

Influence of precommercial thinning on understory vegetation of young-growth Sitka spruce forests in southeastern Alaska

Elizabeth C. Cole, Thomas A. Hanley, and Michael Newton

Abstract: The effects of precommercial thinning on the understory vegetative cover of 16- to 18-year-old spruce–hemlock (*Picea sitchensis* (Bong.) Carrière – *Tsuga heterophylla* (Raf.) Sarg.) stands were studied in seven replicate areas over seven growing seasons postthinning. Vegetative cover was analyzed at the class level, but species-specific effects were examined in relation to their value as food for Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Cowan). When compared with unthinned controls, thinned stands (3.6–6.3 m spacing) had significantly greater understory cover. However, all thinned spacings led to similar understory cover. Conifer cover recovered to about two-thirds of its prethinning level within seven growing seasons posttreatment. Understory nonconiferous cover increased during the first 2–4 years postthinning but began to decline with increasing conifer cover during the next 3 years, nearly reaching pretreatment levels by year 7. In unthinned understories, vegetative cover had declined and was significantly lower than that beneath thinned stands. Summer food resource values for deer were increased by thinning. Winter food resource values were increased by thinning for snow-free conditions but were unaffected for conditions when herb-layer forbs were buried by snow.

Résumé : Les effets de l'éclaircie précommerciale sur le couvert végétal du sous-bois de peuplements mélangés d'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière) et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) âgés de 16–18 ans ont été étudiés dans sept stations (répétitions) pendant sept saisons de croissance suivant l'éclaircie. Le couvert végétal a été analysé au niveau de la classe taxonomique tandis que les effets des traitements sur la valeur de la végétation comme nourriture pour le cerf mulot de Sitka (*Odocoileus hemionus sitkensis* Cowan) ont été examinés par espèce. Le couvert végétal du sous-bois des peuplements éclaircis (espacement variant de 3,6 à 6,3 m) était au départ significativement plus dense que celui des peuplements témoins non éclaircis. Toutefois, le couvert de sous-bois était semblable dans tous les traitements d'éclaircie, peu importe l'espacement. Le couvert de conifères est revenu aux deux tiers de son recouvrement d'avant l'éclaircie en dedans des sept saisons de croissance suivant l'éclaircie. Le couvert des autres espèces a augmenté au cours des deux à quatre premières années suivant l'éclaircie, puis a diminué en lien avec l'augmentation du couvert de conifères durant les trois années suivantes, revenant pratiquement au niveau d'avant l'éclaircie au cours de la septième année; pendant ce temps, le sous-bois des peuplements non traités a décliné et est devenu significativement moins dense que celui des peuplements éclaircis. La valeur des sous-bois pour l'alimentation estivale du cerf a augmenté avec l'éclaircie. La valeur pour l'alimentation hivernale variait selon le couvert de neige : elle augmentait en réponse à l'éclaircie en l'absence de neige mais demeurait semblable à celle des témoins lorsque la neige devenait assez épaisse pour recouvrir la strate herbacée.

[Traduit par la Rédaction]

Introduction

Southeastern Alaska is a temperate rain forest archipelago along the north Pacific coast of North America. Forest landscapes serve a variety of users and interests. Stands managed for timber production are expected to provide productive habitat for wildlife, especially Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Cowan), the major big-game species of the region, which is important to sport and

subsistence hunters, tourism, and local economies. Timber harvest by clear-cutting has been widespread in southeastern Alaska since the early 1950s. Current inventory indicates that approximately 172 000 ha (4% of commercial forest lands) is occupied by stands less than 25 years old (T. Barrett, Forest Inventory and Analysis program, personal communication, 2009), yet research examining responses to silvicultural treatments in young stands has been limited. Forests in southeastern Alaska are dominated by Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), with spruce generally favored in timber management. Natural regeneration is commonly overabundant for optimal tree growth (Harris and Farr 1974). Understory vegetation, an especially important factor for wildlife habitat, is quickly overtopped by young conifers and nearly shaded-out within about 15–35 years stand age (Alaback 1982), depending on the density of regeneration. Thinning treatments have increased understory vegetation abundance in other regions (Harrington and

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Edwards 1999; Thomas et al. 1999; Lindgren et al. 2006) and also increased deer browse (Peitz et al. 1999).

Precommercial thinning (<30 years stand age) has been common throughout southeastern Alaska, but other than the long-term stand density study established by Farr and described by DeMars (2000), no replicated experiments of this kind have been conducted. The Farr study was designed specifically for studying tree growth and yield, but the experimental plots have been used by others to document understory vegetation responses to variation in stand density: P.B. Alaback and J.C. Tappeiner II (unpublished data summarized in Hanley et al. 1989) found that in young stands (20–30 years old), understory vegetation had increased 5–7 years after thinning, with the greatest increase in the shrub component, especially salmonberry (*Rubus spectabilis* Pursh) and blueberry (*Vaccinium ovalifolium* Sm.). Deal and Farr (1994) found similar results but also reported western hemlock regeneration increased in the most widely spaced treatments. Both of those studies reported very little response of herbaceous vegetation, especially low-growing forbs, which are important food sources for black-tailed deer (Parker et al. 1999). The one published study of deer response to thinning in young-growth forest (Doerr and Sandburg 1986) reported a strong preference for the *Vaccinium*-dominated understories of thinned young-growth stands over unthinned stands. The Tongass National Forest has recently embarked on a series of large-scale, long-term studies of young-growth silviculture (McClellan 2008), but results have not been published. There is a need for much more research into understory responses to thinning in southeastern Alaska (Hanley 2005).

The purpose of our study was to compare the effects of precommercial thinning and herbicide treatments on tree growth and understory vegetation. The tree growth study is a long-term study; here, we report only the results for understory vegetation during the first seven growing seasons post-treatment. The first 7 years posttreatment are probably the most dynamic years, with the most profound effects on non-coniferous cover. Our objective was to study the dynamics (multiple years), rather than simply a one-time snapshot analysis. We also wanted to relate the implications of the understory effects to consequences for habitat of black-tailed deer, specifically the food resource base (quantity and quality) for deer.

We had three hypotheses regarding vegetation and three hypotheses regarding deer habitat. Based on the few published results from thinning in the region (P.B. Alaback and J.C. Tappeiner II unpublished data summarized Hanley et al. 1989; Deal and Farr 1994), we expected that (1) the response to thinning would be strong and would change with time, and (2) without herbicides, the understory response would be strongly dominated by shrubs. We also expected that (3) with the addition of herbicide, the shrub component would be reduced and herbs would be favored (Harrington and Edwards 1999). Therefore, we expected the implications for deer food resources to be (1) a significantly increased abundance, especially with wider-spaced thinnings, but (2) of variable quality, especially in winter, depending on whether the shrub response is blueberry, an important winter forage, or salmonberry, a poor winter forage. We expected

(3) the increased forb response from herbicides (vegetation hypothesis 3 above) to be favorable for deer.

Methods

Study areas and treatments

We applied a randomized complete block experimental design involving five thinning treatments (unthinned, 750, 500, 370, and 250 trees/ha, or 3.6–6.3 m average spacing) and two herbicide treatments (treated and untreated) to seven study areas (blocks) of even-aged, Sitka spruce – western hemlock stands 16–18 years old at time of thinning. The seven study areas in southeastern Alaska were located near Hoonah (58.1°N, 135.3°W) (three study areas), on Long Island (54.85°N, 133.0°W) (three study areas), and near Klawock (55.6°N, 133.0°W) (one study area) (Fig. 1). Although the Hoonah and Long Island study areas were clustered, we felt that the high degree of between-site variation in vegetation warranted treating them all as seven separate blocks (Table 1). Study areas were selected on the basis of similar age and the practical costs of silviculture treatments. Study areas were characterized as overstocked with conifers (5 000 to 29 000 trees/ha) and with shrub-dominated (either salmonberry or blueberry), declining understories.

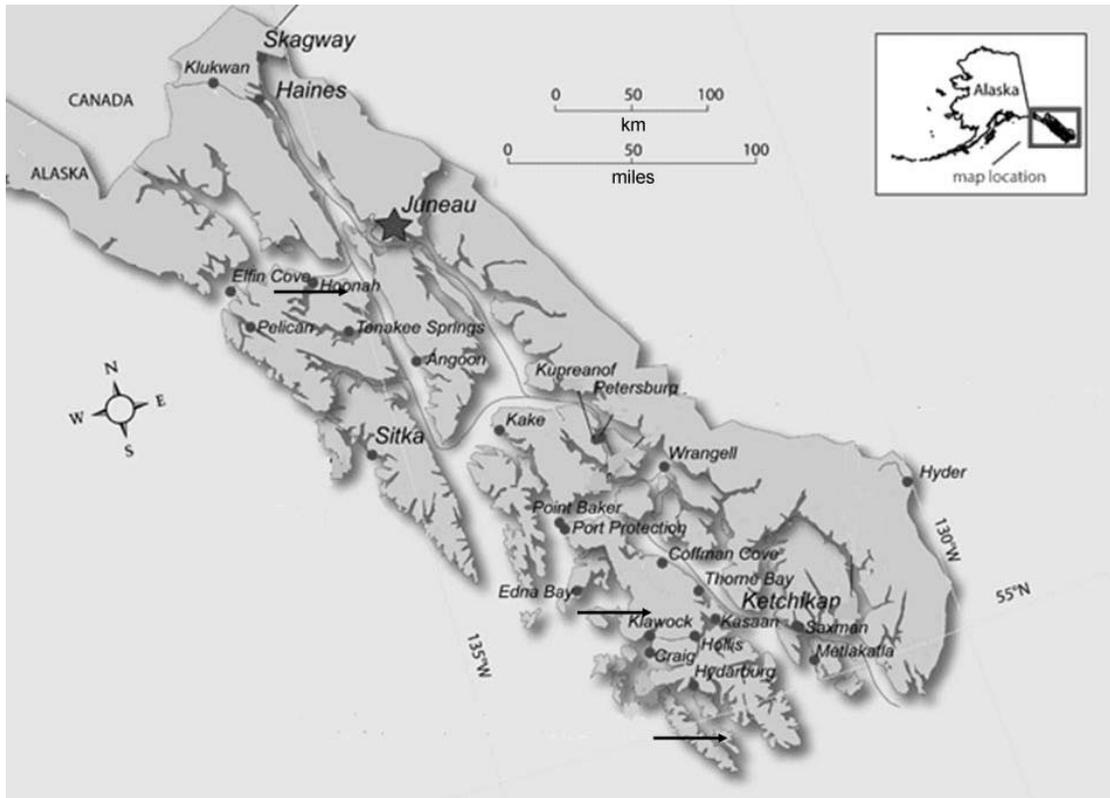
Study areas were located and their 0.2 ha experimental plots (10 per study area) established in 1998. Treatments (five thinning × two herbicide) were assigned randomly to each 0.2 ha plot. Each plot had a 6 m buffer and 0.134 ha central measurement area, with treatment applied uniformly throughout. Thinning treatments were applied in spring 1999 before the growing season began, and herbicide treatments were subsequently applied in August 2000. Thinning was by chain saw with cut trees left in place. Herbicide treatment was a broadcast application of glyphosate at 1.2 kg ae/ha. Imazapyr, at 69 g ai/ha, was added to glyphosate at the Klawock and Long Island areas to strengthen the desired effect of reducing shrub cover.

Data collection

Understory response was measured in terms of species-specific canopy coverage (percentage) in every 0.2 ha treatment plot in 1998 (one growing season prior to thinning), 2000 (immediately before herbicide application), 2002, and 2005, corresponding to years 0, 2, 4, and 7 postthinning. Sampling was done by visually estimating canopy coverage of each species separately in each of six permanently marked subplots of 1.12 m radius in each treatment plot. We used a height of 1.5 m as a cut-off point of availability to deer, so species taller than 1.5 m were estimated for cover both below and above 1.5 m. All sampling in all years was by the same observer revisiting the same sampling subplots. Prior to sampling, the observer calibrated cover estimates with graphic depictions of different cover levels and with measured clumps of vegetation. Some subplots were reevaluated to check for and maintain consistency.

Analysis of food value for deer (see below) required estimates of species-specific biomass (g/m²) rather than canopy coverage, and analysis of food value of shrubs, required estimates of leaves separate from current year's twigs, excluding older stems. Cover-to-biomass regressions were developed for all forage components (each species and part

Fig. 1. Location of study areas in southeastern Alaska. Arrows denote study areas: three were near Hoonah, three were on Long Island, and one was near Klawock. Map courtesy of The Alaska Volcano Observatory (www.avo.alaska.edu).



for shrubs) in the buffer areas of treatment plots in 2005 by a double-sampling technique of estimating cover and then clipping and weighing. Sampling for calibration was performed in fifty plots with 1.12 m radius. Biomass regressions were based on oven-dried weights after drying subsamples to a constant weight at 90 °C for correction factors.

Data analysis

Statistical analyses were conducted with PROC MIXED in SAS software (Statistical Analysis Systems, Cary, North Carolina, version 9.1). Because sampling was conducted on the same subplots through time, a repeated measures covariance matrix was included in the ANOVA. The covariance matrix was selected on the basis of Akaike's Information Criteria and was most commonly the spatial spherical matrix or the unstructured matrix. Time, being a continuous variable, was included as a regression variable in the ANOVA (Littell et al. 1996). This method allows for the examination of trends even if the main effects are not significant and allowed us to plot the dynamics of change over time. For all nonconifer vegetation, initial values (year 0) were included in the trend line. Because conifer canopy coverage was decreased by thinning in year 1, year 0 values were included as a covariate when analyzing conifer canopy coverage. The initial model included year and year² terms and all possible thinning and herbicide treatment interactions with those terms. Nonsignificant ($P > 0.05$) time variables were usually deleted and data reanalyzed, but nonsignificant variables remained in the final model when necessary for convergence.

For most variables, a square root transformation was needed to decrease heterogeneity of variance. The transformation was selected on the basis of predicted and residual values. Additionally, analyses were checked for block \times treatment interactions using Tukey's test for nonadditivity. If the tests were significant ($P < 0.25$), then selected blocks were deleted until the test was no longer significant. All other statistical tests were based on an α level of 0.05. Canopy coverage was summed over all layers for vegetation analyses, but only vegetation <1.5 m in height was used for deer analyses.

After tests indicated no differences among blocks for cover-to-biomass regressions, equations for each major species were developed using PROC REG. These equations provided a reasonable basis for evaluating deer habitat in terms of its food biomass. R^2 values from the cover-to-biomass regressions for forbs and graminoids ranged from 0.82 to 0.99 and for ferns 0.65 to 0.97. For shrubs, correlations varied by shrub component estimated, with foliage generally having better correlations than twigs or stems. For foliage for most species, r^2 values ranged from 0.85 to 0.99. The exceptions to this were salmonberry, with a r^2 value of 0.70 and elderberry with a value of 0.50. Salmonberry (0.45) and red huckleberry twigs (0.59) had lower r^2 values than other shrub species (0.74–0.97). The same was true for salmonberry (0.52) and red huckleberry stems (0.33) when compared with other species (0.68–0.99).

We quantified food value for black-tailed deer (deer-days per hectare) with a food-based nutritional model for deer habitat (<http://cervid.uaa.alaska.edu/deer/> based on work by

Table 1. Block characteristics for precommercial thinning study in southeastern Alaska.

	No. trees per hectare before thinning			Dominant understory vegetation	Mean annual temperature (°C)*	Mean annual precipitation (cm)*	Soil series
	Sitka spruce	Western hemlock	Western redcedar				
Hoonah I	13 796	13 471	0	Salmonberry	5.3	160	Mitlof, Tuxekan–Tonowek
Hoonah II	7 782	5 218	0	Fireweed	5.3	160	Tuxekan–Tonowek
Hoonah III	2 358	11 084	0	Blueberry	5.3	160	Kupreanof–Tuxekan
Klawock IV	4 333	24 496	501	Blueberry, false azalea	7.3	235	Karta, Wadleigh
Long Island V	766	4 569	0	Salmonberry	7.3	269	Sarkar
Long Island VI	2 977	14 503	0	Salmonberry	7.3	269	Sarkar/Ulloa
Long Island VII	5 483	8 342	30	Blueberry	7.3	269	Ulloa

*Data are from the National Climate Data Center (Asheville, North Carolina) from stations in Juneau and Ketchikan. Precipitation has been adjusted from closer stations based on 2–7 years of overlapping data.

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 (one deer for one day) that the food base could support at that specified level of nutritional requirements. The deer-day values provided a quantitative basis for direct comparison of experimental treatment effects combining effects of all species-specific biomass and nutritional quality. Our estimates of food biomass in winter were the summer food biomass values minus all deciduous species or plant parts. Our estimates of the effects of snow on food availability assumed (i) a simple burying effect from ground up, (ii) an estimate of the plant height, and (iii) an assumption of equal distribution of biomass throughout the height profile. 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 database (<http://cervid.uaa.alaska.edu/deer/>) based on the following studies plus other unpublished studies from southeastern Alaska: Hanley and McKendrick (1983), Hanley et al. (1992), McArthur et al. (1993), and Parker et al. (1999). We analyzed the food resources under four different scenarios: two in summer, when metabolic requirements differ for (1) maintenance only versus (2) maintenance plus lactation (reproduction); and two in winter, when forage availability differs greatly for (3) snow-free conditions versus (4) snow depth of 20 cm (enough to bury the ground-layer evergreen forbs but not enough to affect the availability of shrubs). For trend analyses, deer-day values after treatment were expressed as percentages of pretreatment values.

Results

Vegetation responses

Pretreatment canopy coverage was highly variable within blocks (Table 2). Despite the high variability, postthinning treatment trends were fairly consistent among blocks. All vegetation analyses yielded highly significant ($P < 0.01$) differences between thinned and unthinned treatments, no differences ($P > 0.05$) among thinning treatments (750, 500, 370, and 250 trees/ha), and no differences ($P > 0.05$) between herbicide-treated and untreated treatments.

Table 2. Pretreatment canopy coverage for blocks in southeastern Alaska precommercial thinning study.

	% Pretreatment canopy coverage		
	Forb	Shrub	Conifer
Hoonah I	24±4.9 (7–48)	32±4.2 (18–49)	42±6.3 (13–80)
Hoonah II	24±3.6 (7–42)	41±3.9 (26–60)	38±5.4 (11–61)
Hoonah III	18±2.4 (10–34)	48±2.9 (33–61)	37±3.9 (16–64)
Klawock	12±2.7 (3–26)	31±3.4 (12–48)	69±3.5 (49–88)
Long Island I	0.4±0.2 (0–1)	43±2.3 (28–50)	57±4.3 (39–78)
Long Island II	0.3±0.2 (0–2)	40±3.2 (26–55)	61±3.3 (46–78)
Long Island III	5±1.4 (1–13)	36±3.2 (20–52)	54±3.6 (36–70)

Note: Values are the means ± standard errors, with ranges in parentheses.

Not surprisingly, thinning treatments greatly reduced the canopy coverage of conifers when first applied, but conifer cover increased rapidly with time and reached almost two-thirds that of unthinned stands within seven growing seasons postthinning in all but the 250 trees/ha plots (Fig. 2). Thinned stands doubled, some nearly tripled, their conifer coverage (increasing from about 20% to 30% to nearly 60%) within only 7 years, while unthinned stands increased only slightly (increasing from about 80% to 90%).

Total understory vegetation responded directly to both the opening of the conifer canopy with thinning and the rapid recovery of the conifer canopy. Total nonconifer canopy coverage increased steadily during the first 4 years, peaked at about 4 years postthinning, and then decreased steadily to almost prethinning levels (about 55%–60% cover) by year 7 (Fig. 3). Total understory cover steadily decreased in the unthinned treatment plots to about 30% by year 7.

The patterns for both total forbs (Fig. 4) and total shrubs (Fig. 5) were very similar to the pattern for total nonconifer vegetation, although they differed greatly in absolute amounts — forbs ranged from about 6% to 18% cover, while shrubs ranged from about 25% to 45% cover. None of the thinning treatments differed significantly for forbs or shrubs, except from the unthinned treatment in both cases.

Thus, all understory vegetation was released more or less similarly by the thinning treatments. Shrubs were the dominant class at the time of thinning, and they simply retained their dominance as time progressed. Neither shrubs nor forbs appeared to benefit preferentially relative to the other, and both classes were already in decline with the increasing

Fig. 2. Regression trend lines of conifer canopy coverage over time. Regressions differed significantly for thinned (all four densities) versus unthinned treatments but did not differ among thinned treatments. Pretreatment data were collected in the growing season prior to thinning.

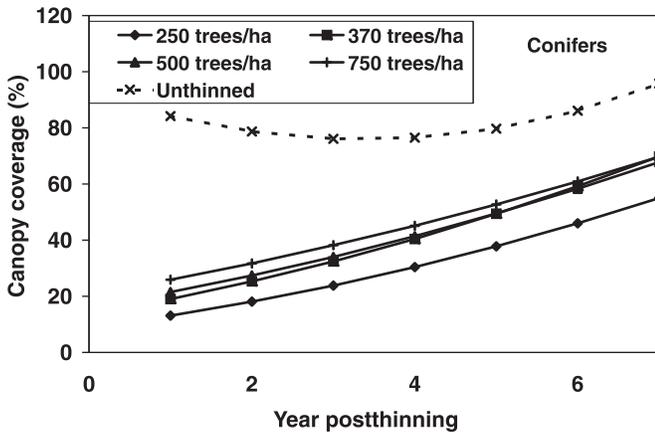
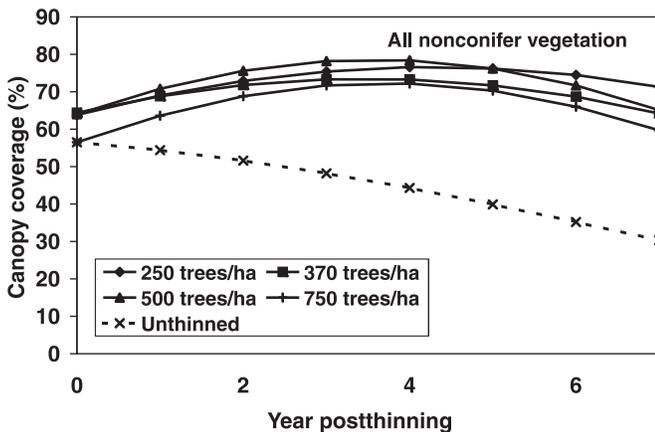


Fig. 3. Regression trend lines of total nonconifer vegetation (i.e., understory) canopy coverage over time. Regressions differed significantly for thinned (all four densities) versus unthinned treatments but did not differ among thinned treatments. Pretreatment data were collected in the growing season prior to thinning.



conifer canopy coverage by year 7. However, the declines were not nearly as great as with the unthinned treatment nor did they reach as low a level.

Individual species responses were not analyzed separately, but general patterns can be seen by comparing their estimated aboveground biomasses at year 7 postthinning (Table 3). The greatest absolute effects were seen in the total forbs and ferns, with certain species like fireweed (*Chamerion angustifolium* (L.) Holub), lady fern (*Athyrium filix-femina* (L.) Roth), and oakfern (*Gymnocarpium dryopteris* (L.) Newm.) responding strongly to thinning and maintaining their relative dominance through time. However, other species, most notably the evergreen forbs (*Cornus canadensis* L., *Coptis asplenifolia* Salisb., *Rubus pedatus* Sm., and *Tiarella trifoliata* L.), which are most important to black-tailed deer in winter (Parker et al. 1999), responded strongly early (as observed in Fig. 4), but had decreased by year 7 (Table 3). Similarly, while some shrubs like salmonberry benefited greatly from thinning and maintained their domi-

Fig. 4. Regression trend lines of total forb canopy coverage over time. Regressions differed significantly for thinned (all four densities) versus unthinned treatments, but did not differ among thinned treatments. Pretreatment data were collected in the growing season prior to thinning.

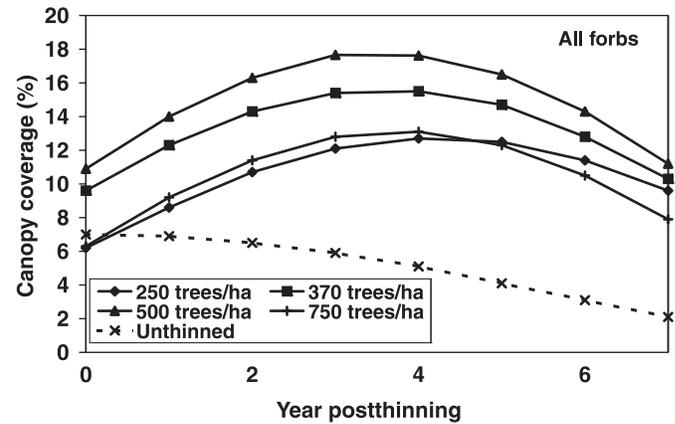
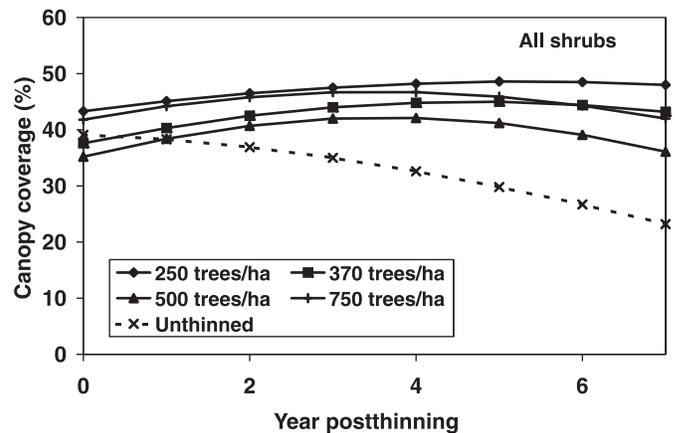


Fig. 5. Regression trend lines of total shrub canopy coverage over time. Regressions differed significantly for thinned (all four densities) versus unthinned treatments, but did not differ among thinned treatments. Pretreatment data were collected in the growing season prior to thinning.



nance, other shrubs like blueberry (*Vaccinium* spp.) did not (note the high standard errors relative to the means). Although still significantly negatively correlated, the relationship between biomass and conifer cover was not as strong in year 7 as in year 0 (Fig. 6). Overall, among-site variation in understory biomass increased greatly after thinning, especially among the low to mid-levels (<80%) of conifer canopy closure. Some sites responded quickly to treatment, while others did not.

Implications for deer food resources

Forb and shrub responses to thinning (Figs. 4 and 5, respectively) generally translated directly into similar responses in deer food resources, with summer food values (both for maintenance and lactation) showing the same temporal patterns as forb and shrub responses. Even after 7 years postthinning, the summer food resources of the thinned treatments were still approximately twice as productive as that of the unthinned treatments (Table 4). Species such as

Table 3. Estimated aboveground biomass (kg/ha oven-dried) of understory vegetation of all treatments (thinning and spraying), calculated across all seven replicate blocks, at 7 years after thinning.

	Thinned		Unthinned	
	Sprayed	Unsprayed	Sprayed	Unsprayed
Forbs				
<i>Chamerion angustifolium</i>	195±109	243±128	0±0	87±59
<i>Circaea alpina</i>	4±2	1±1	0±0	t±t
<i>Cornus canadensis</i>	38±19	28±12	23±2	5±4
<i>Coptis asplenifolia</i>	3±1	1±1	7±6	1±1
<i>Equisetum</i> spp.	3±2	1±1	0±0	0±0
<i>Heracleum maximum</i>	26±26	5±3	0±0	0±0
<i>Lysichiton americanus</i>	6±4	10±7	0±0	3±3
<i>Maianthemum dilatatum</i>	1±t	t±t	t±t	t±t
<i>Rubus pedatus</i>	5±2	4±1	3±2	3±2
<i>Tiarella trifoliata</i>	6±3	3±1	1±t	2±t
Total forbs	287	296	34	101
Ferns				
<i>Athyrium filix-femina</i>	53±22	91±25	4±2	14±12
<i>Blechnum spicant</i>	7±4	12±7	5±4	1±1
<i>Dryopteris expansa</i>	10±3	24±5	3±1	10±4
<i>Gymnocarpium dryopteris</i>	16±8	16±7	2±4	11±1
<i>Polystichum braunii</i>	76±46	28±26	22±20	51±41
Total ferns	162	171	36	87
Graminoids				
<i>Luzula parvifolia</i>	6±3	t±t	t±t	0±0
Unidentified species	14±6	5±3	1±1	0±0
Shrubs*				
<i>Gaultheria shallon</i> leaf	1±t	2±2	0±0	1±1
<i>Menziesia ferruginea</i> leaf	12±5	23±11	28±11	21±12
<i>Menziesia ferruginea</i> twig	6±2	12±6	11±4	10±6
<i>Oplopanax horridus</i> leaf	6±4	19±7	0±0	27±24
<i>Ribes bracteosum</i> leaf	34±12	3±3	0±0	0±0
<i>Ribes bracteosum</i> twig	10±4	1±1	0±0	0±0
<i>Ribes laxiflorum</i> leaf	2±2	1±t	t±t	t±t
<i>Ribes laxiflorum</i> twig	1±1	1±t	t±t	t±t
<i>Rubus spectabilis</i> leaf	131±34	121±29	14±10	37±20
<i>Rubus spectabilis</i> twig	81±21	75±18	9±6	23±13
<i>Vaccinium ovalifolium</i> [†] leaf	148±96	175±79	184±96	71±55
<i>Vaccinium ovalifolium</i> [†] twig	172±111	204±91	214±111	83±64
<i>Vaccinium parvifolium</i> leaf	4±3	3±2	1±1	t±t
<i>Vaccinium parvifolium</i> twig	27±19	18±11	9±8	2±1
Total shrubs	635	658	470	275
Total	1104	1130	541	463

Note: Only species with a mean of ≥ 0.5 kg/ha in at least one treatment are listed. "t" indicates a trace, < 0.5 kg/ha. Values are the means \pm standard errors.

*Shrub values show leaves separate from twigs (current annual growth) because they constituted different forages in the deer forage evaluation; shrub stems (previous years' growth) were not included in the forage evaluation.

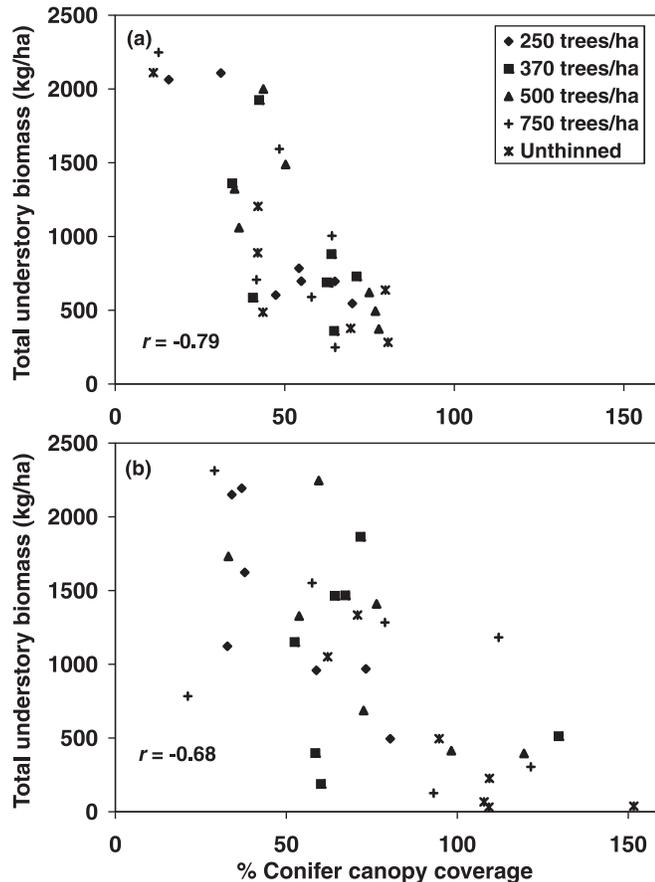
[†]Includes *Vaccinium alaskaense*.

fireweed and salmonberry (Table 3) were especially important contributors to this difference.

Although snow-free winter habitat values (Fig. 7a) paralleled the summer patterns of thinned treatments by being significantly greater than unthinned, there were no significantly different treatment effects from thinning in winter with 20 cm of snow on the ground (Fig. 7b). The availability of evergreen forbs for snow-free conditions drove the snow-free responses, but their burial by 20 cm of snow left

only the shrub component for food. Salmonberry leaves are a relatively high quality summer food, but salmonberry twigs are very poor-quality winter food for black-tailed deer (Hanley and McKendrick 1983; Parker et al. 1999). Blueberry twigs were the primary winter browse for deer, and the inconsistent response by blueberry to thinning translated into nonsignificant effects of thinning on winter food resources for deer when the herb layer of forage was buried by snow.

Fig. 6. Relations between total understory biomass (oven-dried) and conifer canopy coverage in all treatments and study areas, unsprayed herbicide treatment only, (a) prior to thinning and (b) 7 years postthinning.



Summer food values were lower in sprayed plots immediately after spraying because of the effects on fireweed and salmonberry, but by year 7 postthinning (year 5 postherbicide), those species had recovered, and values were similar between sprayed and unsprayed areas. Winter values were unaffected by spraying.

Discussion

In these 16- to 18-year-old stands (at time of thinning), significant understory still existed when they were thinned and the vegetation responded quickly, peaking within only 3–4 years postthinning, as the conifer canopy also quickly expanded. Given the inherent variability in natural vegetation, however, the more subtle differences among thinning treatments (spacing densities) were not significantly different. Thinning had a major effect, but the effect of spacing was minor in the first 7 years. Clason et al. (2008) observed a lack of a spacing response 5 years after thinning to 250–2000 trees/ha in 12- to 14-year-old lodgepole pine (*Pinus contorta* Dougl. Ex Loudon) in British Columbia. It is likely that the abundance of understory vegetation, primarily shrubs, will eventually be dictated by the level of canopy opening (Klinka et al. 1996), as crowns in different-density stands converge at different times. Once canopy closure oc-

curs, then thinning effects may not persist (He and Barclay 2000).

Unfortunately, our herbicide treatment did not provide a strong test of herbicide effects. Weather, application complications, and site variation added statistical noise to our results. Although the applications were made on dry foliage, light-to-hard rain fell on three of the blocks within a few hours of spraying. Ground application was made difficult by the uneven terrain and precommercial thinning slash. Understory response to our herbicide treatment was more variable than we had anticipated, and seven replicates (blocks) might be insufficient for adequately testing herbicide effects in southeastern Alaska.

Thus, with respect to our hypotheses regarding understory response to thinning and herbicides, we conclude the following. (1) Response to thinning was indeed strong and changed greatly with time, although differences among thinned spacings were relatively unimportant throughout the 7 years. (2) Although the understory response was indeed strongly dominated by shrubs, herbs also responded strongly and in proportion to their prethinning relative abundance. Therefore, thinning did not simply release the dominant shrubs at the expense of the herbs; it released all vegetation classes similarly. (3) Our treatments did not provide an adequate test of herbicide effects.

Although broad patterns of understory response obviously translated into implications for black-tailed deer food resources (more understory, more food), subtle differences in species responses played highly significant roles in determining overall effects. Most important were the differential responses of four major forages: fireweed, salmonberry, blueberry, and especially, the group of evergreen forbs (*Cornus canadensis*, *Rubus pedatus*, *Coptis asplenifolia*, and *Tiarrella trifoliata*, which all responded similarly) during the time frame of our study. The evergreen species vary ecologically in terms of shade tolerance and reproduction (Tappeiner and Alaback 1989), and differences among these species may appear later. The evergreen forbs are most important for winter food resources because their high dry-matter digestibility not only provides for high digestible energy but also allows for greater use of more marginal shrub forages, thereby greatly increasing the total food base that can adequately meet metabolic requirements (Parker et al. 1999). The evergreen forbs followed the same temporal pattern as the total forbs as a group (Fig. 4). The second most important winter forage was blueberry twigs, which are especially important when snow covers the herb-layer forbs (Hanley and McKendrick 1985; Parker et al. 1999). Overall, blueberry did not follow the total shrub pattern (Fig. 3), rather it was relatively unresponsive or inconsistent in its response to thinning treatment. At some sites, blueberry appeared to respond slightly to thinning. At other sites, blueberry cover declined throughout the study period. The decline occurred both inside and outside the study areas and was independent of thinning and spraying treatments. Both fireweed and salmonberry, on the other hand, are potential strong competitors within their classes (forbs, shrubs, respectively), and they both are nutritious summer foods for black-tailed deer but very poor (salmonberry twigs) or non-existent (fireweed) winter foods (Hanley and McKendrick 1983; Hanley et al. 1992; McArthur et al. 1993; Parker et

Table 4. Values (deer-days per hectare) of understory vegetation as food resources for black-tailed deer and changes in their values (from pretreatment values) under four different metabolic or winter scenarios for all treatments (thinning and spraying), calculated across all seven replicate blocks, at 7 years after thinning.

	Thinned		Unthinned	
	Sprayed	Unsprayed	Sprayed	Unsprayed
Deer-days*				
Summer				
Maintenance only	752±111	818±177	325±112	303±147
Lactation	301±59	344±85	54±13	153±88
Winter				
Snow free	405±170	390±156	418±179	117±68
Snow depth of 20 cm	246±131	253±118	276±129	74±52
Change in deer-days				
Summer				
Maintenance only	-17±71	107±68	-226±64	-310±106
Lactation	-14±38	59±25	-84±35	-91±28
Winter				
Snow free	72±119	52±105	-138±34	-187±52
Snow depth of 20 cm	57±75	49±75	-65±24	-80±34

Note: Values are the means ± standard errors.

*Calculations were based on the following metabolic requirements and intake rates for summer maintenance only, summer lactation, and winter (both), respectively: metabolizable energy requirement = 9832, 12970, and 4017 kJ/day; digestible protein requirement = 58.6, 107.2, and 9.5 g/day; and daily dry matter intake = 1220, 1340, and 525 g/day (Sadleir 1980; Hanley et al. 1992; Robbins 1993; Parker et al. 1999). For perspective, similar mean (and SE) values for 120 upland old-growth forest stands in the region were 436 (12), 270 (9), 240 (11), and 56 (3) for Summer Maintenance, Summer Lactation, Winter Snow-free, and Winter 20 cm Snow, respectively (M.A. Friberg, Tongass National Forest, unpublished).

al. 1999). Thus, they played a major role in treatment effects on summer food resources of black-tailed deer. Also important, however, is that the spatial distribution of fireweed is highly variable in southeastern Alaska — it is common in some areas and virtually absent or rare in many others.

Therefore, with respect to our hypotheses concerning treatment effects on deer food resources, we conclude the following. (1) Thinning did indeed significantly increase the quantity of food for deer, but thinned spacings had not yet demonstrated differential effects. (2) Salmonberry did indeed play a major role, especially in relation to food quality and especially in summer, but fireweed also played a major very similar role. (3) Although mostly ineffective, the herbicide treatment used here temporarily decreased summer habitat quality for deer through its effect on salmonberry and fireweed.

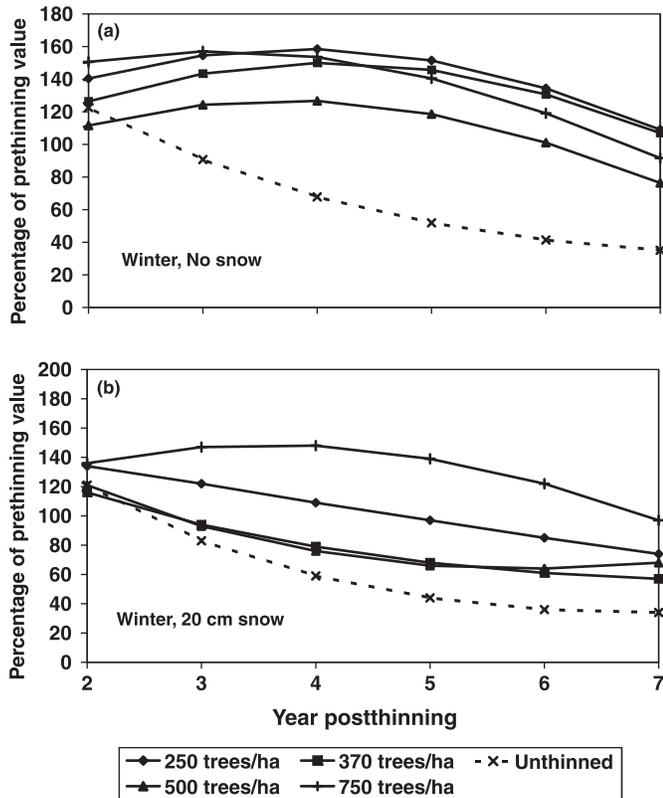
Thinning slash may reduce the value of treatments by interfering with deer access to the forage either by restricting deer movement or by burying the forage beneath slash (Wallmo and Schoen 1980; Hanley 1984). While we recognize that these effects are real, we could not quantify them. The effects are presumably greatest initially and decrease with time but should be expected to vary greatly depending on initial slash loads and probably subsequent weather (e.g., snowpacks). We observed much evidence of deer use of our thinned sites throughout the study, but the forage values quantified here probably represent a maximum potential value that might need to be discounted to an unknown degree, at least in the initial years posttreatment.

It is important to keep in mind that our results come from stands that were 16–18 years old at time of treatment. Although that is a very common age for precommercial sil-

viculture treatments in southeastern Alaska, it certainly is not the only potential age for treatment. Stands at younger ages should be expected to have relatively stronger forb and fern components of their vegetation, while stands of older ages should be expected to be more strongly dominated by shrubs (Alaback 1982). Our results indicate that understory responses to thinning of younger or older stands might likely vary with stronger forb and fern response in younger stands and stronger shrub dominance in older stands — that hypothesis remains to be tested. Conifer canopy response was surprisingly strong and rapid in our study, resulting in understory effects falling almost to pretreatment levels within only 7 years, while understories in unthinned stands had declined well below pretreatment values. As reported by Deal and Farr (1994), we also observed on one block that abundant understory hemlock may decrease nonconiferous understory vegetation. Because the response of understory vegetation to thinning is dependent upon such factors as stand age, thinning density, species present, and site quality, the duration of the effects will be highly variable. We would expect the understory effects to last somewhat longer in widely spaced younger stands, and shorter in older stands but that, too, is another hypothesis for subsequent testing.

Overall, we found that precommercial thinning had strong effects on understory vegetation. The increase of forage above pretreatment levels was relatively short-lived (<10 years) in southeastern Alaska, but thinned stands provided continued higher forage levels than unthinned stands. The consequences for black-tailed deer food resources were strong, especially in absolute abundance of food, but were highly variable, depending on understory species composition and responses. The abundance of primary forage at the

Fig. 7. Regression trend lines of winter food values for black-tailed deer (deer-days per hectare) (a) with snow-free conditions and (b) with 20 cm of snow on the ground. See footnote of Table 4 for metabolic requirements and intake assumptions.



time of thinning was also a factor in how well it released. Fireweed and salmonberry were two species that had strong complicating effects for deer habitat.

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