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Precommercial Thinning: Implications of Early Results From the Tongass-Wide Young-Growth Studies Experiments for Deer Habitat in Southeast Alaska

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Abstract

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This report documents the results from the first "5-year" round of understory responses to the Tongass-Wide Young-Growth Studies (TWYGS) treatments, especially in relation to their effects on food resources for black-tailed deer (*Odocoileus hemionus sitkensis*). Responses of understory vegetation to precommercial silviculture experiments after their first 4 to 8 years posttreatment were analyzed with the Forage Resource Evaluation System for Habitat (FRESH)-Deer model. The studies were conducted in western hemlock (*Tsuga heterophylla*)-Sitka spruce (*Picea sitchensis*) young-growth forests in southeast Alaska. All four TWYGS experiments were studied: (I) planting of red alder (*Alnus rubra*) within 1- to 5-year-old stands; (II) precommercial thinning at narrow and wide spacings (549 and 331 trees per hectare, respectively) in 15- to 25-year-old stands; (III) precommercial thinning at medium spacing (420 trees per hectare) with and without pruning in 25- to 35-year-old stands; and (IV) precommercial thinning at wide spacing (203 trees per hectare) with and without slash treatment versus thinning by girdling in >35-year-old stands. All experiments also included untreated control stands of identical age. FRESH-Deer was used to evaluate the implications for deer habitat in terms of forage resources (species-specific biomass, digestible protein, and digestible dry matter) relative to deer metabolic requirements in summer (at two levels of requirements—maintenance only vs. lactation) and in winter (at six levels of snow depth). Analyses for both summer and winter indicated that in all cases except for Experiment I (red alder planting in 1- to 5-year-old stands), habitat values of all treatments exceeded untreated controls ($P < 0.05$), and earlier treatments yielded greater benefits than did later treatments (i.e., treating at 15 to 25 years of age was more effective than at 25 to 35 years, and at >35 years was least effective). When compared to a wide range of old-growth stands from throughout the region, it was apparent that in summer and winter with low snow depths (≤20 cm) early treatments (15- to 25-year-old stands) yielded better food resources than did old-growth forest, while later treatments (25- to 35-, and 35+ year-old stands) yielded poorer habitat than old growth. These results, however, are from only the first 4 to 8 years posttreatment. The next study of TWYGS responses is scheduled to occur at 9 to 13 years posttreatment.

Keywords: Silviculture, adaptive management, *Odocoileus hemionus*, habitat model, nutrition, understory vegetation, snow.

Summary

The Tongass-Wide Young-Growth Studies (TWYGS) is a large-scale, long-term experimental study of precommercial thinning implemented in 2002 through 2006 as an adaptive management program conducted by the Tongass National Forest in collaboration with the Pacific Northwest Research Station. It was designed as a series of four independent experiments, each involving a different age class of stands with the expectation of monitoring the results at approximately 5-year intervals. This Research Paper reports the results for understory vegetation from the first 5-year round of study, especially in relation to their implications for black-tailed deer (*Odocoileus hemionus*) habitat.

The design of all experiments was that of a randomized complete block analysis of variance with a target of 20 replicates (blocks, widely scattered throughout southeast Alaska) in each. Experiment I compared the planting of red alder (*Alnus rubra*) seedlings at two different densities in recent clearcuts approximately 1 to 5 years old. Experiment II compared precommercial thinning at narrow versus wide spacing in stands 15 to 25 years old. Experiment III compared moderate precommercial thinning alone and in combination with two intensities of pruning in stands 25 to 35 years old. Experiment IV compared wide spacing conventional thinning (with and without slash treatment) with girdling in stands >35 years old. Each TWYGS experiment also included a treatment of untreated control young-growth forest of corresponding age in each experimental block.

Vegetation response was evaluated in terms of its value as food resources for deer using the Forage Resource Evaluation System for Habitat—Deer model to quantify habitat value in units of deer days per hectare, where one deer day is the food required to maintain one adult female deer for one day at user-specified metabolic requirements. This technique provides one quantitative metric that integrates the entire matrix of vegetation biomass and nutritional values into one number that is directly comparable among treatments within experiments, among experiments within TWYGS, and among TWYGS results and other studies of vegetation response to silviculture treatments in the region.

Results indicated the following:

- Total understory biomass of current annual growth is seldom a sufficient measure of habitat quality for deer in southeast Alaska because it most likely (about 80 percent probability in the TWYGS experiments) is composed of too much low-digestibility forage. Dry matter digestibility of forage is also of major importance in evaluating habitat for deer in the region.

- There was no effect of alder-planting treatments in Experiment I, but the various kinds of thinning treatments in Experiments II through IV increased total understory biomass by 3.4 to 5.1 times that of corresponding untreated controls. Relative effects for deer varied with season, metabolic requirements, and snow depths.
- Regardless of observed variation among various studies, it is clear that young clearcuts provide very high amounts of relatively high-quality food for deer in both summer and snow-free winter conditions throughout the region. It is with the closing of their young conifer canopies that their value as habitat drops sharply.
- Precommercial thinning may extend the high habitat values of young clearcuts into an advancing age of young-growth forest, but the stands will likely need further treatments if high habitat values are to be maintained. Pruning combined with thinning might be quite useful as such a secondary treatment.
- For stands that have not been thinned before reaching the relatively large tree sizes typical of ages greater than 35 years, thinning by girdling might be an effective treatment, but careful contract administration is essential when using girdling as a management tool. When girdling is done by chainsaw, too deep a cut leaves the tree with too small an intact bole to sustain wind or snow loads.
- The understory response is stronger with earlier treatment (younger stand age), mostly because there is more understory vegetation already present to serve as nurse stock in younger stands.
- A variety of potential silviculture treatments exists, and they may be applied to a variety of stand ages. Given the importance of landscape heterogeneity to deer, such variety in silviculture may be the optimal way to proceed.

We caution that our TWYGS results are for only the early response of vegetation to silviculture treatments and do not yet include any measures of stand dynamics through time. Future results will be especially important as red alders gain effect (Experiment I), thinned stands begin to close (Experiment II) or not close (Experiment III), and older stands have time to respond more fully (Experiment IV). Quantification of western hemlock (*Tsuga heterophylla*) in the understory, and slash and its rate of decay, will be important features to monitor and compare in all four experiments.

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Introduction

The Tongass-Wide Young-Growth Studies (TWYGS) is a long-term, adaptive management study of silviculture treatments intended to improve habitat for deer and other species. It consists of a series of four experiments involving manipulation of forest overstory along a gradient of stand ages from 1 through >35 years with monitoring intervals of about 5 years each. This report summarizes the results of the first cycle of TWYGS experiments as they relate to habitat for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*).

Even-aged, young-growth forests regenerating from clearcut stands of old growth have long been recognized as problematic habitat for Sitka black-tailed deer in southeast Alaska because of their characteristically sparse understory vegetation (Hanley 1993, Hanley et al. 1989, Schoen et al. 1988, Wallmo and Schoen 1979). Without silvicultural intervention, the usual pattern of secondary succession following clearcutting of western hemlock (*Tsuga heterophylla*)[1]-Sitka spruce (*Picea sitchensis*) forests is one of high biomass and productivity of understory vegetation in the early stage of stand regeneration. This is followed by extremely low levels of understory after crown closure of the dense, young conifers by about 30 years of age through at least the next 100 years (Alaback 1982, 1984). Although departures from that pattern may occur with significant soil disturbance and red alder (*Alnus rubra*) establishment or on poorly productive sites (Hanley 2005), high-lead logging on productive sites has been the dominant harvest technique for the past four decades (McClellan 2005), resulting in the widespread occurrence of dense-canopied young-growth forests throughout the region. As young clearcuts transition into closed-canopy, young-growth forest, their value as habitat for black-tailed deer decreases in direct proportion to their decreasing understory food resources. This habitat decline has social consequences for people of the region because black-tailed deer are the principal big game species for sport hunters and the most important terrestrial animal in local subsistence economies (Brinkman et al. 2007, Mazza 2003). Furthermore, much of the young-growth forest is concentrated in lower elevation areas important as winter range for deer, intensifying the potential impact on local deer populations (Hanley 1984).

Even before problems with deer habitat were noted, there was interest in precommercial thinning of young-growth forests of the region because natural regeneration was almost always denser than optimal for timber production (Ruth and Harris 1979). Early thinning efforts, however, tended to be conservative (spacings

[1] See appendix 1 for full list of common and scientific names with authorities for all plant species identified in this report.

of 749 to 1,329 trees per hectare)[2] (Ruth and Harris 1979) and were conducted early in the successional cycle (often within the first 15 years).[3] Furthermore, none was conducted in an experimental design in which effects on understory vegetation could be measured and compared reliably. When concern about deer habitat emerged as a forest management issue, the best opportunity for assessing the effects of precommercial thinning was Wilbur A. Farr's long-term stand-density study of tree growth and yield (DeMars 2000), which involved manipulation of tree density within gradients of stand age and site index throughout the region. Farr's experimental plots were small (typically 0.4 ha treated with an interior 0.08-ha measurement plot), but treatments were balanced and randomly assigned at each site, their histories were well known, and they provided a reliable basis for studying understory response to thinning intensity (spacing), stand age when treated, and time since treatment.

The initial investigation of understory patterns in the Farr stand-density study revealed that within 5 to 7 years of thinning, understory biomass was greater in stands thinned at younger stand ages (20 to 30 years) than in older ones (39 to 72 years) and did not differ with thinned tree density in young stands but increased significantly with wider spacing in older stands (Alaback and Tappeiner, as reported in fig. 4 of Hanley et al. 1989). However, regardless of stand age or tree spacing, all understories were strongly dominated by shrubs (either salmonberry, *Rubus spectabilis*, or blueberry, *Vaccinium ovalifolium*), while the herb layer (especially important for deer) consistently remained sparse and mostly consisted of ferns rather than forbs. Wide spacing also tended to result in a dense layer of western hemlock seedlings, which, if successful in recruiting into the stand, would result in a second, dense layer of hemlock to the exclusion of understory. The western hemlock response was further verified in another, subsequent study of the Farr sites (Deal and Farr 1994). The lack of a forb response at all thinning intensities, coupled with the western hemlock response at wide spacing, offered poor prospects for thinning as a mitigating tool for deer habitat. The most important winter forages for deer—the evergreen forbs bunchberry dogwood (*Cornus canadensis*), trailing bramble (*Rubus pedatus*), fernleaf goldthread (*Coptis aspleniifolia*), and foamflower (*Tiarella trifoliata*) (Hanley and McKendrick 1983, 1985)—were exactly the species that seemed most unlikely to benefit from thinning. The forbs were shaded out by both the overstory trees in unthinned stands and the dense shrub response in thinned stands. Thus, the challenge of silviculture for deer habitat, and even wildlife habitat more generally, could be primarily focused on growing those four

[2] See table of tree spacings and densities at end of this report for English and metric equivalents.

[3] Unpublished inventory data. On file with: Ben Case, Tongass National Forest, P.O. Box 309, Petersburg, AK, 99833.

species of evergreen forbs (Hanley 1993), a challenge that, based on results from the Farr stand-density study, appeared to be formidable.

Empirical observations of thinned stands, however, indicated a wider range of potential understory responses than was suggested by the Farr stand-density sites. Variation in soil microsites and patterns of disturbance in both the initial logging and subsequent thinning appeared to result in wide variation of understory response within and among stands when treatments were applied at the much larger operational scale of forest management (e.g., several or more hectares, rather than small experimental plots). The need for a large-scale, long-term experimental study of precommercial thinning was recognized in 2001 and became the genesis of the TWYGS experiments, a regionwide adaptive management program conducted by the Tongass National Forest in collaboration with the Pacific Northwest Research Station (McClellan 2008). Under this program, silviculture treatments were applied within a series of experiments, each involving a different age class of young-growth forest, and vegetation responses were monitored at approximately 5-year intervals.

This report documents the results from the first 5-year round of understory responses to the TWYGS treatments, especially in relation to their effects on food resources for black-tailed deer. Note, however, that understory plants also are important food resources for a wide range of animal species not considered in this report. Actual times since treatment varied from 4 to 8 years, but all results analyzed here are "early responses" to silviculture treatment.

The TWYGS program was designed as a series of four independent experiments, each involving a different age class of stands: 1 to 5, 15 to 25, 25 to 35, and >35 years old. Each of the four age classes tested silviculture treatments uniquely appropriate to that age class. All four experiments shared a common set of guidelines.

The TWYGS Experiments

The TWYGS program was designed as a series of four independent experiments, each involving a different age class of stands: 1 to 5, 15 to 25, 25 to 35, and >35 years old. Each of the four age classes tested silviculture treatments uniquely appropriate to that age class. All four experiments shared a common set of guidelines: (1) treatments were practical for application in typical management for timber stand improvement throughout the Tongass National Forest; (2) treatments were expected to increase deer food resources as well as yield of merchantable timber; food resources could be increased by changes in understory plant species composition, biomass, or both; (3) treatments within each experiment differed substantially, enough that differences should be readily apparent even without statistical analysis for discernment; (4) all treatments were applied at an operational scale typical of routine forest management (i.e., several to many hectares rather than small experimental plots); and (5) all treatments were widely replicated throughout the Tongass National Forest in a randomized complete block analysis of variance design with a target of 20 replications per treatment. The treatments were implemented within

Each TWYGS experiment included a treatment of untreated control young-growth forest of corresponding age at each experimental block.

the normal program of timber stand improvement activities by the Tongass National Forest, one or two experiments per year, beginning in 2002 and completed in 2006. (See McClellan 2008 for a full description of history, rationale, and objectives.) The TWYGS experiments were expected to be monitored at 5-year intervals and to continue for about 30 years. Results relevant for deer habitat were expected to be strongly evident within the first 5 to 10 years after treatment, although treatment effects on overstory tree growth would not yet be apparent.

Each TWYGS experiment included a treatment of untreated control young-growth forest of corresponding age at each experimental block. The silviculture treatments of the four experiments were as follows:

- Experiment I compared the planting of red alder seedlings at two different densities (50 versus 200 trees/ha) in recent clearcuts of approximately 1 to 5 years in age. Red alder stands have been found to have very different understories than those of western hemlock-Sitka spruce forests in southeast Alaska (Deal 1997, Hanley and Barnard 1998, Hanley and Hoel 1996, Hanley et al. 2006). Experiment I was designed to determine whether such understory differences could be created by planting red alder seedlings into young clearcuts without the need of extensive soil disturbance. The effects of red alder on understory vegetation, however, were not expected to be evident within the first 5 to 10 years, as more time than that would be needed for the alder to grow large enough to exert a significant effect on understory vegetation and for untreated conifer crowns to approach closure.
- Experiment II compared precommercial thinning at narrow spacing (549 trees/ha) versus wide spacing (331 trees/ha) in stands 15 to 25 years old. Wider spacing was expected to diminish the effects of conifers on understory vegetation, delay conifer crown closure, and thereby increase total understory food resources in both amount and longevity. However, the wide spacing might favor heavy recruitment of western hemlock as reported earlier (Deal and Farr 1994).
- Experiment III compared moderate precommercial thinning (420 trees/ha) alone and in combination with two intensities of pruning[4] (25 versus 50 percent of trees were pruned) in stands 25 to 35 years old. Empirical observations of understory response to experimental pruning treatments (Petruncio 1994) on the Tongass National Forest indicated a highly favorable understory response for deer habitat: pruning appeared to favor a highly productive and species-diverse understory with a strong and long-lasting response

[4] Pruning involves removal of the lower branches of trees by cutting close to the stem, improving wood quality by reducing knots and also increasing light to the understory.

by blueberry shrubs (a key winter browse) and the evergreen forb species so important to deer in southeast Alaska. Pruning is an appropriate silviculture technique for improving wood quality in this age class, although subsequent development of epicormic branches may reduce wood quality in Sitka spruce (Deal et al. 2003). The heavier pruning was expected to yield a stronger and longer lasting understory response.

- Experiment IV compared wide spacing (203 trees/ha) conventional thinning with girdling (killing trees in place by cutting two rings around them, severing the phloem) in stands >35 years old. The cutting and girdling treatments were designed to leave the same density of live residual trees. The conventional thinning also included treatments of the residual slash (residual woody debris) by cutting it into lengths of 1.5 m versus 4.6 m or not at all. Unthinned stands in this age class are often found in non-timber-production sites such as beach buffers and old-growth reserves, where the main objective of thinning is to increase forage availability, not wood production. Conventional thinning in this age class is especially problematic; the large interlocking crowns make it difficult to get cut trees to the ground, and once on the ground they create heavy accumulations of large-diameter slash. Slash is so large and extensive that it likely reduces access to the stand by deer. Suspended slash may directly shade the understory environment, and slash lying on the forest floor occupies potential growing sites, both of these factors thereby inhibiting the understory response to overstory canopy reduction. The bucking of slash was expected to get the wood to the ground and open the understory light environment sooner with pieces cut to shorter lengths than longer lengths or not at all. Girdling was expected to thin the overstory by killing trees left standing in place, whereby the canopy would open with needle loss, followed by small twig and branch loss, and gradually by the falling of semidecomposed trees, resulting in minimal slash accumulation at any one time.

Methods

Stands (Experimental Units of Treatment)

Described in detail by McClellan and DeSanto (N.d)[5] are the rationale for selection of treatments and age classes, the randomized complete block analysis of variance experimental design, and the methods for site selection, treatment layout, and silviculture treatments, including geographic locations, ages, and areas of each stand

[5] McClellan, M.H.; DeSanto, T.L. (No date). Tongass-Wide Young-Growth Studies: study plan and establishment report. Manuscript in preparation.

in all experiments. Experimental blocks (groups of stands with one treatment per stand, each treatment per block) were distributed throughout the Tongass National Forest in all ranger districts except the Yakutat Ranger District and Admiralty Island National Monument. Stand (experimental unit) selection criteria within each block were as follows: (1) site productivity, tree density, and stand composition were required to be relatively uniform; (2) stands must not have been previously thinned or weeded; (3) desired minimum stand size was at least 4 ha; and (4) all stands at each block must be similar and close to one another. In most cases, the experimental units were delineated portions from the same clearcut harvest unit. Each treatment was assigned to one stand at each block randomly by someone other than the field crew who selected the stands. A minimum buffer of at least 30 to 45 m was provided between stands. Although the target number of replicate blocks was 20 for each experiment, the actual number varied from 17 to 23 (table 1).

The experimental treatments were implemented in the following years: Experiment I in 2003, Experiment II in 2002, Experiment III in 2002, and Experiment IV in 2006. No pretreatment data were collected for either overstory or understory. Data from the first cycle posttreatment (this report) were collected in the following years: Experiment I in 2011 (8 years posttreatment), Experiment II in 2007 (5 years posttreatment), Experiment III in 2008 (6 years posttreatment), and Experiment IV in 2010 (4 years posttreatment). The numbers of years posttreatment differ from the idealized 5 because of logistical reasons coupled with a desire to provide a little extra time for the red alders to establish and grow in Experiment I.

Field Sampling (Data Collection)

Data were collected throughout the growing seasons (May through September) of each year. However, understory **biomass** data (described in the last paragraph of this section) were collected only in mid-June through mid-August to try to coincide with the peak of understory phenological development and peak lactation nutritional demands for black-tailed deer in early July. Although many data were collected for overstory trees, only those for overstory canopy cover are described and used in this report. Our focus here is on the understory responses and their implications for food resources for deer. Complete details of the field sampling protocols for all vegetation are described in TWYGS Field Protocol Manuals, Versions 1.3, 1.9, and 2.1 (2008–2011).[6]

[6] Unpublished documents. On file with: Michael H. McClellan and Jeffrey C. Barnard, Forestry Sciences Laboratory, 11175 Auke Lake Way, Juneau, AK 99801.

Table 1—Replicates (blocks) and areas by experiment

Experiment	Blocks	Total area	Average area per stand
		- - - - - - - *Hectares* - - - - - - -	
I	23	359	15.6
II	20	711	35.6
III	19	718	37.8
IV	17	210	12.4

Source: McClellan and DeSanto (manuscript in preparation).

For Experiments II, III, and IV, the basic sampling design focused on five fixed-area plots within each stand.[7] Each plot was square and measured 22.36 m on each side (for an area of 500 m^2), within which all overstory trees were tallied and measured. The location of the plots differed with stand size and shape, but the five plots were distributed as widely as possible within the following constraints: (1) their overall configuration was a square with one plot at each corner and one plot in the very center, (2) corner plots were ≥200 m from one another and ≥25 m from any edge of the stand, and (3) the center plot was ≥100 m from the corner plots. Total overstory canopy coverage was estimated from hemispherical photographs taken at 1.5 m above ground at the center of each of the five plots per stand (one photo per plot, five photos per stand).

Canopy coverage of understory vegetation was estimated within 12 one-square-meter (100- by 100-cm) quadrats in each of the five plots (total of 60 quadrats per stand), with the quadrats systematically located on perpendicular transect lines at distances of 4, 5, and 6 m from plot center (three quadrats on each of four lines). The percentage of canopy cover (vertical projection of outer perimeter of plant canopy to ground) was estimated visually to the following levels of precision: 0 to 1 percent (estimated to nearest 0.1 percent); 1 to 10 percent (estimated to nearest 1 percent); 10 to 30 percent (estimated to nearest 5 percent); 30 to 100 percent (estimated to nearest 10 percent). Canopy coverage was estimated for each species of vascular plants within 1.3 m of the ground, including all tree seedlings and branches, shrubs, and herbs (forbs, grasses, grasslike plants, ferns, clubmosses, and horsetails), but not including bryophytes or lichens.

Sampling for Experiment I involved a different layout, as trees were sampled in an entirely different scheme. All understory vegetation sampling was conducted systematically in 1-m^2 quadrats along three parallel transects run perpendicular

[7] Sampling details for Experiment IV differed slightly from the ideal, as plot layout required modification when treated stands were small, but 60 quadrats for understory vegetation were always sampled systematically in each stand.

to slope with predetermined start and end points located with handheld global positioning system receivers. Transects were of variable length to sample each stand as widely as possible. Quadrats (20 per transect, 60 per stand) were spaced at 3- to 7-m intervals, depending on transect length. Overstory canopy coverage was estimated from hemispherical photos taken in relation to understory transects (start and end points) and overstory plots (total of 6 to 12 photos per stand, depending on size of stand).

Although canopy coverage can be estimated relatively quickly and easily, it is not sufficient for analyzing deer habitat with a food-based model (described below), because deer eat plant biomass, not canopy coverage. Canopy coverage data were obtained for all plant species in all stands at all blocks throughout TWYGS. Understory biomass data, however, could be obtained at only a subset of blocks where electricity, drying ovens, and balances were available. Allometric regression equations were developed and used for converting estimates of canopy coverage (percentage) to estimates of biomass (ovendry weight) of current annual growth for each species, and in the case of woody species, leaves separate from twigs. Biomass of only current annual growth was measured—total aboveground biomass of herbs, only leaves and current year twigs of woody species. Canopy cover-to-biomass equations are known to vary with site environmental conditions, however, especially with stand history and the amount of sunlight (Alaback 1986). Therefore, separate sets of equations were developed for each treatment (and untreated control) within each TWYGS experiment.

In the first two field seasons, 2007 and 2008 (Experiments II and III), biomass regressions were calculated from quadrats that were sampled for canopy coverage as part of the design described above–every middle quadrat of the three quadrats along each transect line at each plot was sampled for biomass (clipped by species, leaves separate from twigs in woody species, and weighed) after canopy coverage was estimated for each species (i.e., one third of the 60 quadrats were double-sampled for both species-specific canopy coverage and biomass). Because of inefficiencies in the double-sampling design, however, a different biomass sampling protocol for the regression data was used for Experiments I and IV: separate 100-m transects were run through the stand, with quadrats spaced at 5-m intervals, and specific species were targeted for each quadrat; the target species was then sampled (both canopy coverage and fresh weight) in quadrats in which it occurred until sufficient samples were obtained throughout the full range of its potential canopy coverage. In other words, systematic sampling targeted species individually to provide a sufficiently wide range of values to calculate a meaningful regression equation for each. In all years, the species within each quadrat were clipped and

weighed (fresh weight) with Pesola spring scales, and several samples of each species were retained each day for oven-drying (24 hours at 100 °C) for dry-weight correction. Sampling for canopy cover-to-biomass regressions was limited to only those experimental blocks accessible from the Prince of Wales Island road system (about one-third of all blocks) each year, and all sampling was restricted to the period mid-June through mid-August. Training and calibration of field crews was conducted for at least 1 month before data collection. The resulting canopy cover-to-biomass regressions were used to convert all estimates of canopy coverage from all stands in the experiment to species-specific estimates of biomass in terms of kilograms per hectare, separately for each treatment.

Quantification of Deer Habitat Value

Vegetation results were analyzed in relation to their potential value as food for black-tailed deer with the Forage Resource Evaluation System for Habitat (FRESH)-Deer model (Hanley et al. 2012); http://cervid.uaa.alaska.edu/deer/Home.aspx. The FRESH model is based on the quantity and quality of available food resources in relation to specified nutritional requirements for deer. It transforms an array of species-specific biomass values (kg/ha) with a matrix of corresponding forage-specific nutritional values (dry matter digestibility and digestible protein[8]) into one measure of habitat value for deer: deer days/ha, where one deer day is the food required to support one animal for one day, with the nutritional requirements of the animal specified by the user on the basis of species, age, sex, body weight, reproductive status, and season. The deer days/ha result is derived from a linear programming model that maximizes the combined biomass of all potential foods while meeting specified minimal constraints for digestible energy and digestible protein concentrations of the combined biomass. The maximum biomass solution (kg/ha) is then divided into the specified daily dry matter intake (g/day) of an adult female Sitka black-tailed deer (our focal animal unit), yielding the number of deer days/ha that the food could support at that specified level of nutritional requirements.

The FRESH model transforms an array of species-specific biomass values (kg/ha) with a matrix of corresponding forage-specific nutritional values (dry matter digestibility and digestible protein) into one measure of habitat value for deer.

[8] Protein is needed for body growth and muscle and tissue maintenance; digestible protein is that fraction of food protein that is digested and assimilated by the animal. Energy is needed to fuel the animal's heat and tissue production, metabolic processes, and activity. Digestible energy is that fraction of a food's gross energy that is digestible and available to the animal. It is the product of a food's gross energy (total energy released upon combustion) and its dry matter digestibility (the fraction of food dry matter that is digestible). Forages vary much more in their dry matter digestibility than in their gross energy, so dry matter digestibility is frequently used as a proxy for digestible energy. Requirements for dry matter digestibility are calculated directly from requirements for digestible energy, assuming a constant value for gross energy and a given daily dry matter intake of food. See Hanley et al. (2012) for more explanation of this and the FRESH-Deer model.

The deer days/ha values provided a quantitative basis for direct comparison of experimental treatments combining effects of all species-specific biomass and nutritional quality. Our summer analysis centered on early July, the time of peak vegetation phenological development and peak lactation requirements for deer in southeast Alaska (Hanley and McKendrick 1985, Parker et al. 1999). For lactation requirements, we used values for one fawn and called that "lactation" (see Hanley et al. 2012 for rationale). Our winter analysis centered on mid-winter (February 1). 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 (1) a simple burying effect from ground up for all species except blueberry and salal (*Gaultheria shallon*), which had logarithmic burial functions, (2) an estimate of the plant height profile of each species, and (3) 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 (leaf, twig) and came from an unpublished database (http://cervid.uaa.alaska.edu/deer/Home.aspx) based on the following studies plus other unpublished studies from southeast Alaska: Hanley and McKendrick (1983), Hanley et al. (1992), McArthur et al. (1993), Parker et al. (1999). All plant species, but only their current annual growth, were considered potential food resources.

We analyzed the food resources under eight different scenarios: two for summer when metabolic requirements differ (for maintenance only, and for maintenance plus lactation), and six in winter when forage availability differs greatly (for snow-free conditions and snow depths of 20, 40, 60, 80, and 100 cm). Snow depth of 20 cm is enough to bury the ground-layer evergreen forbs but not enough to affect the availability of shrubs, while the deeper snow depths progressively bury more shrubs. Stated snow depths are for snow depth in a treeless open area; depth in each stand was reduced as an exponentially decreasing function of overstory canopy cover (Hanley and Rose 1987; see Hanley et al. 2012 for details). Metabolic requirements were the following: for summer maintenance, metabolizable energy (ME) 9839 kJ/day, dry matter digestibility (DMD) 50.0 percent, digestible protein (DP) 4.8 percent, and dry matter intake (DMI) 1220 g/day; for summer maintenance plus lactation, ME 12979 kJ/day, DMD 60.0 percent, DP 8.0 percent, and DMI 1340 g/day; for winter, ME 4019 kJ/day, DMD 48.0 percent, DP 1.8 percent, and DMI 525 g/day (see table 1 of Hanley et al. 2012 for rationale and sources).

Statistical Analysis

Cover-to-biomass regression equations—
All canopy cover-to-biomass regressions were approached as being of the form $Y = aX$, where Y is the biomass (ovendry g/m^2), X is the canopy coverage (percentage), and a is the regression coefficient (slope) with the Y-intercept forced through the origin (0, 0). That is the most simple equation possible for this particular problem. After calculating the equation, residuals were examined for pattern, and adequacy of the equation was judged on the basis of r (correlation coefficient) and r^2 (coefficient of determination). Possible transformations (e.g., arcsine for percentage data), Y-intercepts other than zero, and multiple regressions (e.g., $Y = b_1 + b_2X + b_3X^2$) were considered and used only if they improved the fit sufficiently (determined subjectively).

Silviculture treatment effects—
The treatment effects in each experiment were analyzed in terms of deer habitat value (deer days per hectare) in a randomized complete block analysis of variance with blocked groups of stands as blocks, and silviculture treatments (including untreated control) as treatments. Our analysis focused on deer habitat values rather than any single or group of vegetation variables because the deer habitat values integrate the entire matrix of vegetation biomass and nutritional values into one number that is entirely relevant to deer. No single forage or group of forages is sufficient in itself; it is the interactive effect of all potential forages, their nutritional values, and deer nutritional requirements that determines the food resource value for deer. An alpha level of 0.05 was used throughout as the criterion of statistical significance. All analyses were performed with SAS software (SAS 2004).

Although silviculture treatments were designed to improve food resources for deer and to differ among treatments (as outlined in the "Introduction"), prior scientific investigation of silviculture effects in this region were too limited, and other empirical observations were too equivocal for us to have strong convictions about expected results. Therefore, all hypothesis testing was two-tailed and of null differences among treatments. Because blocks were widely distributed throughout the Tongass National Forest, we considered our scope of statistical inference to be Tongass-wide, recognizing that local patterns of variation may result from environmental factors such as extreme levels of herbivory in areas where deer densities might be exceptionally high.

Our analysis focused on deer habitat values rather than any single or group of vegetation variables because the deer habitat values integrate the entire matrix of vegetation biomass and nutritional values into one number that is entirely relevant to deer.

Results

Cover-to-Biomass Regressions

Understory plant canopy coverage was a strong predictor of biomass, accounting for about 86 percent of the variation in biomass for the species and treatments throughout the four experiments (overall mean $r^2 = 0.857$; see appendix 2 for species- and treatment-specific results). Regression r^2 values ranged from 1.000 to 0.175 (for *Cornus canadensis* and *Rubus spectabilis* twigs, respectively, both in Experiment II). As is common in cover-to-biomass regression relations, cover (a two-dimensional variable) tended to account for variation in biomass much better in strongly two-dimensional species (such as *C. canadensis*) than in strongly three-dimensional species (such as *R. spectabilis*). Regressions for all major species were obtained for all treatments, but lesser species could not be sampled sufficiently for their own equations. Equations from surrogate species (species of similar growth form and appearance, for which we had sufficient data) were used for the lesser species, but in aggregate, total biomass of the lesser species was a relatively small proportion of the total understory. Virtually all regressions took the form $Y = aX$, with only a few including a non-zero Y-intercept. In none of the cases did residuals justify using either data transformations or more complex regressions than simple linear regression.

Sampling efficiency with the double-sampling technique of the first two field seasons (Experiments II and III) suffered from relatively small sample sizes (low frequency of occurrence within the 20 double-sampled quadrats per stand), but efficiency was increased greatly with the switch to targeting specific species in the third and fourth field seasons (Experiments IV and I). All treatments of Experiment I (red alder planting in 1 to 5-year-old stands) were considered similar environments, as the red alder was still a minor part of the vegetation in even the 200 trees/ha treatment, so treatment-specific regressions were not calculated for Experiment 1.

One source of error that we did not account for was variation in degree of browsing by deer. With all regressions based on data from Prince of Wales Island and a moderate degree of browsing, our equations likely overestimated the biomass of shrub twigs and leaves per unit of canopy cover on heavily browsed shrubs at a few sites (blocks) subject to heavy browsing. That bias would have applied equally across all treatments within a block, however, so its effect on the statistical analysis would have been minimal.

Experiment I (Red Alder Planting in 1- to 5-Year-Old Stands, 8 Years Posttreatment)

Stands in Experiment I ranged in age from 2 to 8 years (mean = 4.2) when treated (McClellan and DeSanto, N.d.) so were about 12 years old when sampled posttreatment. The planted red alder trees were only about 5 to 6 m tall and fairly widely scattered in even the densest treatment. The understory of all three treatments was dominated by woody species (shrubs and trees); forbs and ferns were about equally dominant in the herbaceous layer, and graminoids were minor (table 2; woody species also have substantial biomass from prior years' growth, although we did not measure that). No significant differences among treatments were found in deer habitat values (deer days/ha) for either of the two summer or six winter scenarios (table 3). Snow-free winter habitat values exceeded summer values for reproduction requirements (lactation) and were about equal to those for maintenance only. High snow-free values were the result of reduced dry-matter intake rates of deer in winter combined with high amounts of the key evergreen forb species. Habitat value dropped rapidly with increasing snow depth but remained above zero at depths of even 100 cm because of Alaska yellow-cedar (*Chamaecyparis nootkatensis*) remaining above the snowpack. Nutritional quality of Alaska yellow-cedar marginally exceeds deer nutritional requirements in winter (Hanley et al. 2012), so in combination with western hemlock (also available at snow depths of 100 cm), those two conifers provided some suitable food at even our deepest snow depth.

Experiment II (Thinning in 15- to 25-Year-Old Stands, 5 Years Posttreatment)

Stands in Experiment II ranged in age from 17 to 26 years (mean = 21.9) when treated (McClellan and DeSanto, N.d.) so were about 27 years old when sampled posttreatment. Understories were strongly dominated by shrubs, even more so than in Experiment I and especially so in both thinning treatments (table 4). Thinning treatments resulted in shrub biomass levels similar to those of young clearcuts or even greater (compare with table 2), although herbaceous vegetation response was much less. Understory in untreated controls of Experiment II was much less than that of the younger clearcuts of Experiment I.

Both thinning treatments resulted in significantly higher deer habitat value (deer days/ha) than the untreated controls in all scenarios except the deepest snow conditions, where values were very low across all treatments (table 5). In summer, the wider spaced thinning (331 trees/ha) yielded higher habitat value than did the less intense thinning, at both sets of deer nutritional requirements. However, for winter scenarios, no significant differences were found between the two thinning

Table 2—Mean (and standard error) biomass (ovendry current annual growth in kg/ha) of major vegetation groups and five key winter forages, 8 years posttreatment in Experiment I: untreated control and two levels of red alder planting in 1- to 5-year-old stands at time of treatment

	Untreated control	50 trees per hectare	200 trees per hectare
		Kilograms per hectare	
Total forbs	190.04 (28.54)	192.36 (26.59)	163.78 (23.03)
Total ferns	233.55 (26.03)	254.62 (30.82)	240.75 (31.47)
Total graminoids	23.90 (14.04)	30.46 (10.86)	6.34 (2.76)
Total shrubs	375.47 (22.12)	404.74 (26.00)	460.70 (35.66)
Total trees	198.88 (21.25)	224.12 (32.42)	206.54 (25.32)
Key winter forages:			
Coptis aspleniifolia	16.78 (5.07)	10.91 (3.38)	15.12 (5.96)
Cornus canadensis	73.75 (13.35)	58.87 (12.39)	60.30 (12.11)
Rubus pedatus	8.06 (2.02)	10.20 (2.35)	10.95 (3.43)
Tiarella trifoliata	5.40 (1.11)	6.18 (2.15)	3.81 (1.20)
Vaccinium ovalifolium twigs	120.43 (11.67)	124.96 (12.49)	141.62 (17.69)

Note: See appendix 3 for all species-specific data.

Table 3—Mean (and standard error) deer habitat values (deer days/ha) of three treatments in Experiment I, 8 years posttreatment: untreated control and two levels of red alder planting in 1- to 5-year-old stands at time of treatment

	Untreated control	50 trees per hectare	200 trees per hectare
Summer:			
Maintenance only	703.1^a (41.1)	758.4^a (53.4)	718.0^a (58.1)
Maintenance plus lactation	327.7^a (39.2)	377.6^a (40.7)	335.1^a (39.4)
Winter, at snow depths in open:			
0 cm	779.7^a (65.4)	668.1^a (76.2)	705.0^a (90.4)
20 cm	192.9^a (21.4)	166.6^a (17.5)	209.1^a (27.9)
40 cm	129.0^a (17.3)	107.2^a (13.4)	133.7^a (19.6)
60 cm	88.7^a (14.4)	70.6^a (10.7)	87.2^a (14.7)
80 cm	58.0^a (12.0)	43.1^a (8.6)	52.5^a (11.0)
100 cm	29.6^a (10.1)	20.3^a (6.9)	22.7^a (8.4)

Note: Values are for two levels of deer nutritional requirements in summer and six levels of snow depth in winter (snow depth in a treeless open area); means with same superscript within rows do not differ significantly at α of 0.05.

Table 4—Mean (and standard error) biomass (ovendry current annual growth in kg/ha) of major vegetation groups and five key winter forages, 5 years posttreatment in Experiment II: untreated control and two levels of thinning in 15- to 25-year-old stands at time of treatment

	Untreated control	549 trees per hectare	331 trees per hectare
		Kilograms per hectare	
Total forbs	35.77 (10.06)	55.01 (8.58)	108.45 (26.73)
Total ferns	42.53 (15.01)	75.87 (10.54)	131.84 (22.12)
Total graminoids	2.18 (1.96)	1.61 (0.56)	5.62 (1.73)
Total shrubs	171.90 (37.92)	560.60 (42.56)	726.12 (59.41)
Total trees	13.18 (4.10)	35.16 (4.89)	73.84 (17.55)
Key winter forages:			
Coptis aspleniifolia	2.38 (0.90)	4.01 (1.23)	7.04 (4.37)
Cornus canadensis	10.05 (3.45)	24.83 (4.30)	47.26 (15.49)
Rubus pedatus	1.99 (0.64)	8.47 (1.59)	8.99 (2.36)
Tiarella trifoliata	1.69 (0.45)	4.11 (2.54)	3.88 (1.09)
Vaccinium ovalifolium twigs	26.26 (6.87)	69.12 (11.00)	110.57 (20.30)

Note: See appendix 3 for all species-specific data.

Table 5—Mean (and standard error) deer habitat values (deer days/ha) of three treatments in Experiment II, 5 years posttreatment: untreated control and two levels of thinning in 15- to 25-year-old stands at time of treatment

	Untreated control	549 trees per hectare	331 trees per hectare
Summer:			
Maintenance only	194.0^{a} (42.2)	587.8^{b} (43.7)	812.5^{c} (51.2)
Maintenance plus lactation	88.1^{a} (19.4)	232.4^{b} (24.8)	364.3^{c} (31.5)
Winter, at snow depths in open:			
0 cm	103.0^{a} (27.5)	302.2^{b} (37.8)	406.5^{b} (57.3)
20 cm	29.4^{a} (7.70)	92.0^{b} (15.9)	132.4^{b} (25.9)
40 cm	19.6^{a} (4.9)	56.7^{b} (10.1)	77.1^{b} (14.9)
60 cm	12.3^{a} (3.0)	33.7^{b} (6.2)	44.0^{b} (8.4)
80 cm	7.2^{a} (1.7)	17.3^{b} (3.5)	20.5^{b} (1.0)
100 cm	3.1^{a} (3.6)	4.5^{a} (1.9)	2.0^{a} (0.4)

Note: Values are for two levels of deer nutritional requirements in summer and six levels of snow depth in winter (snow depth in a treeless open area); means with same superscript within rows do not differ significantly at α of 0.05.

intensities. Snow-free winter habitat values were similar to those of summer for reproduction (lactation) requirements, and as in Experiment I, all winter values dropped rapidly with increasing snow depth.

Experiment III (Thinning and Pruning in 25- to 35-Year-Old Stands, 6 Years Posttreatment)

Stands in Experiment III ranged in age from 25 to 37 years (mean = 29.0) when treated (McClellan and DeSanto, N.d.) so were about 35 years old when sampled posttreatment. Again, a strong shrub response occurred in all three thinning treatments, with shrubs strongly dominating all understories (table 6), and biomass of untreated controls continued to decrease from levels observed in younger stands (compare with tables 2 and 4). Although the thinning with 25 percent pruning treatment appeared to result in the greatest biomass response, including that of the key winter forages for deer (table 6), differences in deer habitat values among thinning treatments were very few, and none in winter (table 7). All thinning treatments had higher deer habitat values than did the untreated controls in all scenarios except the two deepest snow depths, but only in the summer maintenance-only scenario did a difference among thinning treatments occur—thinning with 25 percent pruning yielding the highest values. As in Experiment II, snow-free winter habitat values were very similar to summer values for reproduction requirements, and all values dropped rapidly with increasing snow depth.

Experiment IV (Thinning by Felling, With or Without Slash Treatment, or Girdling in >35-Year-Old Stands, 4 Years Posttreatment)

Stands in Experiment IV ranged in age from 33 to 60 years (mean = 43.2) when treated (McClellan and DeSanto, N.d.) so were about 47 years old when sampled posttreatment. This experiment included four thinning treatments, and shrubs dominated the understories of each (table 8), while biomass in the untreated controls continued to decline below that of untreated controls in the other three experiments (compare with tables 2, 4, and 6). All thinning treatments resulted in greater summer habitat values for deer than did the untreated controls, but none of the thinning treatments differed from one another (table 9). Results from winter scenarios for deer habitat value were more complicated in Experiment IV than in the other three experiments, with much overlap of nonsignificant differences among treatments (and controls) and with patterns shifting in relation to snow depth. For snow-free conditions, all thinning treatments yielded higher values than did the untreated controls, with thinning by girdling yielding significantly highest values. Thinning by girdling consistently yielded the highest values throughout all winter

Table 6—Mean (and standard error) biomass (ovendry current annual growth in kg/ha) of major vegetation groups and five key winter forages, 6 years posttreatment in Experiment III: untreated control, thinning (to 420 trees/ha) alone, and thinning with two levels of pruning (25 percent and 50 percent of trees) in 25- to 35-year-old stands at time of treatment

	Untreated control	Thinning alone	Thinning with 25 percent pruning	Thinning with 50 percent pruning
		Kilograms per hectare		
Total forbs	7.78 (3.49)	29.98 (8.65)	54.57 (15.88)	26.75 (7.34)
Total ferns	10.56 (4.22)	51.43 (9.23)	80.20 (17.63)	90.48 (21.65)
Total graminoids	0.06 (0.04)	4.23 (2.35)	3.04 (1.15)	2.68 (0.94)
Total shrubs	49.82 (19.36)	221.02 (41.18)	368.00 (71.04)	186.53 (36.41)
Total trees	7.26 (3.89)	11.03 (2.50)	17.46 (3.58)	8.08 (3.44)
Key winter forages:				
Coptis aspleniifolia	0.44 (0.24)	1.98 (1.43)	2.10 (0.85)	2.84 (1.43)
Cornus canadensis	1.78 (1.31)	12.20 (4.01)	23.25 (7.61)	9.43 (2.52)
Rubus pedatus	0.31 (0.21)	2.58 (1.07)	5.33 (1.52)	6.16 (2.21)
Tiarella trifoliata	1.58 (0.81)	0.03 (0.03)	4.46 (1.65)	2.99 (0.98)
Vaccinium ovalifolium twigs	5.62 (2.05)	31.96 (8.10)	46.80 (12.44)	17.86 (4.41)

Note: See appendix 3 for all species-specific data.

Table 7—Mean (and standard error) deer habitat values (deer days/ha) of four treatments in Experiment III, 6 years posttreatment: untreated control, thinning (to 420 trees/ha) alone, and thinning with two levels of pruning (25 percent and 50 percent of trees) in 25- to 35-year-old stands at time of treatment

	Untreated control	Thinning alone	Thinning with 25 percent pruning	Thinning with 50 percent pruning
Summer:				
Maintenance only	60.3^{a} (22.0)	257.4^{b} (43.5)	415.5^{c} (79.1)	235.8^{b} (49.7)
Maintenance plus lactation	29.4^{a} (11.3)	118.6^{b} (19.4)	167.7^{b} (40.6)	103.9^{b} (26.1)
Winter, at snow depths in open:				
0 cm	26.6^{a} (10.0)	125.3^{b} (32.8)	207.5^{b} (51.0)	114.1^{b} (29.8)
20 cm	6.6^{a} (2.3)	31.0^{b} (7.5)	44.3^{b} (11.2)	22.6^{b} (5.7)
40 cm	4.5^{a} (1.5)	19.1^{b} (4.5)	27.1^{b} (6.7)	14.9^{b} (4.0)
60 cm	3.0^{a} (1.0)	11.5^{b} (2.7)	16.2^{b} (3.9)	9.7^{b} (2.8)
80 cm	2.5^{a} (1.0)	6.0^{a} (1.4)	8.5^{a} (2.0)	5.9^{a} (3.6)
100 cm	1.0^{a} (0.5)	1.7^{a} (0.5)	2.3^{a} (0.5)	2.7^{a} (1.2)

Note: Values are for two levels of deer nutritional requirements in summer and six levels of snow depth in winter (snow depth in a treeless open area); means with same superscript within rows do not differ significantly at α of 0.05.

Table 8—Mean (and standard error) biomass (ovendry current annual growth in kg/ha) of major vegetation groups and five key winter forages, 4 years posttreatment in Experiment IV: untreated control, conventional thinning (to 203 trees/ha) alone, thinning with two levels of bucking the slash (to 1.5-m and 4.6-m lengths), and thinning by girdling in >35-year-old stands at time of treatment

	Untreated control	Conventional thinning alone	Thinning with 1.5-m bucking	Thinning with 4.6-m bucking	Thinning by girdling
			Kilograms per hectare		
Total forbs	9.62 (3.75)	20.32 (4.95)	16.52 (4.57)	32.29 (8.88)	26.46 (8.77)
Total ferns	11.53 (5.09)	85.70 (16.86)	29.68 (4.59)	96.44 (17.00)	44.69 (8.41)
Total graminoids	0.00 (0.00)	6.14 (2.83)	2.23 (1.06)	6.43 (4.38)	3.12 (2.12)
Total shrubs	22.28 (9.77)	110.90 (20.67)	104.15 (24.25)	97.20 (19.97)	138.77 (24.09)
Total trees	2.91 (2.04)	33.91 (6.99)	16.73 (3.57)	31.98 (5.92)	17.76 (4.01)
Key winter forages:					
Coptis aspleniifolia	0.11 (0.07)	0 (0)	0.01 (0.01)	0.02 (0.02)	0.15 (0.13)
Cornus canadensis	1.10 (0.81)	3.58 (1.53)	4.80 (3.05)	1.56 (0.55)	3.54 (1.26)
Rubus pedatus	0.79 (0.69)	1.19 (0.56)	1.32 (0.77)	0.74 (0.31)	1.53 (0.68)
Tiarella trifoliata	2.68 (2.13)	6.96 (2.89)	1.44 (0.71)	2.03 (1.50)	11.91 (8.12)
Vaccinium ovalifolium twigs	7.65 (3.66)	10.56 (3.92)	16.15 (7.62)	21.08 (6.24)	29.84 (8.03)

Note: See appendix 3 for all species-specific data.

Table 9—Mean (and standard error) deer habitat values (deer days/ha) of five treatments in Experiment IV, 4 years posttreatment: untreated control, conventional thinning (to 203 trees/ha) alone, thinning with two levels of bucking the slash (to 1.5-m and 4.6-m lengths), and thinning by girdling in >35-year-old stands at time of treatment

	Untreated control	Conventional Thinning alone	Thinning with 1.5-m bucking	Thinning with 4.6-m bucking	Thinning by girdling
Summer:					
Maintenance only	33.3^{a} (12.2)	188.5^{b} (32.3)	127.0^{b} (21.0)	178.2^{b} (23.8)	172.3^{b} (28.2)
Maintenance plus lactation	15.7^{a} (5.8)	98.7^{b} (16.3)	58.2^{b} (7.7)	94.4^{b} (17.1)	80.1^{b} (15.2)
Winter, at snow depths in open:					
0 cm	30.4^{a} (12.7)	96.1^{b} (24.7)	69.5^{b} (25.5)	68.0^{b} (13.1)	119.8^{c} (26.1)
20 cm	7.1^{a} (3.3)	10.5^{a} (3.4)	14.2^{a} (6.3)	20.1^{b} (5.8)	28.0^{b} (7.8)
40 cm	6.6^{a} (3.1)	9.3^{a} (3.0)	12.5^{a} (5.6)	17.8^{b} (3.0)	24.9^{b} (6.9)
60 cm	5.6^{a} (2.6)	7.7^{a} (2.5)	10.3^{a} (4.6)	14.7^{a} (4.2)	20.5^{b} (5.7)
80 cm	4.7^{a} (2.1)	6.0^{a} (1.9)	8.1^{a} (3.6)	11.5^{a} (3.3)	16.2^{b} 4.5)
100 cm	3.7^{a} (1.7)	4.4^{a} (1.4)	5.8^{a} (2.6)	8.4^{a} (2.4)	11.8^{b} (3.2)

Note: Values are for two levels of deer nutritional requirements in summer and six levels of snow depth in winter (snow depth in a treeless open area); means with same superscript within rows do not differ significantly at α of 0.05.

scenarios, but the results for other thinning treatments did not differ from those of the controls in any of the snow depths >0 cm (except for thinning with 4.6-m bucking at 20- and 40-cm snow depths, which were similar to thinning by girdling). Although total shrub response was strong in all thinning treatments (table 8), most of that response was from salmonberry, which is a good summer forage but poor winter forage (Hanley and McKendrick 1983), while the blueberry response was greatest in the thinning by girdling treatment (table 8 and app. 3).

The strong response of thinning by girdling is especially surprising in that failure of the girdling was common among the replicates, making the treatment more similar to conventional thinning alone. The boles of many trees that had been girdled subsequently broke at the girdle, with the tree falling as though it had been felled. Such failure of girdling was widespread through this experiment and widespread through many of its stands, with almost an even distribution of failure ranging from 3 to 96 percent of the girdled trees in a stand (table 10). We did not know when the failures occurred, however, only that they had occurred by the time

Table 10—Effect of girdling failure (percentage of girdled trees found snapped) on deer habitat values (deer days/ha) for two summer scenarios differing in nutritional requirements (maintenance only and maintenance plus lactation) and two winter scenarios differing in open-area snow depth (0 and 20 cm)

Percentage of trees snapped	Summer		Winter	
	Maintenance	Lactation	0 cm snow	20 cm snow
3	186.9	104.4	63.3	10.1
11	40.9	15.1	49.0	7.4
20	8.4	3.4	0.0	0.0
22	382.7	209.2	360.0	0.3
27	140.6	44.8	85.2	15.4
29	422.6	204.6	338.6	87.2
32	112.8	46.9	48.7	16.4
35	165.6	44.2	235.0	92.8
42	24.0	9.2	22.9	4.8
56	194.4	92.3	138.3	53.9
61	151.9	56.9	177.9	62.9
66	101.6	52.7	19.2	1.7
71	168.3	101.1	57.9	6.3
74	70.4	25.7	43.9	18.9
85	230.4	127.8	98.9	0.1
95	299.8	143.5	110.1	27.5
96	228.1	79.8	187.1	70.6
Correlation coefficient	0.139	0.098	-0.069	0.137

Note: The correlation coefficient between percentage of trees snapped and deer days/ha is also shown for each scenario.

that we sampled the stands 4 years after their treatment. The correlation between girdling failure (percentage of trees found snapped) and deer habitat values (deer days/ha) was nil (P > 0.50 in all cases; table 10; $r_{0.50(2),16} = 0.170$).

Discussion

Effects of Logging and Thinning Slash on Habitat Availability

Although effects of slash have not been included in our analyses, one should be aware that slash can be an important variable affecting habitat use by deer.

Abundance of logging and thinning slash (residual woody stems and branches from felled trees) is highly variable within and among treated stands and can be great enough to restrict movement of deer and limit their access to vegetation within a stand. The FRESH model does not include consideration of such effects, as the FRESH analysis is based on just the vegetation alone. If we could predict how a given amount of slash would reduce access by deer, then we could reduce the deer days/ha result accordingly (e.g., a 15-percent reduction in access would result in a 15-percent reduction in the deer days/ha value because the area available to deer would be 15 percent less), but quantitative relations between slash and access by deer are unknown. Therefore, although effects of slash have not been included in our analyses, one should be aware that slash can be an important variable affecting habitat use by deer.

Snow Depth and Its Interaction With Shrubs and Slash

Similarly, modeling the effects of snow with the FRESH model is somewhat problematic for all treatments except the untreated controls of Experiments II through IV because all other treatments had very shrubby understories and large amounts of thinning or logging slash on the ground. The FRESH snow burial process works from the ground up (e.g., a snow depth of 35 cm buries all plant material within 35 cm of the ground surface), which is reasonable within relatively open understories typical of forests. However, in open-grown understories strongly dominated by shrubs, the shrubs may grow so densely that they intercept the snow and hold it above the ground surface, increasing the effective burial depth significantly. Similarly, the same may happen with large amounts of thinning or logging slash lying on the ground. Shrubs and slash together are even more likely to produce that effect. However, we know of no data to quantify the effect. The FRESH snow submodel includes an optional “shrub/slash interaction” coefficient that effectively increases the snow depth when it is assigned a value greater than 1.0 (Hanley et al. 2012), but because the choice of any such value would be subjective in the absence of data, we did not use that option (i.e., we used its default value of 1.0 for all our analyses).

Snow depths of 0 and 20 cm are the most meaningful and important depths to consider. Snow-free conditions occur frequently at lower elevations throughout

winters in southeast Alaska, and the snow-free analysis makes use of the entire understory vegetation. Low-growing evergreen forbs are particularly important contributors to deer habitat in snow-free conditions (Hanley and McKendrick 1984, Hanley et al. 1989, Parker et al. 1999). Snow depth of 20 cm (actually, it is less than that in the stand after being reduced by the effect of overstory canopy) is also an important depth, as it is deep enough to bury the evergreen forbs but unlikely to affect the availability of the shrub layer. Thus, the contrast between snow depths of 0 and 20 cm can be thought in terms of the complete understory vegetation (0 cm) versus only the shrub and tree layers (20 cm). We have analyzed effects of snow at progressively greater depths (40 through 100 cm) to provide perspective of the relative availability and quality of the shrub and tree layers at progressively greater heights above the ground, but the reliability of those results is less than those for the 0- and 20-cm depths. The values for deeper snow are most meaningful for relative (not absolute) comparisons of increasing depth within a treatment and for treatments and experiments at a given depth.

The contrast between snow depths of 0 and 20 cm can be thought in terms of the complete understory vegetation (0 cm) versus only the shrub and tree layers (20 cm). We have analyzed effects of snow at progressively greater depths (40 through 100 cm) to provide perspective of the relative availability and quality of the shrub and tree layers at progressively greater heights above the ground, but the reliability of those results is less than those for the 0- and 20-cm depths.

Limiting Factors

The FRESH analysis not only provides an estimate of the value of a given habitat in deer days/ha, it also identifies the most important factor limiting that value. The habitat value may be limited by either (or both) of the nutritional constraints or the total amount of vegetation biomass available (Hanley et al. 2012). An understanding of potential limiting factors provides insight into the relative tradeoffs between quantity and quality of the forage resources, as quantity and quality are not substitutable for one another (Hobbs and Hanley 1990), and habitat value cannot be determined by simply multiplying the two together (Wallmo et al. 1977).

Examination of limiting factors (digestible protein vs. dry matter digestibility vs. total available biomass) for the four most important nutritional/snow scenarios (summer with two levels of nutritional requirements and winter at snow depths of 0 and 20 cm) across all treatments in each of the four experiments (table 11) reveals several important results:

1. Digestible protein was virtually never the limiting factor; it was limiting in only 1 of the 938 cases analyzed. That result seems common for forb- and shrub-rich forest understories of southeast Alaska (Hanley and McKendrick 1984, Hanley et al. 2006, Parker et al. 1999) even though it contrasts sharply with bunchgrass-dominated habitat of eastern Washington for black-tailed deer (Wagoner 2011, Wagoner et al. 2013) and willow-dominated ranges of south central Alaska for moose (*Alces americanus*) (McArt et al. 2009).

Table 11—Limiting factors

Experiment/scenario	Number of cases	Limiting factor (number of cases)		
		DP	DMD	Biomass
Experiment I:				
Summer, maintenance	51	0	34	17
Summer, lactation	51	0	51	0
Winter, snow-free	51	0	36	15
Winter, 20 cm snow	51	0	51	0
Experiment II:				
Summer, maintenance	48	0	22	26
Summer, lactation	48	0	48	0
Winter, snow-free	48	0	33	15
Winter, 20 cm snow	48	0	48	0
Experiment III:				
Summer, maintenance	52	0	23	29
Summer, lactation	52	0	51	1
Winter, snow-free	52	0	35	17
Winter, 20 cm snow	52	0	52	0
Experiment IV:				
Summer, maintenance	85	0	52	33
Summer, lactation	85	1	84	0
Winter, snow-free	83	0	61	22
Winter, 20 cm snow	81	0	81	0

Note: The limiting factor is that which most limited the total amount of biomass in the solution set, whether it was a nutritional constraint or total biomass availability. Values in the table are the number of cases where the FRESH solution was most limited by digestible protein (DP), dry matter digestibility (DMD), or total available biomass (biomass; i.e., neither DP nor DMD was limiting), and the total number of cases analyzed in each experiment for each of four nutritional/snow scenarios. Number of cases analyzed differed for scenarios within Experiment IV when there was no solution for a case (i.e., 0 deer days/ha).

2. Dry matter digestibility (and by implication, digestible energy) was by far the most common limiting factor (762 of 938 cases, or 81 percent of the cases).
3. In the 19 percent of the cases in which total available biomass (no nutritional limitation) was limiting, it was in summer for maintenance only (low nutritional requirements) and snow-free winter (minimal nutritional requirements combined with high forage quality of evergreen forbs), which are the most relaxed nutritional settings. At higher nutritional requirements in summer (lactation) or poorer quality food resources (only shrubs) in winter, dry matter digestibility was the limiting factor in virtually all cases.

The overwhelming importance of dry matter digestibility (calculated on requirements for digestible energy) as a nutritional limitation emphasizes its importance in evaluating deer habitat and understory response to silviculture in southeast

Alaska. It does not mean that digestible protein is not important; it means only that digestible energy tends to be the most limiting factor in these forest environments, even in summer when protein limitations are most likely. That is why leaves of preferred shrubs (e.g., blueberry, salmonberry, devilsclub [*Oplopanax horridus*] in summer) and especially forbs, which as a group have high dry matter digestibility, are so important to deer. Total understory biomass of current annual growth is seldom a sufficient measure of habitat quality for deer because it most likely (about 80 percent probability in the TWYGS experiments) is composed of too much low-digestibility forage.

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Oval-leaf blueberry (*V. ovalifolium*), a very common and often dominant shrub, illustrates the important tradeoffs among limiting factors. High nutritional requirements for lactation make summer a potentially stressful time in terms of both protein and energy requirements (Parker et al. 1999). As an understory dominant, oval-leaf blueberry often composes much of the available food resources, both within stands and across landscapes. The nutritional quality of its leaves, however, is very different in sunny habitats versus shady forest understories: digestible protein concentrations are lower and dry matter digestibility is greater in sun-grown than shade-grown habitats (Hanley et al. 1992, McArthur et al. 1993, Rose 1989, Van Horne et al. 1988), primarily because of high concentrations of both tannins (reducing protein digestion) and starches (increasing dry matter digestibility) in the sun-grown leaves (Rose 1989, Van Horne et al. 1988). Therefore, although oval-leaf blueberry contributes significantly to the digestible protein component of deer diets in shady forests and very little to the digestible protein component in sunny habitats, its more important role in the overall landscape during summer is its contribution to the digestible energy of diets from sunny habitats. Summer protein requirements in sunny habitats and summer energy requirements in shady forests are met by forages other than oval-leaf blueberry. Thus, oval-leaf blueberry fulfills different dietary roles in different habitats but is not sufficient without other forages. This is an example of the importance of variety both in forages and in habitats for deer.

Protein requirements for deer are relatively low in winter and unlikely to be limiting then, while dry matter digestibility of winter forages (and, therefore, digestible energy) is low and very likely to be limiting in winter, especially when snow is on the ground (Hanley and McKendrick 1985, Parker et al. 1999). Blueberry twigs are the most nutritious common browse forage for deer in winter, yet they only marginally meet the digestible energy requirement then (e.g., see table 1 and appendix 2 in Hanley et al. 2012). That is why the evergreen forbs, with digestible energy concentrations well above required levels, are so important in winter; by mixing evergreen forbs with blueberry twigs in the diet, a much greater proportion

of the available twigs can be included in the FRESH solution set (suitable food supply). The relatively high availability of evergreen forbs in snow-free winter habitats was the driving force behind total forage biomass being the limiting factor in all 29 percent of the snow-free cases that were biomass limited in the TWYGS experiments (all 69 of the 234 cases for snow depth of 0 cm, table 11). However, our analyses assumed that evergreen forbs maintained 100 percent of their summer availability in winter. If that is not true, then our winter snow-free habitat values would be lower, and dry matter digestibility would be the dominant limiting factor even more strongly than we have concluded.

There was no effect of alder-planting treatments in Experiment I, but the various kinds of thinning treatments in Experiments II through IV increased total understory biomass by 3.4 to 5.1 times that of corresponding untreated controls.

Patterns Across Experiments—Vegetation

The experimental design of the TWYGS study was not intended for making statistical comparisons across experiments; however, differences in responses among experiments were large, and general patterns are clearly evident. Understory vegetation of the untreated controls decreased sharply with advancing stand age, with total understory biomass of Experiment IV (>35 years old) being only about 5 percent of that of Experiment I (1 to 5 years old) (47 versus 1022 kg/ha; fig. 1), which is exactly the pattern to be expected for postlogging secondary succession in this region (Alaback 1982). There was no effect of alder-planting treatments in Experiment I, but the various kinds of thinning treatments in Experiments II through IV increased total understory biomass by 3.4 to 5.1 times that of corresponding untreated controls. Although the relative response to silviculture treatment (treatment:control) was greater in the older age classes (3.4:1 versus 5.1:1 versus 4.9:1 for Experiments II, III, and IV, respectively), the decreasing total biomass with advancing stand age resulted in absolute responses being much greater in younger stands than in older stands (887, 385, 231 kg/ha for Experiments II, III, and IV, respectively) (fig. 1). Across all experiments and treatments, shrubs dominated the understory vegetation, and understory composition (proportion of biomass comprised of forbs, ferns, shrubs, etc.) did not differ much between silviculture treatments and untreated controls. Importantly for deer habitat, forbs remained a significant component of all understory plant communities, whether stands had been treated or not–they comprised about 9 to 21 percent of the total current annual growth across all treatments (fig. 1), although ferns tended to be more abundant than forbs throughout.

For perspective, the total understory biomass of current annual growth and its proportional distribution within 31 stands of the most common community types ("Vaal-Coca" and "Vaal-Lyam") of old-growth forest on Admiralty and Prince of Wales Islands, southeast Alaska, was 353 kg/ha, of which 31 percent was forbs, 9

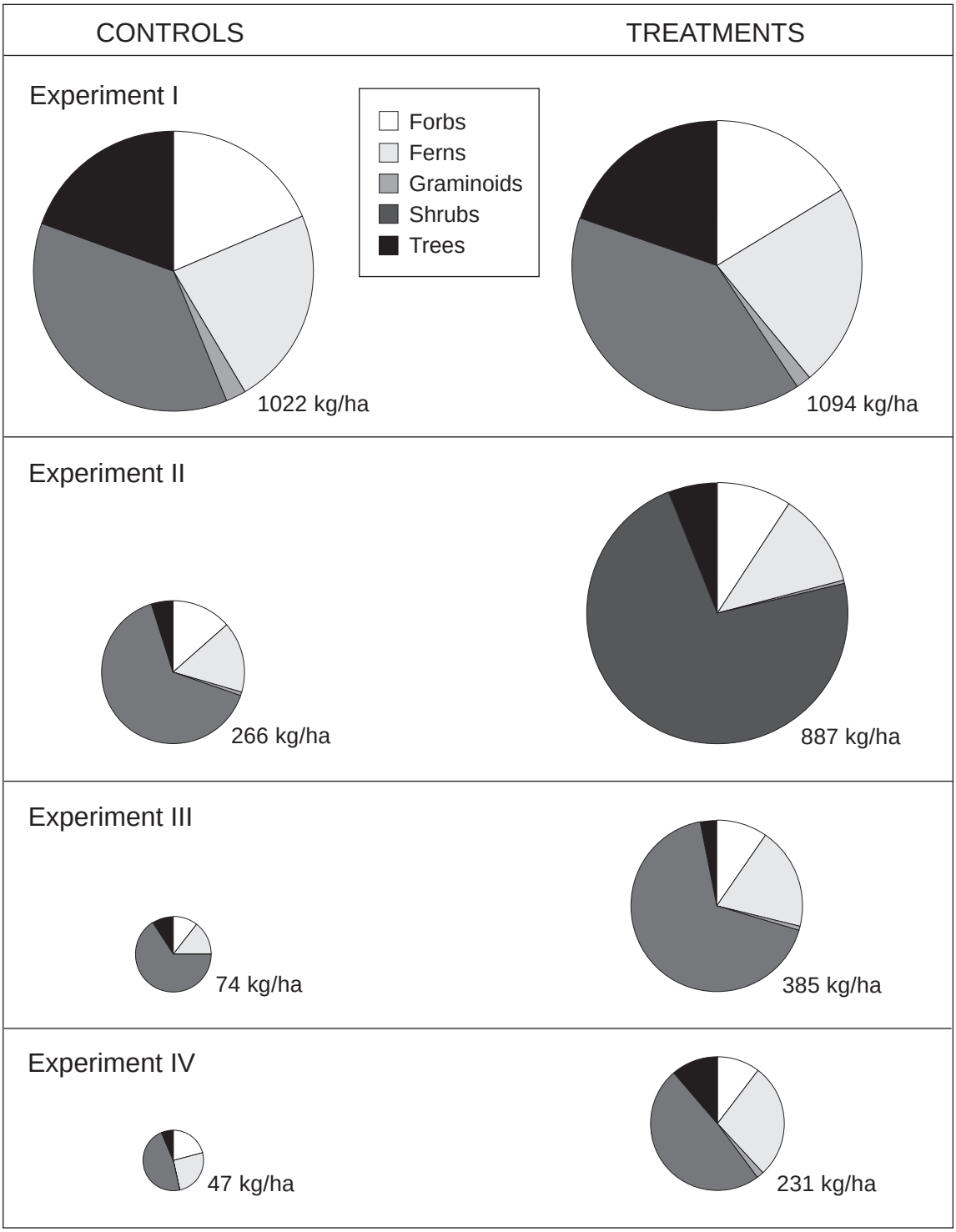

Figure 1—Total biomass (ovendry kg/ha) of current annual growth of understory vegetation and its proportional distribution among forbs, ferns, graminoids, shrubs, and trees in each of the four experiments, shown separately for untreated controls and pooled across all silviculture treatments within each experiment. Circles are proportional to total biomass.

percent ferns, <1 percent graminoids, 49 percent shrubs, and 11 percent tree seedlings (Hanley and Brady 1997). Depending on stand age and treatment, our young-growth stands tended to have more ferns (12 to 28 percent) and fewer forbs (9 to 21 percent) than those old-growth stands.

A comparison of biomass of western hemlock and Sitka spruce within the understory vegetation provides an indication of evidence for or against the potential "hemlock flush" that might be expected in response to thinning young-growth stands (Deal and Farr 1994, Tappeiner and Alaback 1989), as western hemlock was the species reported to exhibit the response. Stands in Experiment I were too young and were not thinned, but the high biomass of western hemlock relative to Sitka spruce occurred in virtually all of the thinning treatments of Experiments II through IV, whereas that pattern did not occur in the untreated controls (table 12).

Table 12—Biomass (ovendry, in kilograms per hectare) of current annual growth of western hemlock (TSHE) and Sitka spruce (PISI) within the understory vegetation in each treatment of Experiments I through IV when sampled posttreatment

Experiment/treatment	Ovendry biomass	
	TSHE	PISI
	Kilograms per hectare	
Experiment I (1 to 5 years old)		
Untreated controls	62.0	55.5
Red alder at 50 trees per hectare	63.4	70.6
Red alder at 200 trees per hectare	63.4	85.5
Experiment II (15 to 25 years old)		
Untreated controls	2.3	8.9
Thinned to 549 trees per hectare	29.5	3.2
Thinned to 331 trees per hectare	44.9	20.1
Experiment III (25 to 35 years old)		
Untreated controls	4.8	2.0
Thinning alone	10.1	0.4
Thinning with 25 percent pruning	11.2	5.1
Thinning with 50 percent pruning	3.9	2.4
Experiment IV (>35 years old)		
Untreated controls	0.5	2.3
Conventional thinning	28.4	4.4
Thinning with 1.5-m bucking	12.7	2.7
Thinning with 4.6-m bucking	26.6	3.7
Thinning by girdling	14.6	2.8

Although four to five years posttreatment is too early to judge the fate of understory hemlock, results from Experiments II through IV will likely be telling in years ahead.

Patterns Across Experiments—Deer Habitat Values

Patterns in deer habitat values (deer days/ha) closely paralleled the patterns in understory biomass, with both summer and winter values greatest in the youngest stands (Experiment I) and decreasing through Experiment IV (figs. 2 and 3). Similarly, all silviculture treatments in Experiments II through IV significantly exceeded their corresponding untreated controls in summer and in all but two treatments of Experiment IV in winter. Although among-treatment differences were apparent in Experiments II and III in summer, very few differences (other than with controls) were evident in winter. For perspective, we also calculated summer and winter habitat values for two sets of old-growth forest understory data: (1) 100 stands from the Accuracy Assessment Study of the Tongass Size-Density Model (Caouette and DeGayner 2005, 2008) from randomly selected stands throughout southeast Alaska (Tongass National Forest, unpublished data on file, Ketchikan and Juneau, Alaska) for the five mid-volume classes (classes 4N, 4S, 5H, 5N, 5S), and

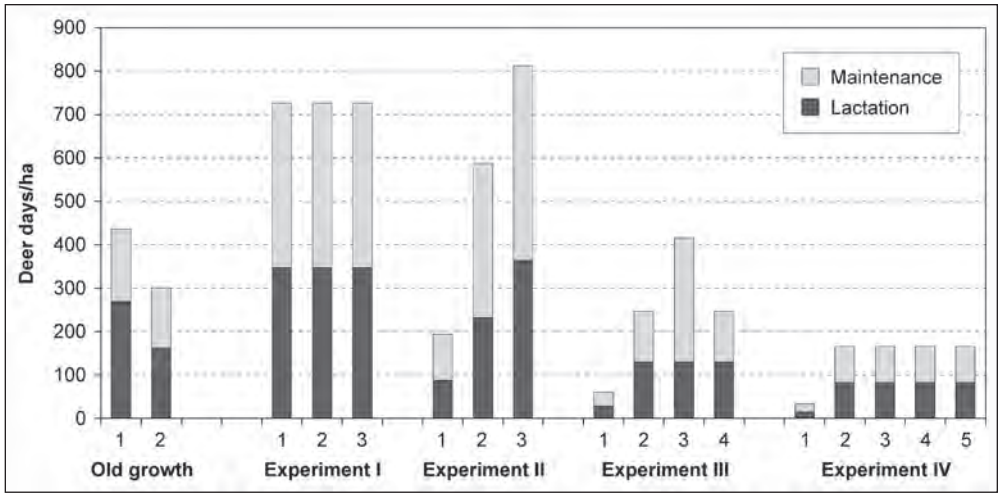

Figure 2—Summer deer habitat values (deer days/ha) for two levels of nutritional requirements (maintenance only and maintenance plus lactation) for all treatments within all four Tongass-Wide Young-Growth Studies (TWYGS) experiments and two data sets for old-growth forests (data set 1 = unpublished Tongass National Forest data for 100 stands of the Size Density Model; data set 2 = 31 stands from Hanley and Brady 1997 for "Vaal-Coca" and "Vaal-Lyam" community types). "Maintenance" values are the full height of the bar; "Lactation" values are the height of only the lower bar. Values of treatments that did not differ ($P > 0.05$) within an experiment have been pooled. TWYGS treatments are as follows: Experiment I (1 = untreated controls; 2 = red alder at 50 trees/ha; 3 = red alder at 200 trees/ha); Experiment II (1 = untreated controls; 2 = thinning to 549 trees/ha; 3 = thinning to 331 trees/ha); Experiment III (1 = untreated controls; 2 = thinning alone; 3 = thinning with 25 percent pruning; 4 = thinning with 50 percent pruning); Experiment IV (1 = untreated controls; 2 = conventional thinning; 3 = thinning with 1.5-m bucking; 4 = thinning with 4.6-m bucking; 5 = thinning by girdling).

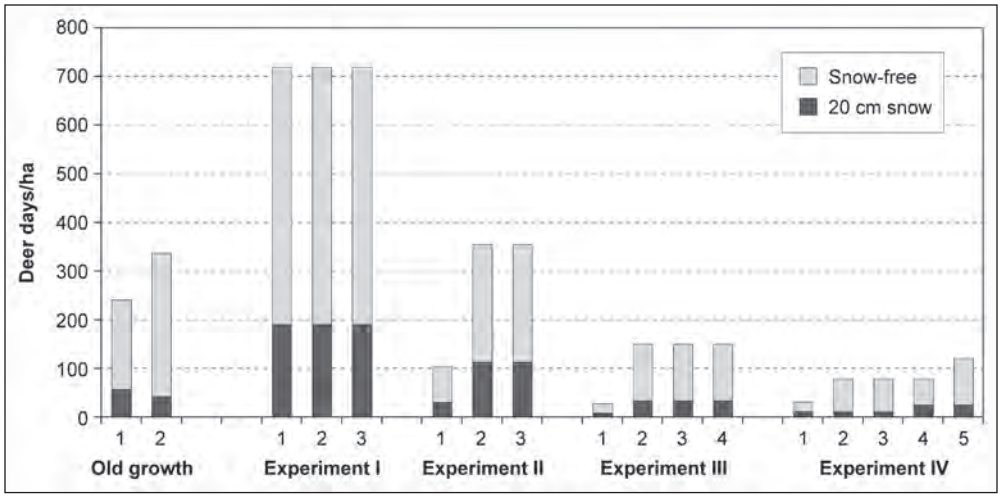

Figure 3—Winter deer habitat values (deer days/ha) for two levels of snow depths (0 cm and 20 cm) for all treatments within all four Tongass-Wide Young-Growth Studies (TWYGS) experiments and two data sets for old-growth forests (data set 1 = unpublished Tongass National Forest data for 100 stands of the Size Density Model; data set 2 = 31 stands from Hanley and Brady 1997 for "Vaal-Coca" and "Vaal-Lyam" community types). "Snow-free" values are the full height of the bar; "20 cm snow" values are the height of only the lower bar. Values of treatments that did not differ ($P > 0.05$) within an experiment have been pooled. TWYGS treatments are as follows: Experiment I (1 = untreated controls; 2 = red alder at 50 trees/ha; 3 = red alder at 200 trees/ha); Experiment II (1 = untreated controls; 2 = thinning to 549 trees/ha; 3 = thinning to 331 trees/ha); Experiment III (1 = untreated controls; 2 = thinning alone; 3 = thinning with 25 percent pruning; 4 = thinning with 50 percent pruning); Experiment IV (1 = untreated controls; 2 = conventional thinning; 3 = thinning with 1.5-m bucking; 4 = thinning with 4.6-m bucking; 5 = thinning by girdling).

The immediate effect of losing the ground-layer evergreen forbs within the first 10 cm of depth is always most pronounced, however, because loss of the forb component of the diet results in a sharp drop in digestible energy as only shrubs and trees remain available.

(2) 31 stands of the two most common community types ("Vaal-Coca" and "Vaal-Lyam") of old-growth forest on Admiralty and Prince of Wales Islands, southeast Alaska (Hanley and Brady 1997). Summer and winter values of old-growth forests exceeded those of untreated controls in all experiments except the young clearcuts of Experiment I, as expected, but thinning treatments exceeded or approached the values for old growth in summer for Experiments II and III (fig. 2) and in winter for Experiment II (fig. 3). The young clearcuts of Experiment I exceeded values for old growth in all of the summer and low-snow winter scenarios analyzed. Although the heaviest thinning treatment of Experiment II (331 trees/ha) yielded exceptionally high values for both summer scenarios (fig. 2), there was nothing exceptional about it in either winter scenario (fig. 3).

The drop in habitat values with increasing snow depth was common to all treatments of all experiments (fig. 4, for Experiments II through IV) and is to be expected with increased burial of forage by snow. The immediate effect of losing the ground-layer evergreen forbs within the first 10 cm of depth is always most pronounced, however, because loss of the forb component of the diet results in a sharp drop in digestible energy as only shrubs and trees remain available. Although

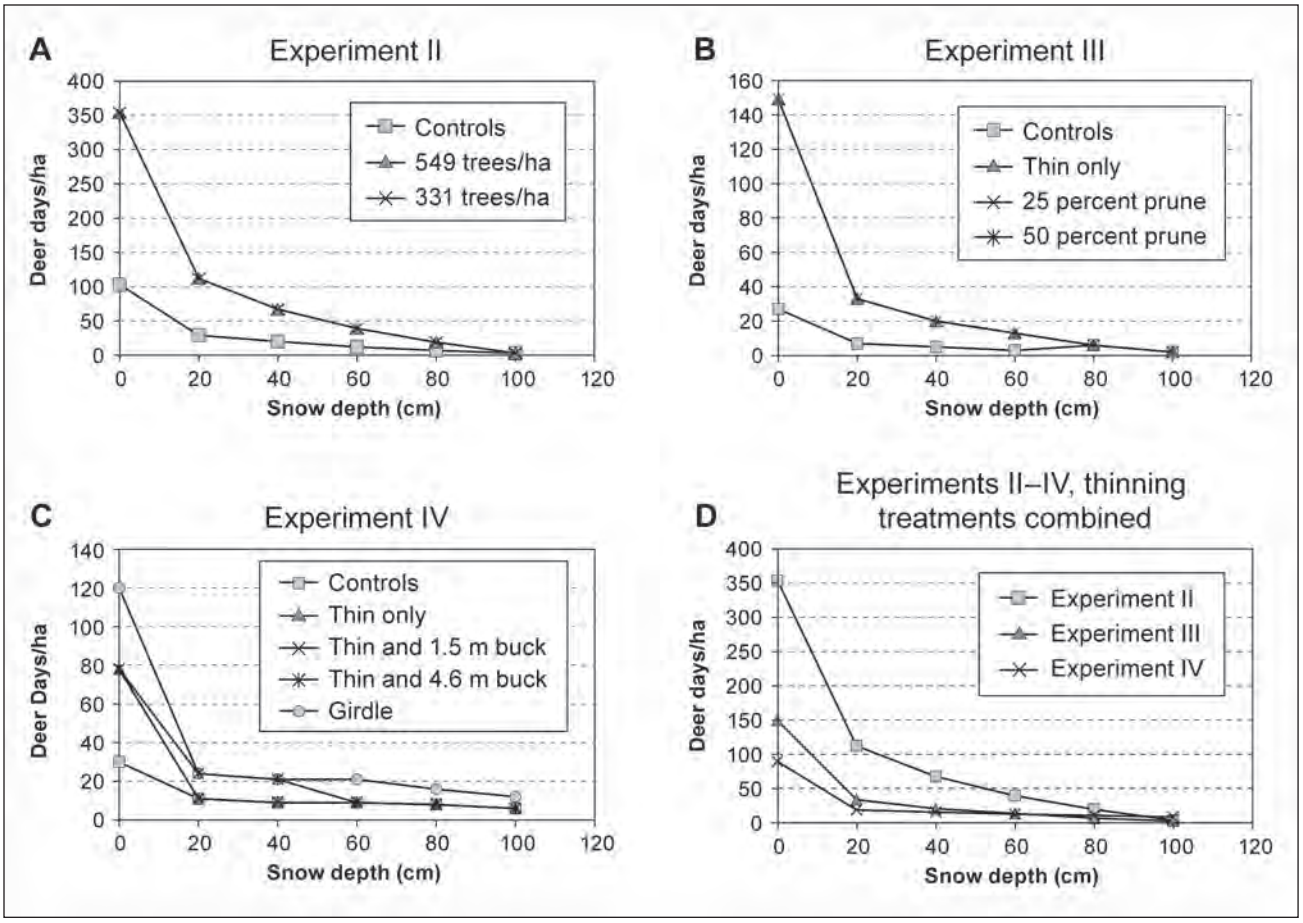

Figure 4—Deer habitat values (deer days/ha) of Tongass-Wide Young-Growth Studies (TWYGS) treatments in relation to increasing snow depth (centimeters in an open, treeless area): (a) Experiment II (untreated controls, thinning to 549 trees/ha, and thinning to 331 trees/ha), (b) Experiment III (untreated controls, thinning only, thinning with 25 percent pruning, and thinning with 50 percent pruning), (c) Experiment IV (untreated controls, conventional thinning, thinning and bucking slash to 1.5-m lengths, thinning and bucking slash to 4.6-m lengths, and thinning by girdling), and (d) all silviculture treatments (exclusive of controls) combined for each experiment. In (a) through (c), values that did not differ between treatments at a given snow depth have been pooled.

the general pattern of silviculture treatments being significantly greater than the untreated controls, and mostly similar to one another within each experiment, repeated in all of thinning Experiments II through IV (figs. 4a through 4c), the magnitudes of the responses differed greatly among experiments, declining with advancing age of the stands (fig. 4d). In both summer (fig. 2) and winter at all snow depths less than 60 to 80 cm (fig. 4), silviculture treatments increased deer habitat value, and the increases were greater with younger stand ages, but treatment effects decreased relative to controls with increasing snow depth. Actual values of dense shrubby and slash-filled habitats might be even lower than indicated by their forages alone, especially with increasing snow depth (see discussion above of "Snow Depth and Its Interaction With Shrubs and Slash").

Management Implications

The TWYGS experiments are the most widespread, comprehensive, and strongly replicated study of young-growth forest management and its effects on black-tailed deer habitat ever conducted in southeast Alaska, but they are not the first. Studies of precommercial thinning (Cole et al. 2010), "commercial" thinning (Zaborske et al. 2002), canopy-gap thinning (Alaback, unpublished report),[9] and even red alder as an alternative pathway of secondary succession (Hanley 2005, Hanley et al. 2006) have been conducted and evaluated with the FRESH model for their implications for deer habitat. Although a long-term study of the effects of pruning on tree growth and wood quality was initiated in the early 1990s (Petruncio 1994), its effects on understory vegetation have not been quantified, so the TWYGS Experiment III is the first analysis of the effects on deer habitat of pruning in the region, and the TWYGS Experiment IV is the first of any kind of study of the effects of thinning by girdling in southeast Alaska. Taken together, all these studies are beginning to develop a scientific basis for managing young-growth forests for Sitka black-tailed deer.

Surprisingly, quantification of species-specific biomass of current annual growth (and plant part) in young clearcuts has seldom been done in southeast Alaska. Aside from the TWYGS Experiment I, the only other study we know of was that by Sealaska Corporation in its Port Frederick lands, northeastern Chichagof Island, as part of an early use of the FRESH model (data collected by R. Johnson of ABR, Inc., under contract with Sealaska Corporation, Juneau, Alaska, unpublished but available on the FRESH-Deer Web site, http://cervid.uaa.alaska.edu/deer/Home.aspx, with permission from R. Wolfe, Sealaska Corp.). The Sealaska data are from five stands 3 to 4 years old and seven stands 6 to 10 years old. Mean habitat values across all 12 stands for the same two summer and two winter scenarios we have analyzed were the following (deer days/ha, mean $\pm$ standard error): summer maintenance only, 2,766 $\pm$ 505; summer lactation, 1,094 $\pm$ 195; winter with 0 cm snow, 1,483 $\pm$ 278; winter with 20 cm snow, 275 $\pm$ 75. Those values are much greater than ours from Experiment I (table 3)—about 3.5 times greater in summer but only about 2 times greater in snow-free winter and 1.5 times greater in winter with 20 cm of snow. Sealaska vegetation included more fireweed (*Epilobium angustifolium*), bunchberry dogwood, and oval-leaf blueberry. Both fireweed

[9] Paul Alaback. An evaluation of canopy gaps in restoring wildlife habitat in second growth forests of southeastern Alaska. Unpublished final report to the Tongass National Forest, Craig and Thorne Bay Ranger Districts, Craig and Thorne Bay, Alaska, dated February 20, 2010. 32 p.

and blueberry contribute to summer habitat values, and bunchberry dogwood is very important in snow-free winter conditions. The relatively high abundance of fireweed in the Sealaska data from the Port Frederick area was most likely a local site effect, as the geographic distribution of fireweed in southeast Alaska is spotty (Hultén 1968). On the other hand, the relatively lower abundance of blueberry and bunchberry dogwood in our data may have been a result of overall higher levels of herbivory by deer at our study sites, as both species are highly preferred by deer, and oval-leaf blueberry is known to decrease in abundance with deer browsing pressure (Hanley 1987). Within our study sites, oval-leaf blueberry plants that were lightly browsed weighed about 3.0 (leaves) to 3.9 (twigs) times more than heavily browsed plants of the same species per unit of canopy coverage (app. 2, Experiment I). Regardless of the variation between and within both data sets, however, it is clear that young clearcuts provide very high amounts of relatively high-quality food for deer in both summer and snow-free winter conditions throughout the region. It is with the closing of their young conifer canopies that their value as habitat drops sharply.

Effects of precommercial thinning of 16- to 18-year-old western hemlock-Sitka spruce stands were studied in seven replicated sites on Prince of Wales and Long Islands, southeast Alaska, by Cole et al. (2010). Treatments were the following: untreated controls, and thinning to 750, 500, 370, and 250 trees/ha. Cole et al. quantified understory vegetation immediately before treatment and 2, 4, and 7 years posttreatment, thereby providing an understanding of the dynamics of change in response to thinning. The Cole et al. results clearly indicated a peak in understory biomass occurring at about 4 years posttreatment, with forbs peaking at about 3 years, and shrubs slowly declining by 7 years posttreatment. Although the Cole et al. treatments included both wider and narrower spacing than did our thinning in Experiment II, the among-site variation and fewer replicates resulted in no significant differences among the Cole et al. treatment effects (other than all thinnings yielding significantly more understory than the untreated controls). Deer habitat values paralleled the pattern in understory dynamics, with all thinnings yielding significantly higher values than those of untreated controls (by about twice as much at year 7 posttreatment) yet not differing among one another. Habitat values of the thinning treatments at 7 years posttreatment for the four seasonal scenarios we have analyzed were the following (deer days/ha, mean $\pm$ standard error): summer maintenance only, 818 $\pm$ 177; summer lactation, 344 $\pm$ 85; winter snow-free, 390 $\pm$ 156; winter 20 cm snow, 253 $\pm$ 118. Those results are similar to the TWYGS Experiment II results for the widest spacing (331 trees/ha, table 5), except that for the winter with 20 cm of snow they were about twice as great as those for the TWYGS

treatments. The latter effect is directly related to the Cole et al. vegetation having about twice as much biomass of oval-leaf blueberry twigs (204 + 91 kg/ha; Cole et al. 2010: table 3) as that of the TWYGS thinnings (table 4). The pattern of stand dynamics in the Cole et al. data indicate that the effects of precommercial thinning within the age class of our Experiment II (15 to 25 years) are likely to be relatively short-lived before they decline with increasing conifer crown closure. Precommercial thinning may extend the high habitat values of young clearcuts into an advancing age of young-growth forest, but the stands will likely need further treatments if high habitat values are to be maintained. Results from our Experiment III indicate that pruning combined with thinning may be quite useful as such a secondary treatment, as Experiment III thinnings increased deer habitat values by about 4 to 6 times those of untreated controls (table 7), even though treatments were applied to stands that had never been treated previously and had already nearly attained conifer crown closure by age 25 to 35 years. Their effect should be expected to be much greater if applied to stands that have already been precommercially thinned earlier. Subsequent rounds of monitoring the Experiment III responses will be especially helpful regarding how long their effects might carry into the young forests' dynamics.

The relatively high rate of failure in many girdled stands emphasizes the importance of careful contract administration when using girdling as a management tool. When girdling is done by chainsaw, too deep a cut leaves the tree with too small an intact bole to sustain wind or snow loads.

For stands that have not been thinned before reaching the relatively large tree sizes typical of ages greater than 35 years, our results from Experiment IV indicate that thinning by girdling might be an effective treatment (table 9). Although those results are for only 4 years posttreatment, they are encouraging in that girdling had already increased deer habitat values by about 4 to 6 times those of untreated controls. Conventional thinning with or without bucking of slash was almost as effective as girdling, but thinning such large trees produces very large sizes and amounts of slash. The girdling results are encouraging, but they also are disconcerting in that we have no idea why they occurred (other than their greater response of oval-leaf blueberry), especially given the complete lack of relation between girdling failure and deer habitat values (table 10). The relatively high rate of failure in many girdled stands emphasizes the importance of careful contract administration when using girdling as a management tool. When girdling is done by chainsaw, too deep a cut leaves the tree with too small an intact bole to sustain wind or snow loads. Experiment IV already has clearly shown the consequences of that.

Land managers have had interest in thinning stands older than those of Experiment IV since at least the mid-1980s when the Tongass National Forest initiated a study of "commercial thinning" called the Second-Growth Management Area Demonstration Project (Zaborske et al. 2002). Strictly speaking, true commercial

thinning (selling the thinned trees at a profit) is unlikely in southeast Alaska (Crone 2005), but thinning of such older, large-treed stands might nevertheless be justifiable for other purposes such as wildlife habitat restoration in certain areas. Stands in the Second-Growth Management study were 42 to 95 years old when treated in 1984 and 1985. Treatments included untreated controls, individual tree selection (even spacing to from 173 to 269 trees/ha), strip thinning (removing all trees within alternating strips 6.1 m wide), and a combination of strip and individual tree selection treatments (thinning included within the leave strips). The study was unevenly replicated at only five sites, so results were limited accordingly. Understory vegetation was measured only once, 13 to 14 years posttreatment, but the data strongly showed two major results: (1) understories of both strip-thinning treatments were strongly dominated by western hemlock seedlings and saplings, which appeared to be thriving at the time of sampling, and (2) the individual tree selection treatment yielded surprisingly favorable results (compared with untreated controls) in terms of deer days/ha when analyzed with the FRESH model.

Although results were discussed by both Zaborske et al. (2002) and Hanley (2005), neither included an analysis of winter habitat values. The original, species-specific data are unpublished but available in the FRESH-Deer database on the FRESH Web site (http://cervid.uaa.alaska.edu/deer/Home.aspx). For the four sites with individual tree selection thinning, results for the four seasonal scenarios we've analyzed are the following (deer days/ha, mean $\pm$ standard error): summer maintenance only, 249 + 68; summer lactation, 52 + 18; winter 0 cm snow, 95 + 37; winter 20 cm snow, 2 + 2.[10] Values were about 3 to 6 times those of the untreated control stands for summer and twice their value in snow-free winter, but the commercial thinning treatments yielded virtually nothing for deer when snow buries the herb layer, because the shrub response at all four sites was mainly from salmonberry (a good summer forage but very poor winter forage) with very little blueberry in the shrub layer (three of the four sites had relatively high levels of immature, decumbent blueberry in the forb layer but virtually no mature, larger plants). The Second-Growth Management study also demonstrated a very strong site-specific response of hemlock seedlings within the individual tree selection treatments (Hanley 2005). Therefore, much remains uncertain about thinning in this age class, yet strongly replicated studies with trees of such size are very expensive.

[10] These summer values differ slightly from those reported in Zaborske et al. (2002) and Hanley (2005) because both of these authors used slightly different user-specified metabolic requirements for the deer and site-specific plant nutritional data rather than the regionwide nutritional database in FRESH-Deer.

Forest managers in southeast Alaska have also been interested in alternatives to conventional thinning, and in the mid-1980s through 1990s, the Tongass National Forest created nearly 600 "canopy gap" treatments throughout Prince of Wales Island alone (Alaback, unpublished report—see footnote 9). Canopy gap treatments in young-growth forest were intended to simulate environmental conditions of small (≤ 0.25-ha) gaps that occur naturally in old-growth forests as a function of wind or disease disturbance (Ott and Juday 2002). Although theoretical considerations might suggest that the newly created gaps would simply respond the same as small clearcuts (Hanley 2005) or fill rapidly with western hemlock regeneration (Deal and Farr 1994), Alaback (unpublished report) found highly favorable understory responses 20 years after treatment in his retrospective study of 76 canopy gap treatments on Prince of Wales Island. Alaback's treatment gaps were 12 to 45 m in diameter, and 30 were surrounded by thinned young-growth forest, while the other 46 were surrounded by untreated young growth. Stands were about 20 to 26 years old when treated. After 20 years posttreatment, Alaback found no significant differences in understory vegetation of thinned versus untreated young-growth forest, but the vegetation within the canopy gaps was significantly greater in species diversity and biomass than that of the surrounding forests. On average, biomass of the key evergreen forbs (*Coptis aspleniifolia, Cornus canadensis, Rubus pedatus, Tiarella trifoliata*) was about 9 times greater in the gaps than in the surrounding forests (15.9 versus 1.8 kg/ha), and that of oval-leaf blueberry was about 5 times greater (219.7 versus 45.4 kg/ha). Alaback used the FRESH model to calculate habitat values for black-tailed deer in two seasonal scenarios, summer with lactation requirements and winter with no snow. His results were as follows (deer days/ha, estimated from figs. 9 and 10 of Alaback, unpublished report): summer lactation, about 65 in gaps versus 15 in thinned forests; snow-free winter, about 45 in gaps versus 3 in thinned forests. Those are very low values of key species biomass and deer habitat value for the surrounding forest (compare with our untreated controls in tables 8 and 9 for similar age stands at time of sampling), especially for the biomass of evergreen forbs, but the significantly higher habitat values of the gaps in both summer and winter are important in that these effects are 20 years after treatment. The significantly greater biomass of blueberry in gaps than surrounding forest indicates that deer habitat values would be correspondingly greater there in winter with snow, too. However, perhaps most surprising of all is that Alaback found no evidence for any sort of western hemlock flush, as tree seedling density did not differ with treatment (was low throughout) or with gap size. The gaps were persisting in time, not filling in with conifers. Thus, he concluded that canopy gap treatments may offer surprisingly long-lasting and effective silviculture treatment for maintaining deer habitat

in young-growth forests of the region, and he developed a model for estimating long-term consequences for deer habitat relative to gap size and frequency on a landscape. The lack of tree response, however, becomes a cost to long-term timber production in a landscape filled with long-persisting gaps.

Silviculture treatments of young-growth forest for deer habitat may be able to take advantage of favorable summer habitat when red alder comprises substantial portions of a forested landscape. Red alder is common in young-growth forests of southeast Alaska where substantial areas of mineral soil were exposed during logging (Ruth and Harris 1979). Although that seldom occurs anymore with high-lead logging, mixed stands of western hemlock-Sitka spruce-red alder, originating in the 1950s through early 1970s, are common in the region. The understory of such stands has been shown to be strongly related to the alder, with significant correlations between percentage of red alder in the stand basal area and total understory biomass ($r^2 = 0.743$), net production of shrubs ($r^2 = 0.758$), and net production of herbs ($r^2 = 0.855$) (see Hanley et al. 2006 for a gradient of young-growth stands aged 38 to 42 years, ranging from 0 to 86 percent red alder by basal area). However, the main understory beneficiaries (or correlates) of the alder in the Hanley et al. (2006) study were salmonberry and deciduous forbs rather than blueberry and evergreen forbs, so although deer habitat value was positively correlated with the red alder in summer ($r^2 = 0.846$), it was not significantly correlated with the alder in winter ($r^2 = 0.246$). Similar patterns in understory biomass and composition have been reported for mixed alder-conifer young growth elsewhere in the region, too (Deal 1997, Hanley and Barnard 1998, Hanley and Hoel 1996). Deer habitat values for the two most strongly alder-dominated stands in the Hanley et al. (2006) study can be calculated from the original data in their table 3 (for stands with 64 and 86 percent red alder overstories), which we have done for the four seasonal scenarios we have been using for comparison (deer days/ha, mean $\pm$ standard error): summer maintenance, 127 $\pm$ 53; summer lactation, 91 $\pm$ 30; winter snow-free, 12 $\pm$ 2; winter 20 cm snow, 0 $\pm$ 0. Thus, the alder can provide much better deer habitat in summer than that of untreated pure conifer young growth (compare with our untreated controls in table 9) and somewhat better than that of Alaback's gap treatments of similar age (above), but the red alder understories are very poor deer habitat in winter, even in snow-free conditions. The greatest value of mixed alder-conifer stands for deer in southeast Alaska on highly disturbed sites, therefore, is in summer within a diverse landscape of other habitats suitable for meeting winter requirements. Future observations of Experiment I will assess whether this pattern exists on sites with less soil disturbance where alder was planted rather than regenerated naturally.

Empirical results from silviculture studies require experimentation and time. Unfortunately, there is no substitute for either.

Landscape diversity is a very important feature in any long-term habitat management plan for deer, as different forages and habitats provide critical food resources in mixed diets and at different times of the year and conditions in winter (Hanley 1993, 1996). The treatments of the TWYGS experiments, coupled with canopy gap treatments, "commercial" thinning in some cases, and even mixed red alder-conifer stands provide a diverse array of potential management practices for creating and maintaining a diverse, young-growth forest landscape of various stand ages, compositions, and structures. Forest managers already seem to understand this, as much interest today is focusing on silviculture treatments that vary in their application, from variable-spaced thinning to "skips and gaps" of treatments. However, our understanding of the long-term consequences of silvicultural manipulations in southeast Alaska, in terms of stand dynamics through time, is only in its infancy today. With the exception of the Cole et al. (2010) study, all studies reviewed above, including the TWYGS experiments, are descriptions of results at one point in time and need repeated measurements. Empirical results from silviculture studies require experimentation and time. Unfortunately, there is no substitute for either.

Conclusions

We consider the results presented in this report to be preliminary, representing just 4 to 8 years posttreatment. Subsequent responses through time and their patterns of temporal dynamics will be more valuable for planning and conducting long-term young-growth forest management programs. The comprehensive experimental approach of the TWYGS experiments, with replicated design and study sites widely scattered throughout southeast Alaska, will allow us to make robust conclusions about the effects of silviculture treatments on deer habitat quality in southeast Alaska. Meanwhile, we have gained several insights from this analysis of short-term results:

1. Although young clearcuts may be highly productive and provide suitable habitat in summer and snow-free conditions, they decline in value rapidly with conifer canopy closure. Without silvicultural manipulation, the resulting young-growth stands become very poor, sparse habitat for deer, as evidenced by the strongly decreasing values of the untreated control stands with increasing stand age in this study and in the studies we reviewed. Once stands have reached the canopy crown closure stage of structure, virtually any sort of disturbance to their overstory is better

than nothing (with the exception, perhaps, of strip thinning). All treatments in all TWYGS experiments and all other studies we reviewed yielded higher quality habitat for deer than that of their untreated, closed-canopy controls.

2. The understory response is stronger with earlier treatment (younger stand age), mostly because there is more understory vegetation already present to serve as nurse stock in younger stands.
3. Precommercial thinning may maintain the favorable conditions of young clearcuts for probably an additional decade beyond normal canopy crown closure, possibly much longer if repeated again and coupled with pruning. However, girdling of older stands also appears promising (very preliminary), as do "commercial thinning" and canopy-gap treatments, and even the red alder pathway of succession. Clearly, a variety of potential treatments exists, and they may be applied to a variety of stand ages. Given the importance of landscape heterogeneity to deer, such variety in silviculture may be the optimal way to proceed.
4. Future results will be especially insightful as red alders gain effect (Experiment 1), thinned stands begin to close (Experiment II) or not close (Experiment III), and older stands have time to respond more fully (Experiment IV). Quantification of western hemlock in the understory, and slash and its rate of decay, will be important features to monitor and compare.

A variety of potential treatments exists, and they may be applied to a variety of stand ages. Given the importance of landscape heterogeneity to deer, such variety in silviculture may be the optimal way to proceed.

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English Equivalents

When you know:	Multiply by:	To get:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Square meters (m^2)	10.76	Square feet
Grams (g)	0.0352	Ounces
Kilograms (kg)	2.205	Pounds
Kilojoules (kJ)	0.948	British Thermal Units (BTU)
Kilojoules per gram (kJ/g)	26.932	BTU/ounce
Kilojoules (kJ)	0.2388	Kilocalories
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

Tree Spacings and Densities

Distance between trees	Distance between trees	Number of trees per acre	Number of trees per hectare
Feet	*Meters*		
9	2.74	538	1329
12	3.66	303	749
14	4.27	222	549
15	4.57	194	479
16	4.88	170	420
17	5.18	151	373
18	5.49	134	331
20	6.10	109	269
23	7.01	82	203
25	7.62	70	173

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Appendix 1: Scientific and Common Names and Plant Codes of All Plant Species in This Report[1]

Species	Common name	Plant code
Actaea rubra (Aiton) Willd.	Red baneberry	ACRU2
Adiantum pedatum L.	Northern maidenhair	ADPE
Alectoria Ach. spp.	Witch's hair lichen	ALECT3
Alnus spp. Mill.	Alder	ALNUS
Angelica genuflexa Nutt.	Kneeling angelica	ANGE2
Andromeda polifolia L.	Bog rosemary	ANPO
Aquilegia formosa Fisch. ex DC.	Western columbine	AQFO
Aruncus sylvester Kostel. ex Maxim.	Bride's feathers	ARSY2
Athyrium filix-femina L. Roth	Common ladyfern	ATFI
Blechnum spicant (L.) Sm.	Deer fern	BLSP
Bromus sitchensis Trin.	Alaska brome	BRSI
Carex deweyana Schwein.	Dewey sedge	CADE9
Carex lyngbyei Hornem.	Lyngbye's sedge	CALY3
Carex mertensii Prescott ex Bong.	Merten's sedge	CAME6
Carex L. spp.	Sedge	CAREX
Chamaecyparis nootkatensis (D. Don) Spach	Alaska cedar	CHNO
Circaea alpina L.	Small enchanter's nightshade	CIAL
Claytonia sibirica L.	Siberian springbeauty	CLSI2
Coptis aspleniifolia Salisb.	Fernleaf goldthread	COAS
Coptis trifolia (L.) Salisb.	Threeleaf goldthread	COTR2
Cornus canadensis L.	Bunchberry dogwood	COCA13
Deschampsia cespitosa (L.) P. Beauv.	Tufted hairgrass	DECA18
Dryopteris dilatata auct. non (Hoffm.) A. Gray	Spreading woodfern	DREX2
Dryopteris expansa (C. Presl.) Fraser-Jenkins & Jermy	Spreading woodfern	DREX2
Drosera rotundifolia L.	Roundleaf sundew	DRRO
Elymus arenarius L.	Sand ryegrass	ELAR
Empetrum nigrum L.	Black crowberry	EMNI
Epilobium angustifolium L.	Fireweed	CHANA2
Epilobium ciliatum Raf.	Fringed willowherb	EPCI
Equisetum arvense L.	Field horsetail	EQAR
Equisetum pratense Ehrh.	Meadow horsetail	EQPR
Equisetum L. spp.	Horsetail	EQUIS
Fauria crista-galli (Menzies ex Hook.) Makino	Deercabbage	NECR2
Galium kamtschaticum Steller ex Schult. & Schult. f.	Boreal bedstraw	GAKA
Galium trifidum L.	Threepetal bedstraw	GATR2
Galium L. spp.	Bedstraw	GALIU
Gaultheria shallon Pursh	Salal	GASH
Gentiana douglasiana Bong.	Swamp gentian	GEDO
Geocaulon lividum (Richardson) Fernald	False toadflax	GELI2
Geranium erianthum DC.	Woolly geranium	GEER2
Geum macrophyllum Willd.	Largeleaf avens	GEMA4
Goodyera oblongifolia Raf.	Western rattlesnake plantain	GOOB2

Gymnocarpium dryopteris (L.) Newman	Western oakfern	GYDR
Heracleum lanatum Michx.	Common cowparsnip	HEMA80
Impatiens noli-tangere L.	Western touch-me-not	IMNO
Kalmia polifolia Wangenh.	Bog laurel	KAPO
Ledum palustre L.	Marsh Labrador tea	LEPA11
Listera cordata (L.) R. Br.	Heartleaf twayblade	LICO6
Listera R. Br. spp.	Twayblade	LISTE
Luzula parviflora (Ehrh.) Desv.	Smallflowered woodrush	LUPA4
Lysichiton americanus Hultén & H. St. John	American skunkcabbage	LYAM3
Maianthemum dilatatum (Alph. Wood) A. Nelson & J.F. Macbr.	False lily of the valley	MADI
Menziesia ferruginea Sm.	Rusty menziesia	MEFE
Mitella pentandra Hook.	Fivestamen miterwort	MIPE
Moehringia L. spp.	Sandwort	MOEHR
Moneses uniflora (L.) A. Gray	Single delight	MOUN2
Oplopanax horridus (Sm.) Miq.	Devilsclub	OPHO
Osmorhiza purpurea (J.M. Coult. & Rose) Suksd.	Purple sweetroot	OSPU
Osmorhiza Raf. spp.	Sweetroot	OSMOR
Oxycoccus microcarpos Turcz. ex Rupr.	Small cranberry	VAOX
Parnassia fimbriata K.D. Koenig	Fringed grass of Parnassus	PAFI3
Picea sitchensis (Bong.) Carrière	Sitka spruce	PISI
Platanthera dilatata (Pursh.) Lindl. ex Beck	Scentbottle	PLDI3
Polystichum braunii (Spenner) Fèe	Braun's hollyfern	POBR4
Potentilla L. spp.	Cinquefoil	POTEN
Prenanthes alata (Hook.) D. Dietr.	Western rattlesnakeroot	PRAL
Ranunculus L. spp.	Buttercup	RANUN
Ranunculus uncinatus D. Don ex G. Don	Woodland buttercup	RAUN
Ribes bracteosum Douglas ex Hook.	Stink currant	RIBR
Ribes laxiflorum Pursh.	Trailing black currant	RILA3
Ribes L. spp.	Currant	RIBES
Rubus chamaemorus L.	Cloudberry	RUCH
Rubus parviflorus Nutt	Thimbleberry	RUPA
Rubus pedatus Sm.	Strawberryleaf raspberry	RUPE
Rubus spectabilis Pursh.	Salmonberry	RUSP
Salix L. spp.	Willow	SALIX
Sambucus racemosa L.	Red elderberry	SARA2
Stellaria crispa Cham. & Schltdl.	Curled starwort	STCR2
Streptopus amplexifolius (L.) DC.	Claspleaf twistedstalk	STAM2
Streptopus Michx. spp.	Twistedstalk	STREP3
Streptopus roseus Michx.	Twistedstalk	STRO4
Streptopus streptopoides (Ledeb.) Frye & Rigg	Small twistedstalk	STST3
Thelypteris phegopteris (L.) Slosson	Long beechfern	PHCO24
Thuja plicata Donn ex D. Don	Western redcedar	THPL
Tiarella trifoliata L.	Threeleaf foamflower	TITR
Tolmiea menziesii (Pursh.) Torr. & A. Gray	Youth on age	TOME
Trientalis latifolia Hook.	Broadleaf starflower	TRBOL
Trisetum cernuum Trin.	Tall trisetum	TRCA21

Trisetum Pers. spp.	Oatgrass	TRISE
Tsuga heterophylla (Raf.) Sarg.	Western hemlock	TSHE
Tsuga mertensiana (Bong.) Carrière	Mountain hemlock	TSME
Urtica dioica L.	Stinging nettle	URDI
Vaccinium alaskaense Howell	Alaska blueberry	VAOV
Vaccinium cespitosum Michx.	Dwarf bilberry	VACA13
Vaccinium L. spp. evergreen	Blueberry	VACCI
Vaccinium ovalifolium Sm.	Oval-leaf blueberry	VAOV
Vaccinium parvifolium Sm.	Red huckleberry	VAPA
Vaccinium uliginosum L.	Bog blueberry	VAUL
Veratrum viride Aiton	Green false hellebore	VEVI
Viola glabella Nutt.	Pioneer violet	VIGL
Viola L. spp.	Violet	VIOLA
Other fern	Other fern	XFERN
Other forb	Other forb	XFORB
Other graminoid	Other graminoid	XGRAM
Other shrub	Other shrub leaf	XSHRUB

[1] Source of nomenclature is PLANTS Database, http://plants.usda.gov/ by genus; plant code = “symbol.”

Appendix 2: Canopy Cover-to-Biomass Regression Equations for Treatments in Each of the TWYGS Experiments[1]

Experiment 1 (1 to 5 years old, plus 8 years posttreatment)

Species code (see app. 1)	Plant part	Y-intercept	All treatments			
			Slope	N	P	r^2
ATFI	Whole	0	2.294	10	<0.001	0.927
ALRU2	Leaf	0	1.650	8	<0.001	0.869
ALRU2	Twig	0	1.087	8	<0.001	0.921
BLSP	Whole	0	1.608	13	<0.001	0.894
CHANA2	Whole	0	3.797	11	<0.001	0.795
CHNO[a]	CAG[b]	0	1.365	12	<0.001	0.855
COAS	Whole	0	0.469	11	<0.001	0.909
COCA13	Whole	0	0.579	11	<0.001	0.920
DREX2	Whole	0	0.583	10	<0.001	0.821
GASH	Leaf	0	0.951	10	<0.001	0.739
GASH	Twig	0	0.228	10	<0.001	0.764
GYDR	Whole	0	0.666	12	<0.001	0.756
LYAM3	Whole	0	1.721	12	<0.001	0.855
MADI	Whole	0	0.476	6	0.007	0.798
MEFE	Leaf	0	0.470	11	<0.001	0.762
MEFE	Twig	0	0.160	11	0.001	0.662
NECR2	Whole	0	0.905	12	<0.001	0.946
OPHO	Leaf	0	1.020	10	0.003	0.643
PHCO24	Whole	0	1.631	10	<0.001	0.940
PICOC	CAG	0	1.289	13	<0.001	0.863
PISI	CAG	0	1.447	11	<0.001	0.778
PTAQ	Whole	0	1.761	13	<0.001	0.871
RIBR	Leaf	0	0.544	9	0.002	0.738
RIBR	Twig	0	0.329	9	0.004	0.669
RILA	Leaf	0	0.355	11	<0.001	0.705
RILA	Twig	0	0.045	11	<0.001	0.765
RUPA	Leaf	0	0.753	11	<0.001	0.961
RUPA	Twig	0	0.454	11	<0.001	0.959
RUPE	Whole	0	0.400	12	<0.001	0.863
RUSP	Leaf	0	0.449	11	<0.001	0.931
RUSP	Twig	0	0.200	11	<0.001	0.865
SARA2	Leaf	0	0.818	9	<0.001	0.855
SARA2	Twig	0	0.529	9	0.001	0.763
TITR	Whole	0	0.502	9	<0.001	0.873
TSHE	CAG	0	0.303	11	0.005	0.563
VAOV[c]	Leaf	0	0.245	8	0.002	0.828
VAOV[c]	Twig	0	0.181	8	<0.001	0.858
VAOV[d]	Leaf	0	0.725	9	<0.001	0.859

VAOV[d]	Twig	0	0.699	9	0.002	0.732
VAPA	Leaf	0	0.678	10	<0.001	0.756
VAPA	Twig	0	1.056	10	<0.001	0.802

[1]All equations are of the form (biomass, ovendry g/m^2) = Y-intercept + slope x (percentage canopy cover).

[a] CHNO, *Chamaecyparis nootkatensis*, current USDA PLANTS name is *Cupressus nootkatensis*, CUNO.

[b] CAG = Current Annual Growth.

[c] Heavily browsed oval-leaf blueberry.

[d] Lightly browsed oval-leaf blueberry.

Experiment II (15 to 25 years old, plus 5 years posttreatment)

Species code (see app. 1)	Plant part	Y-intercept	Untreated control Slope	N	P	r^2
ATFI	Whole	0	1.171	5	<0.001	0.954
BLSP	Whole	0	0.521	3	<0.001	0.998
COAS	Whole	0	1.015	3	0.002	0.996
COCA13	Whole	0	0.912	3	<0.001	1.000
DREX2	Whole	0	0.338	6	<0.001	0.995
GYDR	Whole	0	0.309	5	0.002	0.938
MEFE	Leaf	0	0.677	3	0.001	0.997
RUPE	Whole	0	0.626	3	0.003	0.995
RUSP	Twig	0.137	0.435	5	0.266	0.382
RUSP	Leaf	0.072	0.545	5	0.325	0.315
TITR	Whole	0	0.379	5	<0.001	0.996
TSHE	CAG	0.113	0.059	7	0.462	0.560
VAOV	Twig	0	0.689	5	<0.001	0.992
VAOV	Leaf	0	0.689	5	<0.001	0.992

Experiment II (Continued)

Species code (see app. 1)	Plant part	Y-intercept	549 trees/ha Slope	N	P	r^2
ATFI	Whole	0	0.778	5	<0.001	0.984
BLSP	Whole	0	1.679	4	0.002	0.974
COAS	Whole	0.113	0.641	3	0.068	0.989
COCA13	Whole	0.873	0.403	5	0.061	0.740
DREX2	Whole	0.158	0.657	6	0.065	0.614
grass	Whole	0	1.131	5	0.007	0.868
GYDR	Whole	0.345	0.401	6	0.004	0.902
MEFE	Twig	0	0.233	6	0.002	0.871
MEFE	Leaf	0.184	1.325	6	0.002	0.933
OPHO	Leaf	0.819	0.156	3	0.797	0.098
PISI	CAG	0.111	0.235	6	0.132	0.472
RUPE	Whole	0	1.110	5	<0.001	0.970
RUSP	Twig	2.501	0.201	7	0.351	0.175
RUSP	Leaf	1.681	0.847	7	0.078	0.495
TITR	Whole	-0.004	0.656	3	0.035	0.931
TSHE	CAG	1.796	0.333	7	0.141	0.380

VAOV	Twig	-0.605	0.478	7	0.032	0.634
VAOV	Leaf	4.257	0.688	7	0.273	0.233

Experiment II (Continued)

Species code (see app. 1)	Plant part	331 trees/ha				
		Y-intercept	Slope	N	P	r^2
ATFI	Whole	0	1.379	6	<0.001	0.991
BLSP	Whole	0.262	1.377	6	0.001	0.943
COCA13	Whole	0	0.849	6	<0.001	0.998
DREX2	Whole	0	1.020	6	<0.001	0.985
EPAN	Whole	0.001	0.561	3	0.042	0.996
grass	Whole	0	1.067	6	<0.001	0.932
GYDR	Whole	0.358	0.235	6	0.069	0.605
LYAM3	Leaf	0	1.932	4	0.001	0.982
MADI	Whole	0	1.014	4	0.006	0.941
MEFE	Twig	0.218	0.122	7	0.023	0.677
MEFE	Leaf	0	1.040	7	<0.001	0.911
PISI	CAG	0.056	1.155	5	<0.001	0.984
RIBES	Twig	0	0.372	3	0.015	0.971
RIBES	Leaf	0	0.774	4	0.043	0.793
RUPE	Whole	0.267	0.549	6	0.001	0.942
RUSP	Twig	4.489	0.151	7	0.580	0.065
RUSP	Leaf	3.331	1.160	7	0.116	0.418
TITR	Whole	0.129	0.495	4	0.268	0.537
TSHE	CAG	0.476	0.922	7	0.111	0.428
VAOV	Twig	-1.561	0.796	7	0.012	0.748
VAOV	Leaf	4.804	0.944	7	0.153	0.361
VAPA	Twig	0	1.950	3	0.048	0.906
VAPA	Leaf	0	3.706	3	0.079	0.848

Experiment III (25 to 35 years old, plus 6 years posttreatment)

Species code (see app. 1)	Plant part	Untreated control				
		Y-intercept	Slope	N	P	r^2
ATFI	Whole	0	0.594	4	<0.001	0.988
BLSP	Whole	0	0.412	5	<0.001	0.955
COAS	Whole	0	0.439	4	<0.001	0.996
COCA13	Whole	0	1.033	4	<0.001	0.991
DREX2	Whole	0	0.368	5	<0.001	0.964
GYDR	Whole	0	0.300	4	0.001	0.982
MEFE	Twig	0	0.128	2	0.167	0.933
MEFE	Leaf	0	0.274	2	0.032	0.998
RUPE	Whole	0	0.257	4	0.005	0.950
RUSP	Twig	0	0.238	4	0.091	0.668
RUSP	Leaf	0	0.642	4	0.161	0.535
TITR	Whole	0	0.424	3	0.009	0.983
TSHE	CAG	0	0.254	3	0.009	0.983
VAOV	Twig	0	0.117	5	0.061	0.625
VAOV	Leaf	0	0.461	5	0.001	0.939

Experiment III (Continued)

Species code (see app. 1)	Plant part	Y-intercept	Thinning only			
			Slope	N	P	r^2
ATFI	Whole	0	0.704	5	<0.001	0.958
BLSP	Whole	0	1.041	5	0.008	0.854
COAS	Whole	0	0.430	5	0.011	0.838
COCA13	Whole	0	0.709	5	0.003	0.911
DREX2	Whole	0	0.462	5	<0.001	0.954
grass	Whole	0	1.753	3	0.022	0.956
GYDR	Whole	0	0.597	5	0.001	0.940
MEFE	Twig	0	0.059	4	0.063	0.735
MEFE	Leaf	0	0.317	4	0.039	0.804
OPHO	Leaf	0	0.830	3	0.070	0.865
PHCO24	Whole	0	0.638	3	0.035	0.931
PISI	CAG	0	0.336	4	0.063	0.737
RUPE	Whole	0	0.374	5	<0.001	0.974
RUSP	Twig	0	0.317	5	<0.001	0.972
RUSP	Leaf	0	0.703	5	0.001	0.944
TITR	Whole	0	0.593	5	0.004	0.904
TSHE	CAG	0	0.427	5	0.006	0.875
VAOV	Twig	0	0.243	5	0.031	0.727
VAOV	Leaf	0	0.604	5	0.003	0.918

Experiment III (continued)

Species code (see app. 1)	Plant part	Y-intercept	Thin and prune 25 percent of trees			
			Slope	N	P	r^2
ATFI	Whole	0	0.875	5	<0.001	0.977
BLSP	Whole	0	1.268	4	0.003	0.966
COAS	Whole	0	0.665	4	0.011	0.913
COCA13	Whole	0	0.768	5	<0.001	0.992
DREX2	Whole	0	0.912	5	0.009	0.848
grass	Whole	0	1.112	3	0.100	0.810
GYDR	Whole	0	0.676	5	<0.001	0.969
LYAM3	Leaf	0	1.630	3	0.015	0.970
MEFE	Twig	0	0.116	5	0.005	0.893
MEFE	Leaf	0	0.685	5	0.001	0.946
PISI	CAG	0	1.369	5	<0.001	0.973
RUPE	Whole	0	0.731	5	<0.001	0.974
RUSP	Twig	0	0.288	5	0.004	0.894
RUSP	Leaf	0	0.984	5	<0.001	0.954
TITR	Whole	0	0.683	4	<0.001	0.998
TSHE	CAG	0	0.485	5	0.015	0.809
VAOV	Twig	0	0.431	5	0.002	0.922
VAOV	Leaf	0	1.448	5	0.005	0.884

Experiment III (Continued)

Species code (see app. 1)	Plant part	Y-intercept	Thin and prune 50 percent of trees			
			Slope	N	P	r^2
ATFI	Whole	0	1.488	4	0.002	0.971
BLSP	Whole	0	1.867	4	<0.001	0.992
COAS	Whole	0	0.543	2	0.158	0.940
COCA13	Whole	0	0.615	5	<0.001	0.979
DREX2	Whole	0	0.549	5	<0.001	0.966
GYDR	Whole	0	0.608	5	<0.001	0.988
MEFE	Twig	0	0.104	2	0.106	0.973
MEFE	Leaf	0	0.750	2	0.069	0.988
PISI	CAG	0	0.635	3	0.070	0.865
RUPE	Whole	0	0.860	5	0.001	0.939
RUSP	Twig	0	0.252	5	<0.001	0.999
RUSP	Leaf	0	0.786	5	<0.001	0.971
TITR	Whole	0	0.745	4	0.015	0.896
TSHE	CAG	0	0.128	4	0.041	0.798
VAOV	Twig	0	0.197	5	<0.001	0.960
VAOV	Leaf	0	0.682	5	<0.001	0.994
VAPA	Twig	0	0.312	2	0.148	0.947
VAPA	Leaf	0	0.345	3	0.090	0.828

Experiment IV (>35 years old, plus 4 years posttreatment)

Species code (see app. 1)	Plant part	Y-intercept	Untreated control			
			Slope	N	P	r^2
ATFI	Whole	0	0.263	12	<0.001	0.946
COCA13	Whole	0	0.279	10	<0.001	0.904
DREX2	Whole	0	0.157	11	<0.001	0.750
GYDR	Whole	0	0.135	11	<0.001	0.848
LYAM3	Leaf	0	0.512	7	0.002	0.817
MEFE	Twig	0	0.017	9	0.008	0.606
MEFE	Leaf	0	0.135	9	<0.001	0.939
OPHO	Leaf	0	0.240	12	<0.001	0.918
PHCO24	Whole	0	0.484	11	<0.001	0.885
RIBR	Twig	0	0.196	9	0.001	0.756
RIBR	Leaf	0	0.301	9	<0.001	0.794
RILA	Twig	0	0.060	4	0.005	0.950
RILA	Leaf	0	0.399	4	0.006	0.943
RUSP	Twig	0	0.250	11	<0.001	0.817
RUSP	Leaf	0	0.407	11	<0.001	0.821
SARA2	Twig	0	0.234	9	<0.001	0.809
SARA2	Leaf	0	0.366	9	0.001	0.748
TITR	Whole	0	0.161	8	<0.001	0.848
TSHE	CAG	0	0.161	11	<0.001	0.831
VAOV	Twig	0	0.278	11	<0.001	0.716
VAOV	Leaf	0	0.262	11	<0.001	0.852

Experiment IV (Continued)

Species code (see app. 1)	Plant part	Y-intercept	Thin by felling only			
			Slope	N	P	r^2
ATFI	Whole	0	0.557	10	<0.001	0.800
COCA13	Whole	0	0.363	7	<0.001	0.938
DREX2	Whole	0	0.602	11	<0.001	0.837
GYDR	Whole	0	0.423	10	<0.001	0.862
LYAM3	Leaf	0	0.475	3	0.002	0.996
MEFE	Twig	0	0.152	9	<0.001	0.871
MEFE	Leaf	0	0.330	9	<0.001	0.909
OPHO	Leaf	0	0.492	9	<0.001	0.890
PHCO24	Whole	0	0.641	11	<0.001	0.784
RIBR	Twig	0	0.257	7	0.003	0.792
RIBR	Leaf	0	0.432	7	0.003	0.795
RILA	Twig	0	0.227	11	<0.001	0.902
RILA	Leaf	0	0.609	11	<0.001	0.887
RUSP	Twig	0	0.470	9	<0.001	0.779
RUSP	Leaf	0	0.637	9	<0.001	0.859
SARA2	Twig	0	0.814	11	<0.001	0.877
SARA2	Leaf	0	1.022	11	<0.001	0.878
TITR	Whole	0	0.414	10	<0.001	0.961
TSHE	CAG	0	0.667	11	<0.001	0.804
VAOV	Twig	0	0.460	10	<0.001	0.776
VAOV	Leaf	0	0.395	10	<0.001	0.820

Experiment IV (Continued)

Species code (see app. 1)	Plant part	Y-intercept	Thin and buck slash to 1.5 m			
			Slope	N	P	r^2
ATFI	Whole	0	0.462	7	<0.001	0.871
COCA13	Whole	0	0.490	8	<0.001	0.935
DREX2	Whole	0	0.169	11	<0.001	0.989
GYDR	Whole	0	0.528	11	<0.001	0.736
LYAM3	Leaf	0	1.056	10	<0.001	0.921
MEFE	Twig	0	0.790	8	<0.001	0.817
MEFE	Leaf	0	1.615	8	<0.001	0.874
OPHO	Leaf	0	0.680	8	<0.001	0.929
PHCO24	Whole	0	0.464	10	<0.001	0.918
RIBR	Twig	0	0.274	6	0.003	0.862
RIBR	Leaf	0	0.730	6	<0.001	0.947
RILA	Twig	0	0.372	4	0.040	0.801
RILA	Leaf	0	0.682	4	0.010	0.920
RUSP	Twig	0	0.260	9	0.018	0.525
RUSP	Leaf	0	0.640	9	<0.001	0.798
SARA2	Twig	0	0.287	7	<0.001	0.946
SARA2	Leaf	0	0.439	7	<0.001	0.860
TITR	Whole	0	0.246	7	0.005	0.765
TSHE	CAG	0	0.416	10	<0.001	0.769
VAOV	Twig	0	0.340	9	0.003	0.700
VAOV	Leaf	0	0.363	9	0.012	0.569

Experiment IV (Continued)

Species code (see app. 1)	Plant part	Y-intercept	Thin and buck slash to 4.6 m			
			Slope	N	P	r^2
ATFI	Whole	0	1.006	9	<0.001	0.767
COCA13	Whole	0	0.309	8	<0.001	0.915
DREX2	Whole	0	0.730	11	<0.001	0.819
GYDR	Whole	0	0.552	8	0.001	0.803
LYAM3	Leaf	0	0.717	6	<0.001	0.908
MEFE	Twig	0	0.273	9	0.132	0.261
MEFE	Leaf	0	0.421	7	0.002	0.833
OPHO	Leaf	0	0.386	10	<0.001	0.899
PHCO24	Whole	0	0.621	9	<0.001	0.804
RILA	Twig	0	0.211	10	0.001	0.720
RILA	Leaf	0	0.456	10	<0.001	0.978
RUSP	Twig	0	0.308	7	<0.001	0.898
RUSP	Leaf	0	0.574	7	0.003	0.799
SARA2	Twig	0	0.472	8	0.020	0.564
SARA2	Leaf	0	0.414	8	<0.001	0.863
TITR	Whole	0	0.236	8	<0.001	0.875
TSHE	CAG	0	0.651	9	<0.001	0.915
VAOV	Twig	0	0.701	9	0.017	0.530
VAOV	Leaf	0	0.569	9	<0.001	0.943

Experiment IV (Continued)

Species code (see app. 1)	Plant part	Y-intercept	Thin by girdling			
			Slope	N	P	r^2
ATFI	Whole	0	0.300	10	<0.001	0.886
COCA13	Whole	0	0.320	7	<0.001	0.963
DREX2	Whole	0	0.192	11	<0.001	0.767
GYDR	Whole	0	0.414	10	<0.001	0.981
LYAM3	Leaf	0	1.050	5	0.034	0.715
MEFE	Twig	0	0.259	8	0.008	0.662
MEFE	Leaf	0	0.662	8	<0.001	0.885
OPHO	Leaf	0	0.386	10	<0.001	0.899
PHCO24	Whole	0	0.472	9	<0.001	0.887
RIBR	Twig	0	0.252	9	<0.001	0.957
RIBR	Leaf	0	0.915	9	<0.001	0.868
RILA	Twig	0	0.233	8	<0.001	0.818
RILA	Leaf	0	0.532	8	0.001	0.797
RUSP	Twig	0	0.729	8	0.015	0.592
RUSP	Leaf	0	0.864	8	<0.001	0.841
SARA2	Twig	0	0.418	12	<0.001	0.698
SARA2	Leaf	0	0.369	12	<0.001	0.916
TITR	Whole	0	0.545	13	<0.001	0.865
TSHE	CAG	0	0.525	9	<0.001	0.827
VAOV	Twig	0	0.658	7	0.010	0.693
VAOV	Leaf	0	0.581	7	0.002	0.829

[1]All equations are of the form (biomass, ovendry g/m^2) = Y-intercept + slope x (percentage canopy cover).

Appendix 3: Species-Specific Results (Oven-dry Biomass in Kilograms Per Hectare, Mean and Standard Error) From All TWYGS Treatments by Experiment

Experiment I (1 to 5 years old, plus 8 years posttreatment)

Species	Plant part[a]	Untreated control		Alder at 50 trees/ha		Alder at 200 trees/ha	
		Mean	SE	Mean	SE	Mean	SE
Forbs:							
Aconitum delphiniifolium	W	2.08	1.86	<0.01	<0.01	—	—
Actaea rubra	W	1.86	1.86	0.11	0.11	—	—
Aruncus dioicus	W	—	—	7.39	6.35	6.44	6.44
Chamerion angustifolium[b]	W	8.92	4.23	7.62	4.60	13.93	7.57
Circaea alpina	W	<0.01	<0.01	0.01	0.01	0.08	0.07
Claytonia siberica	W	0.13	0.12	0.01	0.01	<0.01	<0.01
Coptis aspleniifolia	W	16.78	5.07	10.91	3.38	15.12	5.96
Cornus canadensis	W	73.75	13.35	58.87	12.39	60.30	12.11
Cornus suecica	W	0.50	0.26	0.15	0.10	0.44	0.24
Epilobium ciliatum	W	—	—	0.04	0.03	0.01	0.01
Equisetum arvense	W	—	—	0.42	0.38	0.01	0.01
Equisetum spp.	W	0.58	0.54	0.69	0.47	0.04	0.04
Galium spp.	W	0.05	0.04	0.01	0.01	0.02	0.01
Heracleum maximum	W	—	—	2.91	2.65	—	—
Lysichiton americanus	W	41.77	10.16	55.27	15.37	25.39	6.67
Maiathemum dilatatum	W	7.79	2.67	6.86	2.40	7.28	3.10
Nephrophyllidium crista-galli	W	6.19	4.17	4.37	1.94	2.49	1.64
Platanthera spp.	W	—	—	0.47	0.47	—	—
Prenanthes alba	W	0.10	0.07	0.12	0.07	0.12	0.08
Rubus pedatus	W	8.06	2.02	10.20	2.35	10.95	3.43
Sanguisorba canadensis	W	—	—	0.04	0.03	—	—
Streptopus amplexifolius	W	16.14	8.88	15.69	5.78	15.71	8.45
Streptopus spp.	W	1.58	0.77	2.19	1.44	1.59	0.96
Streptopus streptopoides	W	<0.01	<0.01	0.02	0.02	<.01	<.01
Tiarella trifoliata	W	5.40	1.11	6.18	2.15	3.81	1.20
Tolmiea menziesii	W	—	—	—	—	0.01	0.01
Trientalis europaea arctica	W	<0.01	<0.01	0.20	0.20	0.03	0.02
Viola glabella	W	0.03	0.02	<0.01	<0.01	<0.01	<0.01
Viola spp.	W	0.09	0.08	0.05	0.02	<0.01	<0.01
Total forbs		190.04	28.54	192.36	26.59	163.78	23.03
Ferns:							
Adiantum pedatum	W	0.05	0.04	0.67	0.51	1.59	0.94
Athyrium filix-femina	W	103.80	21.38	121.04	14.83	116.04	23.08
Blechnum spicant	W	73.83	14.80	59.41	15.56	62.55	15.26
Dryopteris expansa	W	12.67	3.88	10.21	3.75	11.46	4.52

Gymnocarpium drypoteris	W	23.42	3.33	25.49	5.23	21.32	4.28
Phegopteris connectilis	W	9.77	4.75	24.47	14.40	8.70	4.74
Pteridium aquilinum	W	8.53	7.54	15.38	10.22	19.09	15.03
Total ferns		233.55	26.03	254.62	30.82	240.75	31.47
Graminoids:							
Carex laeviculmis	W	—	—	1.89	1.89	—	—
Carex spp.	W	2.63	1.96	5.48	4.18	1.31	0.95
Juncus spp.	W	—	—	—	—	0.12	0.12
Luzula spp.	W	—	—	0.25	0.19	—	—
Unknown grass	W	21.26	13.97	22.85	9.31	4.91	2.27
Total graminoids		23.90	14.04	30.46	10.86	6.34	2.76
Shrubs:							
Gaultheria shallon	L	8.98	8.98	6.71	6.71	15.41	12.76
Gaultheria shallon	T	2.15	2.15	1.51	1.51	3.69	3.06
Ledum groenlandicum	L	—	—	4.04	3.59	4.38	3.08
Ledum groenlandicum	T	—	—	4.30	3.82	4.66	3.28
Linnaea borealis	W	0.13	0.11	0.31	0.27	2.87	2.12
Menziesia ferruginea	L	34.39	6.48	33.87	7.53	32.70	5.94
Menziesia ferruginea	T	11.70	2.20	11.53	2.56	11.13	2.02
Oplopanax horridium	L	9.65	3.18	26.95	10.10	25.21	8.86
Ribes spp.	L	0.94	0.62	0.71	0.49	0.73	0.49
Ribes spp.	T	0.12	0.08	0.09	0.06	0.09	0.06
Ribes bracteosum	L	0.56	0.34	0.19	0.14	0.81	0.57
Ribes bracteosum	T	0.34	0.21	0.12	0.09	0.49	0.35
Ribes lacustre	L	1.03	0.71	1.66	0.86	1.10	0.78
Ribes lacustre	T	0.13	0.09	0.21	0.11	1.10	0.78
Ribes laxiflorum	L	0.15	0.15	0.35	0.24	0.11	0.08
Ribes laxiflorum	T	0.02	0.02	0.04	0.03	0.01	0.01
Rubus parviflorus	L	2.04	1.07	2.06	1.44	1.86	1.10
Rubus parviflorus	T	1.23	0.64	1.24	0.87	1.12	0.66
Rubus spectabilis	L	21.44	6.04	19.97	7.13	22.04	4.31
Rubus spectabilis	T	9.56	2.69	8.91	3.18	9.83	1.92
Sambucus racemosa	L	1.02	0.42	2.71	1.07	0.55	0.25
Sambucus racemosa	T	0.66	0.27	1.76	0.69	0.36	0.16
Vaccinium caespitosum	W	—	—	—	—	0.20	0.20
Vaccinium ovalifolium	L	124.77	12.09	129.46	12.94	146.72	18.33
Vaccinium ovalifolium	T	120.43	11.67	124.96	12.49	141.62	17.69
Vaccinium spp. immature	W	2.06	1.19	3.21	1.33	5.62	2.05
Vaccinium oxycoccos	W	0.06	0.05	0.02	0.02	0.03	0.02
Vaccinium parvifolium	L	8.46	2.76	6.42	2.08	12.58	3.78
Vaccinium parvifolium	T	13.18	4.30	10.01	3.25	19.61	5.90
Vaccinium vitis-idaea	W	0.27	0.27	1.82	1.82	0.25	0.25
Total shrubs		375.47	22.12	404.74	26.00	460.70	35.66

Trees:							
Alnus rubra	L	5.47	5.47	4.63	2.28	16.38	7.15
Alnus rubra	T	3.60	3.60	3.05	1.50	10.79	4.71
Alnus viridis sinuata	L	—	—	0.30	0.30	—	—
Alnus viridis sinuata	T	—	—	0.20	0.20	—	—
Chamaecyparis nootkatensis	CAG	2.36	1.74	1.57	1.53	3.83	2.28
C. nootkatensis seedlings	W	5.25	2.64	2.83	1.86	2.06	1.30
Malus fusca	L	0.97	0.97	—	—	—	—
Malus fusca	T	0.64	0.64	—	—	—	—
Pinus contorta contorta	CAG	0.24	0.24	3.57	3.51	2.10	1.85
Pinus contorta contorta seedlings	W	0.27	0.27	1.92	1.75	2.87	2.81
Picea sitchensis	CAG	17.17	16.19	26.99	26.04	62.22	19.61
Picea sitchensis seedlings	W	38.34	11.24	43.57	10.83	23.23	6.75
Thuja plicata	CAG	9.15	6.24	6.42	3.92	8.96	4.36
Thuja plicata seedlings	W	16.97	6.54	10.30	3.80	10.28	5.04
Tsuga heterophylla	CAG	31.66	7.36	35.60	6.70	37.88	6.26
Tsuga heterophylla seedlings	W	30.36	3.93	27.80	4.16	25.56	3.56
Tsuga mertensiana	CAG	0.93	0.64	1.58	1.16	0.36	0.20
Tsuga mertensiana seedlings	W	1.26	0.77	1.00	0.67	0.02	0.02
Total trees		198.88	21.25	224.12	32.42	206.54	25.32
Total biomass (all species)		1021.96	40.26	1108.00	48.45	1080.05	63.32

[a] Plant parts: W = whole plant; L = leaf; T = twig; CAG = current annual growth (twigs and needles together).
[b] *Chamerion angustifolium* is *Epilobium angustifolium*.

Experiment II (15 to 25 years old, plus 5 years posttreatment)

Species	Plant part[a]	Untreated control		Thin to 549 trees/ha		Thin to 331 trees/ha	
		Mean	SE	Mean	SE	Mean	SE
Forbs:							
Caltha leptosepala	W	—	—	—	—	0.02	0.02
Chamerion angustifolium	W	—	—	—	—	0.09	0.08
Circaea alpina	W	0.73	0.73	0.02	0.02		
Clintonia uniflora	W	—	—	—	—	0.01	0.01
Coptis aspleniifolia	W	2.38	0.90	4.01	1.23	7.04	4.37
Cornus canadensis	W	10.05	3.45	24.83	4.30	47.26	15.49
Drosera rotundifolia	W	—	—	—	—	<0.01	<0.01
Galium spp.	W	—	—	—	—	0.01	0.01
Galium trifidum	W	0.02	0.02	—	—	0.06	0.04
Galium triflorum	W	—	—	—	—	<0.01	<0.01
Heracleum maximum	W	1.62	1.62	—	—	0.62	0.62
Linneaea borealis	W	—	—	0.12	0.12	0.07	0.05
Listera convallarioides	W	0.02	0.02	0.01	0.01	0.04	0.04
Listera cordata	W	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Lysichiton americanum	W	14.85	7.21	7.49	4.46	30.34	13.43

Maianthemum dilatatum	W	1.18	0.64	4.95	3.58	8.74	5.58
Moneses uniflora	W	0.01	0.01	0.05	0.04	0.16	0.15
Prenanthes alba	W	0.03	0.03	—	—	0.06	0.06
Ranunculus uncinatus	W	—	—	<0.01	<0.01	—	—
Rubus pedatus	W	1.99	0.64	8.47	1.59	8.99	2.36
Saxifragia mertensia	W	0.06	0.06	—	—	—	—
Stellaria calycantha	W	—	—	—	—	<0.01	<0.01
Stellaria crispa	W	—	—	—	—	<0.01	<0.01
Streptopus amplexifolius	W	1.02	0.43	0.92	0.67	0.76	0.49
Streptopus lanceolatus	W	—	—	—	—	0.01	0.01
Streptopus spp.	W	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Streptopus streptopoides	W	—	—	—	—	<0.01	<0.01
Tiarella trifoliata	W	1.69	0.45	4.11	2.54	3.88	1.09
Trientalis europa arctica	W	—	—	—	—	0.05	0.05
Vertrum viride	W	0.02	0.02	—	—	—	—
Viola glabella	W	0.08	0.08	—	—	0.19	0.13
Unknown forb	W	—	—	—	—	0.01	0.01
Total forbs		35.77	10.06	55.01	8.58	108.45	26.73
Ferns:							
Athyrium filix-femina	W	32.72	13.53	18.95	4.44	65.96	14.55
Blechnum spicant	W	1.77	1.13	11.73	4.39	10.63	4.43
Dryopteris expansa	W	4.04	1.26	30.68	5.67	44.01	12.52
Gymnocarpium drypoteris	W	3.67	1.08	12.95	2.80	10.45	1.63
Phegopteris connectilis	W	0.14	0.08	0.33	0.31	0.37	0.27
Polypodium glycyrrhiza	W	0.20	0.20	—	—	0.17	0.17
Polystichum munitum	W	—	—	1.24	1.24	0.25	0.25
Unknown fern	W	—	—	—	—	<0.01	<0.01
Total ferns		42.53	15.01	75.87	10.54	131.84	22.12
Graminoids:							
Carex spp.	W	1.73	1.73	0.31	0.18	1.23	0.78
Cymophyllus fraseri	W	—	—	0.01	0.01	0.02	0.02
Unknown grass	W	0.45	0.25	1.29	0.46	4.36	1.61
Total graminoids		2.18	1.96	1.61	0.56	5.62	1.73
Shrubs:							
Menziesia ferruginea	L	22.02	8.20	107.55	26.56	66.56	12.93
Menziesia ferruginea	T	7.58	2.82	18.63	4.66	9.88	1.57
Oplopanax horridus	L	8.15	2.43	11.27	3.71	8.60	2.27
Ribes spp.	L	0.03	0.03	1.25	0.85	2.47	1.44
Ribes spp.	T	0.01	0.01	0.57	0.38	1.19	0.69
Ribes bracteosum	L	2.21	2.02	0.31	0.31	2.41	1.39
Ribes bracteosum	T	1.00	0.92	0.14	0.14	1.09	0.63
Ribes lacustre	L	0.26	0.15	1.14	0.82	5.85	3.68
Ribes lacustre	T	0.12	0.07	0.51	0.37	2.65	1.67

Ribes laxiflorum	L	1.28	1.28	1.69	1.34	0.19	0.18
Ribes laxiflorum	T	0.58	0.58	0.77	0.61	0.09	0.08
Rubus parviflorus	L	—	—	0.18	0.12	0.92	0.90
Rubus parviflorus	T	—	—	0.08	0.06	0.42	0.41
Rubus spectabilis	L	20.04	8.89	103.19	16.13	193.43	23.61
Rubus spectabilis	T	16.76	7.11	44.19	4.55	65.73	3.07
Salix spp.	L	—	—	0.02	0.02	—	—
Salix spp.	T	—	—	0.01	0.01	—	—
Sambucus racemosa	L	0.33	0.31	0.92	0.65	3.36	2.04
Sambucus racemosa	T	0.15	0.14	0.42	0.29	1.52	0.92
Vaccinium caespitosum	L	0.26	0.26	—	—	—	—
Vaccinium caespitosum	T	0.12	0.12	—	—	—	—
Vaccinium ovalifolium	L	55.19	14.43	150.61	15.80	197.72	24.08
Vaccinium ovalifolium	T	26.26	6.87	69.12	11.00	110.57	20.30
Vaccinium oxycoccos	L	—	—	—	—	0.03	0.03
Vaccinium oxycoccos	T	—	—	—	—	0.03	0.03
Vaccinium parvifolium	L	6.25	3.97	31.50	13.72	33.70	11.47
Vaccinium parvifolium	T	3.29	2.09	16.58	7.22	17.73	6.04
Total shrubs		171.90	37.92	560.60	42.56	726.12	59.41
Trees:							
Alnus spp.	L	—	—	—	—	1.24	1.24
Alnus spp.	T	—	—	—	—	0.18	0.18
Alnus rubra	L	1.24	1.24	1.58	1.58	3.55	1.91
Alnus rubra	T	0.18	0.18	0.36	0.36	0.46	0.26
Alnus sinuata viridis	L	—	—	—	—	2.31	1.58
Alnus sinuata viridis	T	—	—	—	—	0.28	0.20
Chamaecyparis nootkatensis	CAG	0.08	0.08	—	—	0.29	0.17
Picea sitchensis	CAG	8.88	3.49	3.23	0.47	20.05	6.86
Thuja plicata	CAG	0.38	0.18	0.47	0.16	0.57	0.20
Tsuga heterophylla	CAG	2.34	0.60	29.45	3.71	44.91	11.57
Tsuga mertensiana	CAG	0.08	0.08	0.07	0.07	—	—
Total trees		13.18	4.10	35.16	4.89	73.84	17.55
Total biomass (all species)		265.57	58.89	728.28	53.07	1045.82	67.24

[a] Plant parts: W = whole plant; L = leaf; T = twig; CAG = current annual growth (twigs and needles together).
[b] *Chamerion angustifolium* is *Epilobium angustifolium*.

Experiment III (25 to 35 years old, plus 6 years posttreatment)

Species	Plant part[a]	Untreated control		Thinning alone		Thin and 25 percent prune		Thin and 50 percent prune	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Forbs:									
Actaea rubra	W	0.01	0.01	0.06	0.06	0.07	0.07	—	—
*Chamerion angustifolium**	W	—	—	0.08	0.05	—	—	0.01	0.01
Circaea alpina	W	0.19	0.18	0.08	0.05	0.17	0.09	<0.01	<0.01
Clintonia uniflora	W	0.18	0.13	0.65	0.39	0.19	0.12	0.55	0.35
Coptis aspleniifolia	W	0.44	0.24	1.98	1.43	2.10	0.85	2.84	1.43
Cornus canadensis	W	1.78	1.31	12.20	4.01	23.25	7.61	9.43	2.52
Epilobium ciliatum	W	—	—	0.01	0.01	—	—	0.03	0.03
Equisetum arvense	W	0.01	0.01	0.29	0.27	0.13	0.13	0.01	0.01
Galium spp.	W	—	—	—	—	0.05	0.05	<0.01	<0.01
Galium trifidum	W	—	—	—	—	0.02	0.02	0.02	0.02
Galium triflorum	W	—	—	—	—	0.03	0.02	0.02	0.02
Heracleum maximum	W	—	—	—	—	0.67	0.67	—	—
Linneaea borealis	W	—	—	—	—	0.29	0.29	—	—
Listera convallarioides	W	—	—	—	—	—	—	0.01	0.01
Listera cordata	W	<0.01	<0.01	—	—	<0.01	<0.01	<0.01	<0.01
Lysichiton americanum	W	1.99	1.64	5.55	3.42	15.57	6.15	1.36	0.79
Maianthemum dilatatum	W	0.10	0.05	4.04	1.81	0.87	0.46	1.17	0.60
Moneses uniflora	W	0.16	0.14	0.05	0.04	0.02	0.01	0.09	0.05
Orthilia secunda	W	—	—	—	—	0.03	0.03	0.01	0.01
Platanthera stricta	W	—	—	0.03	0.03	0.01	0.01	—	—
Prenanthes alba	W	0.09	0.09	0.21	0.21	0.29	0.24	0.12	0.11
Ranunculus unci0tus	W	<0.01	<0.01	—	—	—	—	<0.01	<0.01
Rubus pedatus	W	0.31	0.21	2.58	1.07	5.33	1.52	6.16	2.21
Stellaria crispa	W	—	—	<0.01	<0.01	0.01	0.01	—	—
Streptopus amplexifolius	W	—	—	0.20	0.12	0.12	0.07	0.40	0.26
Streptopus lanceolatus	W	0.63	0.63	0.99	0.98	0.72	0.71	1.08	1.08
Streptopus spp.	W	0.07	0.05	0.28	0.28	0.01	0.01	0.43	0.43
Streptopus streptopoides	W	—	—	—	—	—	—	0.04	0.03
Tiarella trifoliata	W	1.58	0.81	—	—	4.36	1.65	2.95	0.98
Tiarella trifoliata unifoliata	W	—	—	0.03	0.03	0.10	0.10	0.04	0.04
Viola glabella	W	—	—	—	—	0.58	0.43	—	—

Urtica diocia	W	—	—	—	—	—	—	0.01	0.01
Unknown orchid	W	—	—	—	—	—	—	<0.01	<0.01
Unknown forb	W	0.02	0.01	0.01	<0.01	—	—	<0.01	<0.01
Total forbs		7.78	3.49	29.98	8.65	54.57	15.88	26.75	7.34
Ferns:									
Adiantum pedatum	W	—	—	—	—	—	—	0.02	0.02
Athyrium filix-femina	W	2.69	1.33	8.91	1.91	16.69	6.22	18.41	6.04
Blechnum spicant	W	0.49	0.14	17.13	5.29	27.17	11.21	43.48	16.45
Dryopteris expansa	W	2.74	0.91	9.83	2.96	20.87	3.86	9.64	2.12
Gymnocarpium drypoteris	W	2.47	1.22	14.75	3.40	14.97	5.29	17.44	5.68
Phegopteris connectilis	W	0.43	0.25	0.81	0.33	0.60	0.34	1.49	0.79
Polypodium glycyrrhiza	W	0.03	0.02	—	—	0.03	0.03	0.02	0.02
Polystichum braunii	W	0.45	0.45	—	—	0.26	0.26	—	—
Total ferns		10.56	4.22	51.43	9.23	80.20	17.63	90.48	21.65
Graminoids:									
Carex spp.	W	<0.01	<0.01	0.45	0.33	0.71	0.47	1.31	0.70
Unknown grass	W	0.06	0.04	3.80	2.33	2.34	0.95	1.40	0.38
Total graminoids		0.06	0.04	4.23	2.35	3.04	1.15	2.68	0.94
Shrubs:									
Gaultheria shallon	L	—	—	—	—	—	—	0.07	0.07
Ledum groenlandicum	L	—	—	—	—	—	—	<0.01	<0.01
Menziesia ferruginea	L	3.45	1.47	7.89	2.01	29.90	6.91	23.41	7.40
Menziesia ferruginea	T	1.60	0.68	1.47	0.38	5.03	1.16	3.24	1.02
Oplopanax horridus	L	4.41	2.75	15.16	4.68	17.49	8.15	12.66	6.20
Ribes bracteosum	L	1.58	1.15	0.75	0.51	1.54	1.38	0.08	0.08
Ribes bracteosum	T	0.76	0.55	0.36	0.24	0.74	0.66	0.04	0.04
Ribes lacustre	L	0.03	0.03	0.43	0.25	1.01	0.42	0.15	0.08
Ribes lacustre	T	0.02	0.02	0.21	0.12	0.48	0.20	0.07	0.04
Ribes laxiflorum	L	—	—	—	—	0.09	0.09	0.02	0.02
Ribes laxiflorum	T	—	—	—	—	0.04	0.04	0.01	0.01
Rubus parviflorus	L	—	—	0.29	0.29	1.58	1.04	0.57	0.57
Rubus parviflorus	T	—	—	0.14	0.14	0.76	0.50	0.27	0.27
Rubus spectabilis	L	6.15	3.96	52.72	13.21	71.21	19.64	41.65	10.07
Rubus spectabilis	T	2.27	1.46	23.59	6.01	20.32	5.81	13.31	3.22

Sambucus racemosa	L	—	—	2.61	2.15	9.02	5.29	5.42	3.72
Sambucus racemosa	T	—	—	0.85	0.70	2.93	1.72	1.81	1.20
Vaccinium caespitosum seedlings	W	<0.01	<0.01	—	—	—	—	—	—
Vaccinium caespitosum	L	0.70	0.70	—	—	—	—	—	—
Vaccinium caespitosum	T	0.20	0.20	—	—	—	—	—	—
Vaccinium spp. immature	W	0.05	0.02	0.13	0.03	0.14	0.04	0.09	0.02
Vaccinium ovalifolium	L	22.13	8.07	79.63	20.18	157.29	41.81	61.85	15.27
Vaccinium ovalifolium	T	5.62	2.05	31.96	8.10	46.80	12.44	17.86	4.41
Vaccinium parvifolium	L	0.45	0.37	1.70	0.68	1.68	1.06	1.99	0.60
Vaccinium parvifolium	T	0.41	0.33	1.54	0.61	1.52	0.96	1.80	0.55
Vaccinium vitis-idaea	W	<0.01	<0.01	—	—	—	—	—	—
Total shrubs		49.82	19.36	221.02	41.18	368.00	71.04	186.53	36.41
Trees:									
Alnus rubra	L	—	—	—	—	0.13	0.09	—	—
Alnus rubra	T	—	—	—	—	0.05	0.04	—	—
Chamaecyparis nootkatensis	CAG	0.03	0.03	—	—	0.27	0.16	1.29	1.25
Picea sitchensis seedlings	W	0.02	0.01	0.05	0.02	0.05	0.02	0.05	0.03
Picea sitchensis	CAG	1.99	1.38	0.35	0.12	5.01	2.09	2.38	1.35
Thuja plicata	CAG	0.43	0.35	0.51	0.27	0.00	0.00	<0.01	<0.01
Tsuga heterophylla seedlings	W	0.04	0.02	0.04	0.01	0.04	0.01	0.06	0.02
Tsuga heterophylla	CAG	4.78	2.59	10.08	2.40	11.11	2.31	3.80	1.28
Tsuga mertensiana seedlings	W	—	—	—	—	<0.01	<0.01	—	—
Tsuga mertensiana	CAG	—	—	—	—	0.12	0.10	—	—
Total trees		7.26	3.89	11.03	2.50	17.46	3.58	8.08	3.44
Total biomass (all species)		74.16	26.51	317.75	51.87	524.00	94.60	314.56	59.82

[a] Plant parts: W = whole plant; L = leaf; T = twig; CAG = current annual growth (twigs and needles together).
[b] *Chamerion angustifolium* is *Epilobium angustifolium*.

Experiment IV (>35 years old, plus 4 years posttreatment)

Species	Plant part[a]	Untreated control		Conventional thin		Thin and 1.5-m buck		Thin and 4.6-m buck		Thin by girdling	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Forbs:											
Aruncus dioicus	W	—	—	0.17	0.15	—	—	0.27	0.27	0.01	0.01
Chamerion angustifolium[b]	W	—	—	0.17	0.10	0.04	0.03	0.05	0.03	0.07	0.04
Circaea alpina	W	1.01	0.86	1.85	1.10	0.82	0.62	1.94	1.16	2.51	1.44
Claytonia siberica	W	<0.01	<0.01	—	—	<0.01	<0.01	—	—	—	—
Clintonia uniflora	W	0.31	0.29	0.20	0.20	—	—	0.04	0.04	—	—
Coptis aspleniifolia	W	0.11	0.07	—	—	0.01	0.01	0.02	0.02	0.15	0.13
Cornus canadensis	W	1.10	0.81	3.58	1.53	4.80	3.05	1.56	0.55	3.54	1.26
Epilobium ciliatum	W	—	—	0.22	0.17	0.01	0.01	0.04	0.04	0.02	0.02
Equisetum arvense	W	—	—	0.04	0.04	—	—	—	—	—	—
Galium spp.	W	—	—	—	—	—	—	<0.01	<0.01	0.05	0.05
Galium trifidum	W	—	—	0.17	0.11	—	—	—	—	—	—
Galium triflorum	W	—	—	—	—	—	—	—	—	0.06	0.06
Listera cordata	W	<0.01	<0.01	—	—	—	—	—	—	0.01	0.01
Lysichiton americanus	W	1.80	1.38	3.80	2.39	5.84	2.83	10.45	5.52	4.89	2.98
Maiathemum dilatatum	W	1.62	1.39	1.56	1.25	1.71	1.54	12.24	7.92	0.68	0.36
Mitella pentandra	W	—	—	0.07	0.05	0.02	0.02	0.93	0.84	0.63	0.42
Moneses uniflora	W	0.05	0.04	0.02	0.02	0.06	0.06	0.02	0.02	0.04	0.03
Prenanthes alba	W	—	—	—	—	—	—	—	—	0.01	0.01
Ranunculus uncinatus	W	—	—	0.13	0.13	—	—	—	—	0.02	0.02
Rubus pedatus	W	0.79	0.69	1.19	0.56	1.32	0.77	0.74	0.31	1.53	0.68
Streptopus amplexifolius	W	0.18	0.14	0.15	0.11	—	—	—	—	—	—
Streptopus spp.	W	—	—	0.01	0.01	—	—	0.01	0.01	0.01	0.01
Tiarella trifoliata	W	2.68	2.13	6.96	2.89	1.44	0.71	2.03	1.50	11.91	8.12
Tolmiea menziesii	W	—	—	0.10	0.07	—	—	1.68	1.06	0.32	0.22
Viola glabella	W	—	—	0.04	0.04	—	—	0.06	0.06	<0.01	<0.01
Viola spp.	W	0.03	0.03	—	—	0.01	0.01	0.15	0.12	—	—
Unknown forb	W	0.10	0.06	0.06	0.05	0.44	0.37	0.06	0.04	—	—
Total forbs		9.62	3.75	20.32	4.95	16.52	4.57	32.29	8.88	26.46	8.77

Ferns:											
Adiantum pedatum	W	<0.01	<0.01	0.31	0.23	—	—	0.06	0.05	0.07	0.07
Athyrium filix-femina	W	2.25	1.39	15.61	3.53	5.62	1.36	31.74	8.90	7.00	2.48
Blechnum spicant	W	1.59	1.01	15.00	7.06	5.02	1.90	5.13	1.99	9.86	2.81
Dryopteris expansa	W	3.22	0.88	34.06	8.29	5.48	1.60	32.50	7.67	7.57	2.27
Gymnocarpium drypoteris	W	2.23	0.80	15.91	3.60	11.84	3.48	20.69	6.53	16.23	3.52
Phegopteris connectilis	W	2.75	2.27	4.10	1.28	1.50	0.72	6.24	2.42	3.84	1.26
Polystichum braunii	W	<0.01	<0.01	0.58	0.30	—	—	0.09	0.09	0.12	0.12
Pteridium aquilinum	W	—	—	0.12	0.12	—	—	—	—	—	—
Total ferns		11.53	5.09	85.70	16.86	29.68	4.59	96.44	17.00	44.69	8.41
Graminoids:											
Carex spp.	W	—	—	—	—	—	—	0.16	0.16	—	—
Unknown grass	W	—	—	6.14	2.83	2.23	1.06	6.27	4.39	3.12	2.12
Total graminoids		0.00	0.00	6.14	2.83	2.23	1.06	6.43	4.38	3.12	2.12
Shrubs:											
Menziesia ferruginea	L	0.46	0.22	2.08	0.56	21.12	5.67	2.29	0.66	4.89	1.60
Menziesia ferruginea	T	0.06	0.03	0.96	0.26	10.33	2.77	1.49	0.43	1.91	0.63
Oplopanax horridus	L	0.29	0.14	3.48	1.20	1.45	0.77	1.49	0.62	3.28	1.55
Ribes spp.	L	—	—	—	—	0.02	0.02	—	—	—	—
Ribes spp.	T	—	—	—	—	0.01	0.01	—	—	—	—
Ribes bracteosum	L	<0.01	<0.01	2.68	2.52	0.33	0.32	—	—	0.23	0.19
Ribes bracteosum	T	<0.01	<0.01	1.59	1.50	0.12	0.12	—	—	0.06	0.05
Ribes lacustre	L	—	—	2.87	1.43	1.93	1.18	0.78	0.53	0.90	0.51
Ribes lacustre	T	—	—	1.07	0.53	1.05	0.65	0.36	0.25	0.39	0.22
Ribes laxiflorum	L	<0.01	<0.01	0.31	0.19	0.18	0.17	2.79	2.17	0.88	0.65
Ribes laxiflorum	T	<0.01	<0.01	0.12	0.07	0.07	0.06	1.29	1.00	0.24	0.18
Rubus parviflorus	L	—	—	—	—	0.05	0.05	0.18	0.17	0.79	0.63
Rubus parviflorus	T	—	—	—	—	0.02	0.02	0.08	0.08	0.22	0.17
Rubus spectabilis	L	3.29	1.74	27.84	6.82	21.87	7.36	27.55	9.08	32.90	8.71
Rubus spectabilis	T	2.02	1.07	20.51	5.02	8.87	2.99	14.80	4.88	27.76	7.35
Salix spp.	L	—	—	0.58	0.58	—	—	—	—	—	—
Salix spp.	T	—	—	0.46	0.46	—	—	—	—	—	—
Sambucus racemosa	L	0.11	0.11	13.69	6.17	0.90	0.49	1.62	1.00	1.61	0.65
Sambucus racemosa	T	0.07	0.07	10.91	4.92	0.59	0.32	1.84	1.14	1.83	0.73
Vaccinium ovalifolium	L	7.20	3.45	9.06	3.36	17.28	8.15	17.12	5.07	26.36	7.10

Vaccinium ovalifolium	T	7.65	3.66	10.56	3.92	16.15	7.62	21.08	6.24	29.84	8.03
Vaccinium spp. immature	W	0.33	0.14	0.21	0.10	0.28	0.15	0.32	0.18	0.59	0.36
Vaccinium parvifolium	L	0.29	0.27	0.74	0.54	0.30	0.20	0.94	0.60	1.16	0.80
Vaccinium parvifolium	T	0.30	0.29	0.86	0.63	0.28	0.19	1.16	0.74	1.32	0.90
Total shrubs		22.28	9.77	110.90	20.67	104.15	24.25	97.20	19.97	138.77	24.09
Trees:											
Alnus rubra	L	0.04	0.04	1.15	0.67	1.14	1.03	1.69	0.94	0.26	0.20
Alnus rubra	T	0.02	0.02	0.85	0.67	0.46	0.42	0.91	0.50	0.22	0.17
Alnus viridis	L	0.10	0.10	—	—	0.01	0.01	—	—	—	—
Alnus viridis	T	0.06	0.06	—	—	<0.01	<0.01	—	—	—	—
Chamaecyparis nootkatensis	CAG	—	—	—	—	<0.01	<0.01	—	—	—	—
Picea sitchensis	CAG	2.29	1.85	4.35	1.23	2.73	0.77	3.71	1.54	2.75	0.99
Thuja plicata	CAG	0.01	0.01	0.01	0.01	0.09	0.07	—	—	0.13	0.10
Tsuga heterophylla	CAG	0.38	0.19	14.76	5.68	5.91	1.39	6.69	2.39	7.03	2.89
Tsuga heterophylla seedlings	W	0.09	0.04	13.65	3.50	6.79	2.49	19.90	5.25	7.58	2.55
Total trees		2.91	2.04	33.91	6.99	16.73	3.57	31.98	5.92	17.76	4.01
Total biomass (all species)		46.87	17.17	258.04	39.52	169.01	27.27	264.92	29.98	230.79	33.86

[a] Plant parts: W = whole plant; L = leaf; T = twig; CAG = current annual growth (twigs and needles together).
[b] *Chamerion angustifolium* is *Epilobium angustifolium*.

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