# Composition and development of conifer regeneration in thinned and unthinned natural stands of western hemlock and Sitka spruce in southeast Alaska

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Received October 15, 1993

Accepted October 26, 1993

Deal, R.L., and Farr, W.A. 1994. Composition and development of conifer regeneration in thinned and unthinned natural stands of western hemlock and Sitka spruce in southeast Alaska. Can. J. For. Res. **24**: 976–984.

Natural regeneration of understory conifers was studied in 1988, 9–14 years after thinning of even-aged stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) on upland sites in southeast Alaska. Two age-classes of stands were compared: young stands, <30 years old that before thinning had open forest canopies and understories of conifer regeneration, shrubs, herbs, and forbs; and older stands, 31–98 years old, that before thinning had closed forest canopies and little or no understory vegetation. In 1988, dominant understory conifers in young stands were 2–4 m tall, and about the same age as trees in the overstory. In the older stands there was dense new regeneration that germinated 2–3 years after thinning and averaged 0.6–1.5 m tall. Seventy-two to 100% of all regeneration was hemlock. The rest was Sitka spruce. The amount of regeneration increased and the percentage of hemlock decreased with increasing thinning intensity. Thinning of young stands on upland sites appears to benefit understory conifers, which rapidly expand to fill in the available growing space. Heavy thinning in older stands promotes dense germination of understory conifers making it difficult for other understory plants to become established.

Deal, R.L., et Farr, W.A. 1994. Composition and development of conifer regeneration in thinned and unthinned natural stands of western hemlock and Sitka spruce in southeast Alaska. Can. J. For. Res. **24** : 976–984.

La régénération naturelle des conifères en sous-étage a été étudiée en 1988, soit 9 à 14 ans après une éclaircie dans des peuplements équiennes de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et d'épinette de Sitka (*Picea sitchensis* (Bong.) Carr.) sur des stations bien drainées dans le sud-est de l'Alaska. Deux catégories d'âge de peuplement ont été comparées : les peuplements jeunes, moins de 30 ans, qui présentaient des couverts ouverts et un sous-étage de régénération résineuse, d'arbustes et d'herbacées avant l'éclaircie; et les peuplements plus âgés, 31 à 98 ans, qui présentaient des couverts fermés avec peu ou pas de végétation en sous-étage avant l'éclaircie. En 1988, les conifères dominants dans le sous-étage des peuplements jeunes atteignaient 2 à 4 m de hauteur et avaient sensiblement le même âge que ceux du couvert principal. Dans les plus vieux peuplements, on observait une nouvelle régénération, dense, qui a germé 2 à 3 ans après l'éclaircie et qui atteignait en moyenne 0,6 à 1,5 m de hauteur. La pruche constituait 72 à 100% de l'ensemble de la régénération, le reste étant formé d'épinette de Sitka. La quantité de régénération augmentait et le pourcentage de pruche diminuait avec une augmentation de l'intensité de l'éclaircie. L'éclaircie pratiquée dans de jeunes peuplements sur stations bien drainées semble bénéficier aux résineux du sous-étage qui s'étendent rapidement pour combler l'espace de croissance disponible. Une éclaircie forte dans des peuplements plus âgés favorise une germination dense de résineux en sous-étage, rendant difficile l'installation d'autres plantes.

[Traduit par la rédaction]

## Introduction

Old-growth stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) cover most commercial forest lands in southeast Alaska (Hutchison and LaBau 1975; USDA Forest Service 1991). They have multiple-aged, highly variable stand structures, with abundant and diverse understory vegetation (Alaback 1982*a*, 1984).

Clear-cutting is converting many of the old-growth stands into naturally regenerated even-aged stands of hemlock and spruce with more uniform stand structures. Both species are prolific seed producers (Godman 1953; James 1959; Harris 1967, 1969), and conifer regeneration is generally excessive after logging (Harris 1967; Harris and Farr 1974; Deal et al. 1991). These new even-aged stands close in 20–30 years, and most or all understory vegetation is then shaded out (Alaback 1984). Throughout most of the stand's projected 100- to 150-year rotation (USDA Forest Service 1991), there is significantly less understory plant cover than typically is found in old-growth stands. The U.S. Forest Service is trying to maintain the understory cover for a longer period of time through precommercial thinning of 10- to 20-year-old stands.

Little is known about the development of understory vegetation in thinned stands. Limited research, however, suggests that thinning of young even-aged stands may have little beneficial effect on maintaining understory cover (Alaback and Herman 1988). Our study examined the response (9–14 years) of understory conifers in thinned and unthinned even-aged stands. In particular, we investigated the effects that stand age-class (younger and older) and thinning intensity (heavy, medium, light, and unthinned) have on amount, composition, and development of understory conifers.

## Methods

### *Plot selection and treatment*

Five young stands (<30 years old) and 15 older stands (31–98 years old) were studied covering a wide range of sites, ages, species composition, and stocking representative of productive upland even-aged stands of western hemlock and Sitka spruce in southeast Alaska (Fig. 1). Stands were selected at random from 60 stands that were available for study (Farr and Ford 1988). Stands ranged in age from 12 to 98 years, and overstory stocking before thinning ranged from 530 to 13 400 trees/ha

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Printed in Canada / Imprimé au Canada

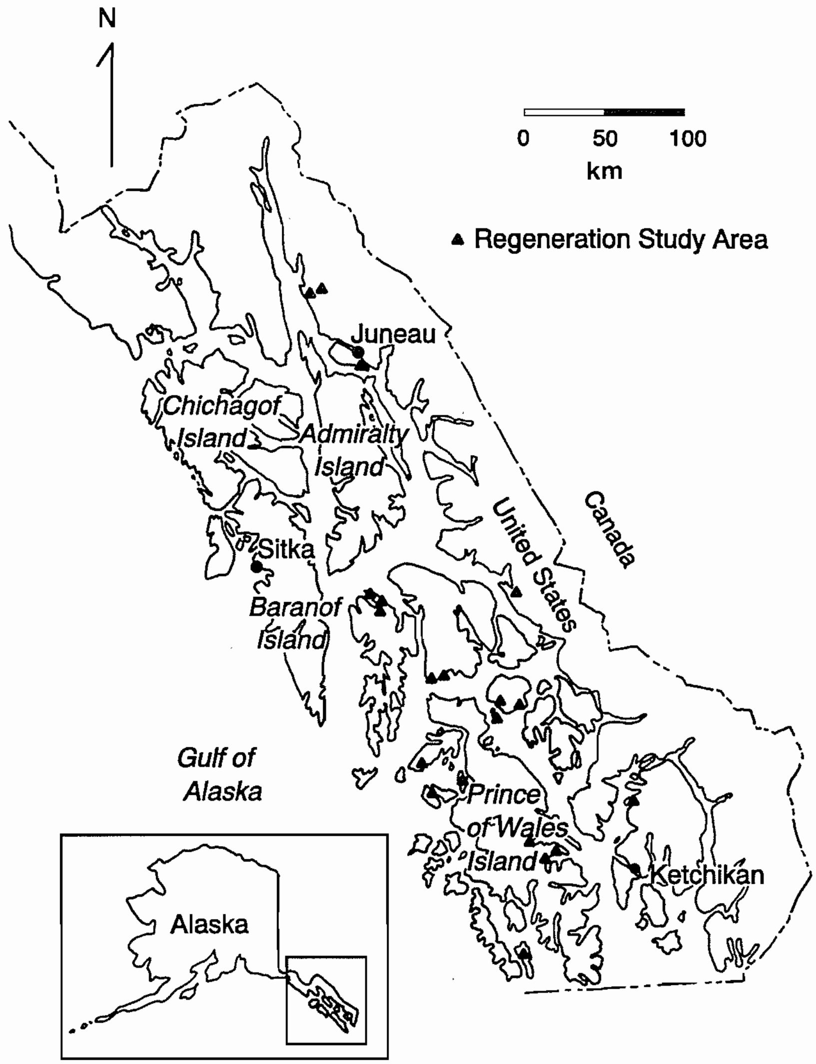


FIG. 1. Location of 20 regeneration study areas in southeast Alaska.

(Table 1). All were well-stocked natural stands, free of residuals from the former stand. Those <70 years old were of logging origin; older stands originated from windthrow. Site index (50 years at 1.3 m; Farr 1984) of spruce and hemlock ranged from 18 to 37 m and 12–36 m, respectively (Table 1).

The experiment used an incomplete block design incorporating a split-plot structure replicated five times in young stands and 15 times in older stands. Four randomly assigned thinning treatments (unthinned, light, medium, and heavy) were applied with a single replication of 0.405-ha (1-acre) plots in each stand. Eighteen of the 20 stands contained all treatments, one 60-year-old stand had a single replication of a medium thinning, and one 95-year-old stand contained three thinned plots and no unthinned control. All plots were thinned between May 1974 and May 1979. Leave trees were selected and marked on each plot to obtain as uniform a spacing as possible. All other trees greater than 0.6 m (2 ft) in height were cut. Trees on thinned plots in young stands were spaced to 2.4, 3.7, or 4.9 m (light, medium, and heavy thinning). Spacing in the older stands ranged from 2.4 m for small-diameter lightly thinned plots on poorer sites to about 7 m for large-diameter heavily thinned plots on the best sites.[2] Species composition after thinning was highly variable ranging from 94% spruce to 100% hemlock (Table 1).

[2]Farr, W.A. 1976. The effects of stand density upon growth and yield of hemlock-spruce stands in coastal Alaska. Revised study plan. Study on file, Forestry Sciences Laboratory, 2770 Sherwood Lane, Suite 2A, Juneau, AK 99801.

*Assessment*

Each 0.405 ha treatment plot contained a 0.08-ha (0.2-acre) interior measurement plot. The area around the interior measurement plot served as a uniform buffer. Tree boles greater than 10 cm in diameter were removed from interior measurement plots in older stands (>30 years old) to simulate harvest after a commercial thin. Diameter at breast height (DBH; 1.3 m) was recorded for all leave trees on the interior plots, and total height and height to live crown were measured on 20–30 trees selected at random from across the range of tree diameters. All plots were remeasured at 2- to 4-year intervals after thinning.

Nine 0.001 62 ha circular (4-milacre; 2.27-m radius) subplots were permanently established on an equally spaced grid within each interior measurement plot. During the summer of 1988, on these subplots, all new and advance regeneration taller than 6 cm was tallied by species into one of seven English measure height classes. When converted to metric units, the height classes were 0 (6–15 cm); 1 (16–46 cm); 2 (47–76 cm); 3 (77–107 cm); 4 (108–137 cm); 5 (138–169 cm); and 6 (>170 cm). Regenerated individuals in classes 0–5 were defined as seedlings, those in class 6 were saplings. Diameter at breast height was recorded for all saplings.

Destructive sampling to evaluate patterns of height growth took place on six small areas carefully selected between the nine interior subplots to preserve the subplots. If possible, one tree of each size class and species recorded on the subplots was selected at random from each sampling area. Occasionally, height classes were pooled or sample trees were cut in the buffer strips to

TABLE 1. Plot statistics before and after thinning and 9–14 years later when inventoried, by age-class and thinning intensity

| Age-class and thinning intensity | Site index | | Before thinning | | | | After thinning | | | When inventoried | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Spruce (m) | Hemlock (m) | Age (years) | Trees (no./ha) | Basal area ($m^2$/ha) | Spruce (%) | Trees (no./ha) | Basal area ($m^2$/ha) | Spruce (%) | Age (years) | Trees (no./ha) | Basal area ($m^2$/ha) | Spruce (%) |
| **Young stands**[a] | | | | | | | | | | | | | |
| Heavy thin ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 26.8 | 25.8 | 19 | 4064.9 | 14.5 | 43.0 | 410.2 | 2.6 | 50.6 | 32 | 405.4 | 14.6 | 52.0 |
| Range | 21–32 | 22–33 | 12–27 | 2965–6425 | 9–16 | 3–68 | 395–420 | 2–5 | 13–70 | 25–40 | 370–420 | 4–34 | 13–70 |
| Medium thin ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 25.6 | 26.2 | 19 | 3296.4 | 15.9 | 47.0 | 689.4 | 5.1 | 47.4 | 32 | 726.5 | 22.0 | 48.4 |
| Range | 23–32 | 24–33 | 12–27 | 1421–4510 | 4–26 | 27–83 | 556–729 | 1–5 | 40–67 | 25–40 | 717–741 | 13–40 | 38–66 |
| Light thin ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 29.4 | 26.8 | 19 | 4638.2 | 19.1 | 47.8 | 1564.2 | 8.3 | 45.8 | 32 | 1648.2 | 34.6 | 47.0 |
| Range | 25–34 | 22–33 | 12–27 | 3286–6374 | 9–32 | 9–65 | 1310–1680 | 3–14 | 14–59 | 25–40 | 1594–1680 | 20–54 | 15–59 |
| Unthinned ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 28.8 | 26.5 | 19 | 5271.3 | 18.7 | 31.0 | 5271.3 | 18.7 | 31.0 | 32 | 7646.4 | 47.7 | 31.4 |
| Range | 22–37 | 22–34 | 13–27 | 1715–7962 | 4–35 | 11–48 | 1715–7962 | 4–35 | 11–48 | 26–40 | 4600 – 12 425 | 22–82 | 11–42 |
| **Older stands**[b] | | | | | | | | | | | | | |
| Heavy thin ($n$ = 14) | | | | | | | | | | | | | |
| Mean | 27.6 | 23.3 | 59 | 3869.7 | 64.7 | 26.9 | 340.3 | 22.0 | 41.2 | 70 | 321.0 | 29.8 | 42.6 |
| Range | 18–37 | 16–30 | 31–98 | 530–7858 | 44–92 | 5–68 | 94–420 | 11–44 | 0–94 | 42–109 | 161–420 | 17–44 | 0–92 |
| Medium thin ($n$ = 15) | | | | | | | | | | | | | |
| Mean | 27.4 | 23.2 | 60 | 4633.2 | 67.3 | 24.9 | 625.9 | 27.5 | 34.9 | 71 | 572.5 | 38.8 | 35.4 |
| Range | 21–37 | 14–35 | 32–98 | 927–9637 | 49–86 | 2–54 | 346–803 | 13–53 | 3–71 | 43–109 | 260–741 | 20–64 | 3–73 |
| Light thin ($n$ = 14) | | | | | | | | | | | | | |
| Mean | 27.3 | 22.9 | 60 | 5312.8 | 66.6 | 26.4 | 1128.8 | 37.1 | 34.3 | 71 | 1052.9 | 48.8 | 34.6 |
| Range | 21–36 | 12–34 | 32–98 | 939 – 13 455 | 49–109 | 2–60 | 420–1680 | 14–57 | 2–92 | 43–109 | 420–1680 | 26–70 | 0–91 |
| Unthinned ($n$ = 13) | | | | | | | | | | | | | |
| Mean | 29.4 | 25.1 | 57 | 3450.1 | 59.6 | 29.8 | 3450.1 | 59.6 | 29.8 | 68 | 2648.2 | 67.4 | 29.2 |
| Range | 18–34 | 17–36 | 32–98 | 840–9541 | 33–78 | 5–76 | 840–8854 | 33–78 | 5–76 | 43–109 | 642–8100 | 41–94 | 3–80 |

[a]Stands <30 years old when thinned.
[b]Stands 31–98 years old when thinned.

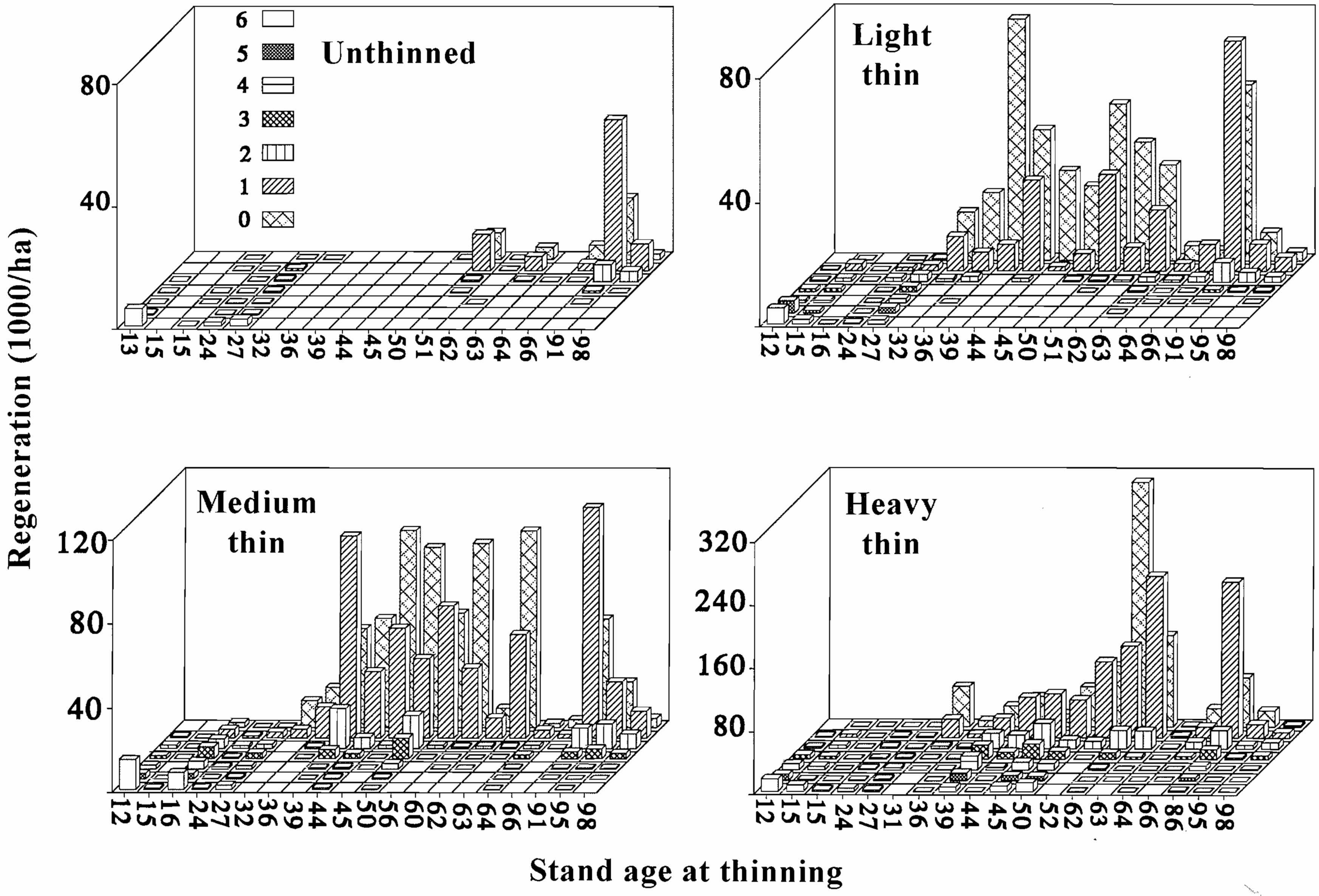


FIG. 2. Size class distribution of regeneration in unthinned and thinned stands in southeast Alaska. Size classes are 0 (6–15 cm), 1 (16–46 cm), 2 (47–76 cm), 3 (77–107 cm), 4 (108–137 cm), 5 (138–169 cm), and 6 (>170 cm). Note that the scale of the *y*-variable differs among treatments.

reduce numbers of trees cut on interior plots. A total of 1213 trees was sampled, averaging about 16 trees per plot. All sample trees were cut at ground level and later processed at a field camp or in the laboratory. Basal diameter and age, DBH (for saplings), total height, and yearly height growth for the previous 15 years were recorded for each sample tree. Sections that were difficult to measure were taken into the laboratory, oven-dried at 70°C, and processed (Harrington and Deal 1982). Ages then were counted under a dissecting microscope.

Number of seedlings and saplings, species percentages, ages of seedlings and saplings, and mean heights of the 1000 tallest regenerated trees per hectare were used as response variables in analyses of variance of means of treatment combinations. Regression models also were developed to predict the amount of regeneration and percentage of hemlock regeneration per hectare in young and older stands, 9–14 years after thinning as functions of number and basal area of overstory trees and percentage of overstory in hemlock.

## Results

Amount, composition, and size of conifer regeneration 9–14 years after thinning were related to overstory and understory pretreatment conditions. When thinned, the young stands had open tree canopies and understories of advance conifer regeneration, shrubs, herbs and forbs, and the older stands had closed tree canopies with little or no understory vegetation.

### *Amount of regeneration*

Older plots had more but smaller regeneration than on young plots 9–14 years after thinning ($p < 0.0001$). Total number of seedlings and saplings also increased with thinning intensity ($p < 0.0001$). There was no significant interaction between age class and thinning intensity ($p < 0.5252$).

Unthinned plots of all ages had the least average amount of regeneration (Table 2). There was, however, considerable difference between plots. Young unthinned plots averaged about 2800 seedlings and saplings per hectare, and older unthinned plots averaged about 9900 small seedlings per hectare. No saplings were recorded on the older unthinned plots. Five of 18 unthinned plots had no regeneration (Fig. 2). Four of them were 36–45 years old, an age when the overstories of unthinned stands are typically very dense. Amount of regeneration in unthinned plots generally increased in stands 50 years of age or older.

Numbers of seedlings and saplings contrasted more in thinned than in unthinned stands. Young, lightly thinned plots averaged about 6000 seedlings and saplings per hectare and older, lightly thinned plots about 47 000 seedlings per hectare, or 2 to 4.5 times the number recorded on unthinned plots of the same age (Table 2). More than 25 000 seedlings per hectare were recorded on most older, lightly thinned plots (Fig. 2) and all were small seedlings, averaging <60 cm tall. Medium thinned plots had about twice as much regeneration as that recorded on lightly thinned plots: about 15 000 and 87 000 trees per hectare on young and older plots, respectively. Heavily thinned plots had the most regeneration, about three times the amount found on lightly thinned plots and 33–70% more than recorded on medium thinned plots (Table 2). Young, heavily thinned plots averaged about 20 000 seedlings and saplings per hectare and older, heavily thinned plots about 147 000 trees per hectare. Three heavily thinned plots had over 300 000 seedlings and saplings per hectare.

### *Species composition of regeneration*

Seventy-two to 100% of regeneration was western hemlock (Table 2). The remainder was Sitka spruce. The percentage of hemlock was significantly higher in older stands than in young stands ($p < 0.0001$). The percentage of hemlock was highest in unthinned stands and lowest in stands receiving the heaviest thinning ($p < 0.001$). There also was an interaction between overstory age class (young or older) and thinning intensity ($p < 0.0194$). Regeneration in young stands ranged from 90% hemlock on unthinned plots to 72% hemlock on heavy and medium thinned plots (Table 2). Percentage of hemlock in older stands ranged from 100% on unthinned plots to 91% on heavily thinned plots.

### *Regeneration age*

Most regeneration on young plots was advance regeneration present when the plots were thinned. It was a mixture of seedlings and small saplings. Regeneration on older plots was mostly new regeneration that germinated 2–3 years after thinning (Table 2). It was still of seedling size except for some small saplings on the heavily thinned plots.

Mean seedling age was older in young stands than in older stands ($p < 0.0001$) and mean seedling age was older on unthinned plots than on thinned plots ($p < 0.0021$). Interaction between overstory age class and thinning intensity was marginally significant ($p < 0.0417$). Mean age of seedlings on young plots that received light, medium, and heavy thinnings was 16.4 ± 0.82 (mean ± SE; $n = 29$), 16.7 ± 0.73 ($n = 40$), and 16.1 ± 0.64 ($n = 46$) years, respectively. Saplings on the young plots were about 6 years older than the seedlings. Seedlings on older plots that received light, medium, and heavy thinnings were 9.1 ± 0.24 ($n = 283$), 8.6 ± 0.19 ($n = 287$), and 8.6 ± 0.15 ($n = 364$) years old, respectively.

### *Height of regeneration*

Regeneration on young thinned plots was mostly 1–3 m tall with saplings >2 m commonly tallied on young heavily thinned plots (Table 2). Percentage of regeneration on young plots >46 cm tall was 76, 84, and 89% on light, medium, and heavy thinned plots, respectively. Most regeneration on older plots was <47 cm tall; few trees over 1 m tall were recorded except on heavily thinned plots. Percentage of regeneration on older plots >46 cm tall was 7, 11, and 26% on light, medium, and heavy thinned plots, respectively. No regeneration was found on 36- to 45-year-old unthinned plots (Fig. 2).

Mean height of the 1000 tallest regenerated trees per hectare was taller in young stands than in older stands ($p < 0.0001$) and also differed by thinning intensity ($p < 0.001$). Interaction between age class and thinning intensity was nonsignificant ($p < 0.5299$). Mean height of the 1000 tallest regeneration in young stands averaged 2–4 m (Table 2). Tallest regeneration in older stands ranged from about 21 cm on the unthinned plots to 1.5 m on the heavily thinned plots (Table 2). Differences in mean height were largely due to tree age; regeneration on the young plots was older than regeneration on older plots.

### *Height growth of regeneration*

Height growth of hemlock and spruce regeneration was highly variable within and between plots. There was no clear evidence that one species outgrew the other in height after thinning (Fig. 3). Both responded to thinning. Height growth was greatest on the heavily thinned plots.

TABLE 2. Means and ranges for regeneration 9–14 years after thinning, by age-class and thinning intensity

| Age-class and thinning intensity | Stand age when thinned (years) | Time since thinning (years) | All Regeneration | | | Seedlings | | | | Saplings | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Total (no./ha) | Hemlock (%) | Top height (m)[a] | Total (no./ha) | Hemlock (%) | Mean height (m) | Mean age (years) | Total (no./ha) | Hemlock (%) | Mean height (m) | Mean age (years) |
| **Young stands[b]** | | | | | | | | | | | | | |
| Heavy thin ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 19 | 13 | 19 513 | 72 | 4.3 | 12 913 | 71 | 1.5 | 16.1 | 6600 | 74 | 3.7 | 21.2 |
| Range | 12–27 | 13–14 | 3979 – 41 647 | 64–88 | 2.3–5.9 | 2058 – 25 387 | 58–90 | 0.2–1.6 | 8–32 | 1922 – 16 260 | 58–86 | 1.7–7.9 | 11–32 |
| Medium thin ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 19 | 13 | 14 627 | 72 | 3.5 | 9468 | 72 | 1.2 | 16.7 | 5159 | 67 | 3.2 | 22.3 |
| Range | 12–27 | 13–14 | 1030 – 31 354 | 64–80 | 1.7–5.0 | 479 – 23 191 | 55–86 | 0.2–1.6 | 7–25 | 548 – 14 341 | 40–76 | 1.7–8.2 | 15–33 |
| Light thin ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 19 | 13 | 6229 | 75 | 2.3 | 4500 | 71 | 0.9 | 16.4 | 1729 | 77 | 2.4 | 23.6 |
| Range | 12–27 | 13–14 | 274 – 10 498 | 67–85 | 0–3.9 | 205–9057 | 50–87 | 0.2–1.6 | 9–24 | 69–5145 | 50–100 | 1.7–6.1 | 15–33 |
| Unthinned ($n$ = 5) | | | | | | | | | | | | | |
| Mean | 19 | 13 | 2813 | 90 | 2.4 | 919 | 82 | 1.1 | 20.6 | 1894 | 94 | 2.3 | 25.4 |
| Range | 13–27 | 13–14 | 0–6380 | 74–100 | 0–4.5 | 0–2744 | 50–100 | 0.2–1.6 | 17–23 | 0–5696 | 77–100 | 1.7–5.5 | 16–33 |
| **Older stands[c]** | | | | | | | | | | | | | |
| Heavy thin ($n$ = 14) | | | | | | | | | | | | | |
| Mean | 59 | 11 | 147 494 | 91 | 1.5 | 145 651 | 85 | 0.9 | 8.6 | 1843 | 99 | 2.1 | 12.7 |
| Range | 31–98 | 9–13 | 5627 – 462 508 | 72–99 | 0.9–3.3 | 5558 – 462 438 | 72–99 | 0.2–1.6 | 3–24 | 0 – 11 253 | 97–100 | 1.7–4.3 | 9–24 |
| Medium thin ($n$ = 15) | | | | | | | | | | | | | |
| Mean | 60 | 11 | 86 729 | 95 | 0.9 | 86 660 | 95 | 0.6 | 8.6 | 69 | 100 | 2.0 | — |
| Range | 32–98 | 9–13 | 5763 – 175 165 | 85–100 | 0.3–1.9 | 5763 – 175 165 | 85–100 | 0.2–1.6 | 4–29 | 0–756 | 100 | 1.7–2.4 | — |
| Light thin ($n$ = 14) | | | | | | | | | | | | | |
| Mean | 60 | 11 | 46 597 | 96 | 0.6 | 46 597 | 96 | 0.6 | 9.1 | 0 | — | — | — |
| Range | 32–98 | 9–13 | 8302 – 138 389 | 92–100 | 0.3–0.9 | 8302 – 138 389 | 92–100 | 0.2–1.6 | 3–27 | 0 | — | — | — |
| Unthinned ($n$ = 13) | | | | | | | | | | | | | |
| Mean | 57 | 11 | 9912 | 100 | 0.2 | 9912 | 100 | 0.3 | 11.0 | 0 | — | — | — |
| Range | 32–98 | 9–13 | 0 – 76 091 | 97–100 | 0.0–0.9 | 0 – 76 091 | 97–100 | 0.2–1.2 | 4–27 | 0 | — | — | — |

[a]Mean height of 1000 tallest regenerated trees per hectare.
[b]Stands <30 years old when thinned.
[c]Stands 31–98 years old when thinned.

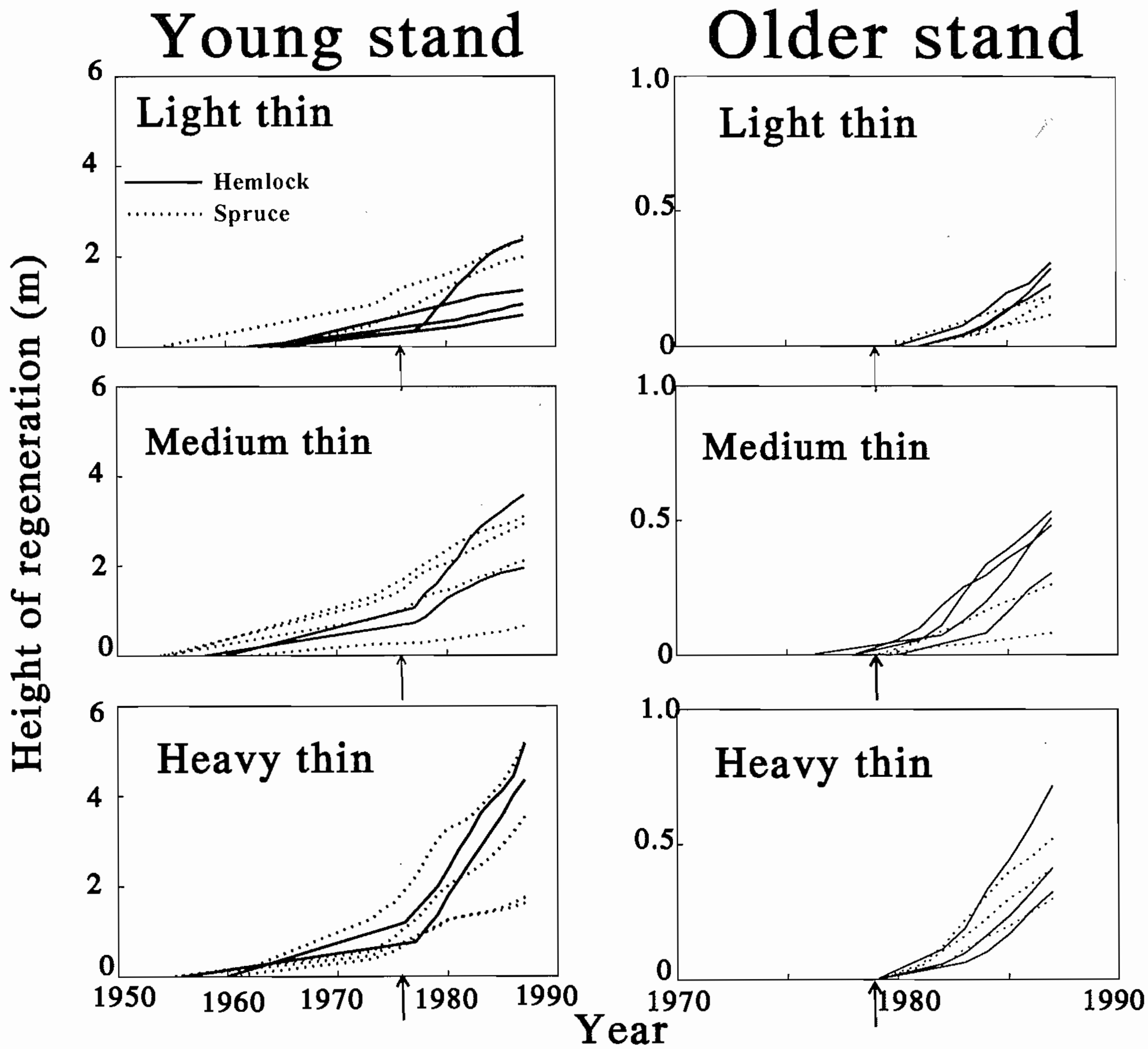


FIG. 3. Height-growth reconstructions of individual western hemlock and Sitka spruce regeneration on young (<30 years) and older (31–98 years) thinned plots. Arrow indicates thinning date. Note that the scales of the *x*- and *y*-variables differ among plots.

*Effects of overstory on amount and composition of regeneration*

The amount of regeneration on young thinned plots was inversely related to overstory basal area ($R^2$ = 0.82, Table 3). Amount of regeneration on older thinned plots was related to the number of overstory trees ($R^2$ = 0.26). Percentage of hemlock regeneration on young thinned plots was related to the natural logarithm of overstory basal area ($R^2$ = 0.47). Percentage of hemlock regeneration on older thinned plots was related to the inverse of overstory basal area squared and percentage of overstory hemlock basal area ($R^2$ = 0.32).

## Discussion

*Effects of thinning on conifer regeneration*

Stand condition at the time of thinning determined the type of regeneration response. Thinning of young stands prolonged survival and development of understory conifers. Thinning of older closed canopy stands initiated germination of new regeneration.

Even-aged stands of western hemlock and Sitka spruce typically pass through well-defined stages of stand development. A major disturbance, such as clear-cutting or a massive windthrow event, where all or most of the overstory is removed, is followed by rapid growth of existing herbs, shrubs, forbs, and advance conifer regeneration and the germination of new regeneration. This stand-initiation stage (Oliver and Larson 1990) typically lasts 15–30 years in the hemlock–spruce forests of southeast Alaska (Alaback 1982*b*, 1984). During this stage, conifer crowns expand to form a dense canopy that eventually shade out the understory vegetation. A stem-exclusion stage follows canopy closure (Oliver and Larson 1990) and lasts 50–100 or more years. During this stage, there is little or no understory vegetation other than mosses on the forest floor (Alaback 1982*a*; Harcombe 1986). This stage is followed by the slow reinvasion of shrubs, herbs, forbs, and conifers as light conditions gradually improve in the understory (Connell and Slatyer 1977; Oliver 1981; Alaback 1982*a*). In the absence of another major disturbance, the overstory will, over several hundred years, develop into a multiaged old-growth stand (White 1979; Oliver 1981; Alaback 1982*b*; Deal et al. 1991).

In this study, thinning delayed the stem-exclusion stage in young stands, and in older stands added a new initiation phase or hastened the onset of the understory-reinitiation stage. Stands less than 30 years old still had understory conifers that originated from the stand-initiating disturbance and they rapidly expanded to fill in the available growing space provided by thinning. Their expansion seemed to

TABLE 3. Regression models with regression $R^2$, MSE, and $P$ for amount of regeneration per hectare and percentage of hemlock regeneration on thinned, even-aged hemlock–spruce plots 9–14 years after thinning

| Dependent variable | $n$ | $B_0$ | $B_1$ | $X_1$ | $B_2$ | $X_2$ | $R^2$ | MSE | $P$ |
|---|---|---|---|---|---|---|---|---|---|
| Regeneration (no./ha) | | | | | | | | | |
| Thinned young plots | 15 | 5563.2 | 340 280.62 | 1/BA | −106 289.35 | $1/BA^2$ | 0.822 | 5 458.0 | 0.0001 |
| Thinned older plots | 43 | 0.0 | 42 774 439.00 | 1/T | | | 0.263 | 82 825.0 | 0.0011 |
| Percent hemlock | | | | | | | | | |
| Thinned young plots | 15 | 47.6 | 8.432 | ln(BA) | | | 0.468 | 5.61 | 0.0054 |
| Thinned older plots | 43 | 95.0 | −4 339.588 | $1/BA^2$ | 0.060 05 | %OH | 0.316 | 5.16 | 0.0005 |

NOTE: $n$, number of observations; $B_0$, intercept; $B_1$ and $B_2$, slope coefficients of the regression line; $R^2$, coefficient of determination; MSE, mean square error; $T$, number of overstory trees (trees/ha); BA, overstory basal area ($m^2$/ha); %OH, percentage of overstory basal area in western hemlock.

exclude new germinants. Older stands were in the stem-exclusion stage of development when they were treated. They had little, if any, residual understory. New hemlock and spruce regeneration became established in those stands within the first 2–3 years after thinning.

Composition of understory conifers was related to overstory stand age-class. Sixty-four to 88% of all regeneration in young stands, 13–14 years after thinning, was western hemlock. Regeneration in older stands ranged from 72 to 100% hemlock. High percentages of hemlock regeneration were due to several factors. Hemlock stands tend to have dense canopies (Gholz 1982; Stewart 1986). This favors hemlock regeneration because hemlock is more shade tolerant than spruce (Harris and Farr 1974; Minore 1979; Harris 1990). High percentages of hemlock also may be due to disturbance history. Little forest floor disturbance occurred during thinning of these research plots as merchantable stems (>10 cm in diameter) were removed from the plots by hand. Site disturbance from logging usually results in a mixed soil seed bed, an increase in nitrate nitrogen associated with warming of the soil, and an increase in organic decomposition, which favors the establishment of spruce regeneration (Taylor 1929, 1934; Gregory 1960; Harris and Farr 1974; Deal et al. 1991). A study of regeneration survival and long-term stand development (Deal 1987) showed that spruce seedlings have lower rates of mortality and higher probabilities of reaching sapling size than hemlock. With time, the percentage of understory spruce should increase, although the total number of spruce will stay less than hemlock.

Few studies have investigated the effect of thinning on understory conifer regeneration in the coastal hemlock–spruce forest type. In this study, the conifer regeneration that was present in thinned stands 9–14 years after thinning was abundant for all treatments and age classes. Amounts of understory conifer regeneration were much higher than previously reported for thinned hemlock–spruce stands in coastal Oregon (Alaback and Herman 1988). The larger numbers for southeast Alaska may be related to weather, rooting medium, and competing vegetation. Abundant moisture is present throughout the year in southeast Alaska where both hemlock and spruce are prolific seed producers (Godman 1953; Harris 1967, 1969). Hemlock–spruce stands tend to be more dense in southeast Alaska than in coastal Washington and Oregon (Meyer 1937; Barnes 1962; Harris and Farr 1974). Hemlock regeneration germinates mostly on logs and organic substrates (Christy and Mack 1984; Harmon and Franklin 1989), which are very abundant in southeast Alaska. Competing vegetation also may be an important variable; there is greater diversity, abundance, and growth of shrubs in the Pacific Northwest than in southeast Alaska.

*Overstory–understory relations*

Overstory stand height, vigor, and intensity of thinning in even-aged stands will determine if understory conifers will eventually grow to the overstory. Some large advance regeneration has reached the lower levels of the overstory in some of the younger plots. Some of this regeneration may survive as the overstory canopy closes. The early height advantage of dominant trees, however, has been shown to be maintained in this forest type (James and Gregory 1959; Harris 1967; Deal et al. 1991). Unless new disturbance events provide additional growing space, it is unlikely that many of the understory trees will successfully compete with trees in the overstory. Most regeneration in the young stands will eventually be shaded out. Understory conifer regeneration may have a better chance of long-term survival in older, heavily thinned stands because there will be fewer trees in the overstory and their canopies will develop at a slower rate as they age.

We did not study the development of the understory shrubs after thinning but have observed that they responded to the additional light and growing space, particularly on young plots that were heavily thinned. The larger shrubs have formed a cover layer 1–2 m tall that is shading out the shorter shrubs, herbs, and forbs. The conifer regeneration in turn is overtopping the shrubs and may soon shade it out.

Thinning of the older stands resulted in the rapid germination of several thousand conifers per hectare especially on plots that received a medium or heavy thinning. Nine to 14 years after the older plots were heavily thinned, they averaged 134 000 hemlock and 13 000 spruce germinants per hectare. Mean height of the tallest 1000 germinants per hectare was 1.5 m. Growth of these understory conifers will no doubt be slowed as the overstory expands to fill the additional growing space (Farr and Harris 1971). Although it is unlikely that the understory conifers will eventually compete with the overstory, they have already formed a significant second layer, making it difficult for other understory plants to become established.

## Conclusion

Thinning of dense, young (<30 years old) even-aged stands of western hemlock and Sitka spruce in the uplands of southeast Alaska allowed established understory conifers to rapidly fill the available growing space to the exclusion of new germinants. In the older stands, there was little, if any, understory vegetation at the time of thinning. Two to 3 years later there was a prolific reinvasion of predominantly hemlock regeneration. Observed reestablishment of other understory species has been very slow, leading to the conclusion that reestablishment of diverse and abundant understories in depauperate stands is a difficult, if not impossible, short-term task. Before other plants are able to germinate, develop, and compete, they will be shaded out by hemlock regeneration. Understory plants seem more competitive if thinning is performed in young stands where they are already well established. Even there, however, it may be difficult to maintain a productive diverse understory for a long time because aggressive understory conifers will outgrow the other species and shade them out, or the overstory canopy will close and shade out the understory.

**Acknowledgements**

The authors gratefully acknowledge the field assistance of D. Bassett and P. Reid and the helpful reviews of P. Alaback, D. DeBell, D. DeMars, K. O'Hara, J. Hazard, J. Zasada, and two anonymous reviewers.

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