented the establishment of other understory plants. Stand dynamics, tree species composition, and stand structure are integral components of overstory–understory interactions and strongly influence understory plant community structure.

The tree size structure of these partially cut stands may also be an important factor for maintaining understory plant diversity and abundance. The residual trees remaining after partial cutting grew rapidly and were a dominant component of the current stand (Deal 1999). Immediately after cutting there were few trees on these plots greater than 70 cm DBH, and these cut stands had very different tree size structures than the old-growth stands prior to cutting (Deal and Tappeiner 2001). Sixty years after cutting, however, these stands had similar numbers of large-sized (>100 cm DBH) trees compared with the old-growth stands, and these similar structures were largely a result of the growth of the medium-diameter trees into the larger diameter classes. Following partial cutting there is often a wide range of large and small trees left in the residual stands, and these stands develop and form structurally complex, multilayered forest canopies. The heterogeneous stand structures that develop after partial cutting are much more similar to old-growth stands than to the uniform young-growth stands that develop after clear-cutting. Alaback (1984) found that several structural differences between old-growth stands and young-growth stands were related to differences in canopy density and canopy structure. These stand structures may influence light levels that are critical for understory plant development (Alaback 1984; Tappeiner and Alaback 1989). The presence of large and small residual trees after partial cutting creates structural heterogeneity and complex overstory–understory interactions, and these structures may be important for maintaining abundant and diverse understory plant communities.

It is important to remember that these stands were cut to provide specific wood products such as spruce sawtimber and hemlock pilings, and cutting occurred without a goal of maintaining understory species or the complex stand structures found in old-growth forests. Nevertheless, I found that these partially cut stands had high species diversity and maintained understory plant abundance over a moderately wide range of cutting intensity. Partial cutting may closely mimic the natural disturbance regime of southeast Alaska. This region is dominated by high frequency, low- to medium-magnitude wind disturbances (Harris 1989; Lertzman et al. 1996; Nowacki and Kramer 1998). Large-scale catastrophic events such as stand replacing fires are rare. Frequently, some of the original stand remains after a blowdown, creating complex multiaged or uneven-aged stands. The complex structures left after partial cutting may create conditions similar to natural, low-intensity disturbances that are common in the region. Further investigation of mechanisms controlling stand responses to partial cutting appears warranted to improve understanding and to develop management guidelines for new silvicultural systems in southeast Alaska.

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