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Responses of Southeast Alaska Understory Species to Variation in Light and Simulated Herbivory

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Cover: Upper photo shows a blueberry bush that has been heavily browsed by deer in a southeast Alaska forest; current use has greatly reduced its current annual growth of leaves and twigs, while past use has resulted in a "hedged" growth form of stunted plant size and shortened twigs. Lower photo shows an exclosure in an even-aged, young-growth forest on Admiralty Island in southeast Alaska. Constructed 21 years before the photo was taken, the exclosure has protected vegetation within it from herbivory by black-tailed deer.

Abstract

Hanley, Thomas A.; Barnard, Jeffrey C. 2014. Responses of southeast Alaska understory species to variation in light and simulated herbivory. Res. Pap. PNW-RP-599. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 22 p.

Responses to variation in light intensity, simulated herbivory by clipping, and their interaction were studied over three seasons in a factorial experimental design. Six major species of southeast Alaska forest understories were studied, each as a separate experiment: bunchberry, *Cornus canadensis* L.; threeleaf foamflower, *Tiarella trifoliata* L.; oval-leaf blueberry, *Vaccinium ovalifolium* Sm.; salmonberry, *Rubus spectabilis* Pursh; devilsclub, *Oplopanax horridus* (Sm.) Miq.; and western hemlock, *Tsuga heterophylla* (Raf.) Sarg. Seedlings of each species were grown in plastic grow pots under three intensities of light in an outdoor garden experiment—full sun in the open (100 percent incident light) and under two natural forest canopies, red alder (*Alnus rubra* Bong.; about 17 percent incident light) and young-growth conifers (about 1.7 percent incident light). Plants within each light treatment were subjected to simulated herbivory by clipping the current year's growth at the end of the first and second growing season at three intensities of clipping—0-percent removal, 50-percent removal, and 100-percent removal (75-percent removal for western hemlock). At the end of the third growing season, mean percentage survival was determined and total biomass (both below- and aboveground ovendry weight) of each surviving plant was measured. Factorial analyses of variance, conducted at the α level of 0.10, indicated that for survival, light was a significant main effect for only three of the six species, and clipping was a significant main effect for only one of the species (salmonberry, which also was the only species having a significant light by clipping interaction effect). Treatment effects were much stronger for mean plant size, however, with light having a significant main effect on all six species, clipping having a significant main effect on all but one species (devilsclub), and three of the six species having significant light by clipping interaction effects. Overall, the results emphasized the predominant importance of light in determining plant responses to herbivory, although the light by clipping interaction effect was not as strong as hypothesized.

Keywords: Autecology, clipping, black-tailed deer, silviculture, survival, growth, biomass, browsing, grazing.

Summary

Responses to variation in light intensity, simulated herbivory by clipping, and their interaction were studied over three seasons in a factorial experimental design. Six major species of southeast Alaska forest understories were studied, each as a separate experiment: bunchberry, threeleaf foamflower, oval-leaf blueberry, salmonberry, devilsclub, and western hemlock. Principal forest management implications of the results are as follows:

- Light intensity within forest understories, especially in closed-canopy young-growth stands, is an overwhelmingly important environmental factor affecting both survival and, especially, growth of understory plants. Loss of plant tissue through herbivory is also an important environmental factor, but its interaction with light is frequently only an additive rather than interactive effect.
- Clipping has a stronger influence on reducing plant size than on reducing survival (at least within a 3-year timeframe) in most species. Reduction in plant size should interact with foraging efficiency to produce a negative feedback loop that reduces subsequent herbivory by animals the size of deer.
- However, foraging patch size (area of relatively uniform vegetation) and overall density of deer within the surrounding landscape will interact in determining the intensity of herbivory for individual plants and patches of vegetation.
- Therefore, all considerations of potential effects of herbivory within a silviculture context must be made at a landscape scale, considering the overall suitability of habitat and deer densities, because the level of herbivory experienced within any given stand will be strongly influenced by its larger landscape context. Herbivory is not a factor that can be evaluated and managed at the stand scale alone.

Introduction

Young-growth, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)–Sitka spruce (*Picea sitchensis* (Bong.) Carrière) forests of southeast Alaska are commonly very depauperate in understory vegetation from the time the canopy closes in the regenerating stand (about 25 to 35 years) through anticipated age of harvest rotation at about 100 years or more (Alaback 1982, 1984). Availability of light in the understory environment appears to be the principal limiting factor affecting plant establishment (Tappeiner and Alaback 1989) and growth (Hanley et al. 2014, Rose 1990).

Once plants are established, their growth rates are strongly dependent on the quantity of light, and species differ in their growth curves in relation to light (production of biomass as a function of intensity of light): greenhouse light trials with five common species showed substantial differences in growth curves in relation to light (Hanley et al. 2014). All four understory species (bunchberry, *Cornus canadensis* L.; oval-leaf blueberry, *Vaccinium ovalifolium* Sm.; salmonberry, *Rubus spectabilis* Pursh; and devilsclub, *Oplopanax horridus* (Sm.) Miq., grew more than western hemlock at low intensities (<4 mol m^{-2} day^{-1}), while western hemlock did best at high intensities of light (>15 mol m^{-2} day^{-1}). Growth rates among the non-conifer species also changed with light intensities: bunchberry was greatest relative to the others at lowest light, and blueberry and devilsclub were greatest at highest light. In manipulation field experiments with the same species, four of the five species showed greater production under a red alder (*Alnus rubra* Bong.) canopy than under a conifer canopy (bunchberry responded the same to both light treatments), but soil type was important only for two species (Hanley et al. 2014). Understory light intensity was low in both forest canopies but was more than a full order of magnitude greater under alder (about 19.5 percent of unobstructed incident light) than under conifers (about 1.7 percent).

Interestingly, all five species in the above field experiments survived and grew (albeit slowly) when planted as seedlings under the conifer canopy, even though the conifer understory was nearly devoid of vascular vegetation. All plants were protected by fencing from mammalian herbivores. A similar understory response to fencing was observed by Hanley (1987) in an examination of understory response to deer exclosures in southeast Alaska: the one exclosure that occurred in an even-aged stand (about 80 years old, at Pybus Bay on Admiralty Island) had a total vascular understory biomass of 782 kg/ha inside the exclosure and only 31 kg/ha outside. Although 60 percent of the biomass within the 21-year-old exclosure consisted

of western hemlock seedlings, 309 kg/ha was in the form of shrubs and herbs. The low biomass of understory outside the exclosure was typical of that expected for stands of that age (Alaback 1982), yet the exclosure demonstrated that herbivory by Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) had played a major role in the understory vegetation at the Pybus Bay site. The combination of the field experiments (Hanley et al. 2014) and the earlier Pybus Bay observations indicates that mammalian herbivory might be an important factor in understory dynamics at low levels of light such as commonly occur in young-growth, even-aged stands—where plants can survive but cannot withstand browsing. However, until our experiments reported here, there have been no experimental tests of that idea.

We tested the hypotheses that both (1) survival and (2) growth of understory plants exposed to simulated herbivory by clipping are interactive with the intensity of light in the environment. Specifically, we expected that survival and growth would decrease with increasing intensity of clipping (amount of living tissue removed) and with decreasing intensity of light and, especially, that the interactive effects of high clipping and low light would be significantly greater than an additive effect.

Methods

The experiments were conducted in Juneau, Alaska, in an outdoor "garden" setting with all plants growing in 3.8-liter plastic grow pots and commercial potting soil through three growing seasons. We used six species of understory plants: the evergreen forbs bunchberry and threeleaf foamflower (*Tiarella trifoliata* L.); the shrubs oval-leaf blueberry, salmonberry, and devilsclub; and the conifer western hemlock, all of which are common understory species and significant in black-tailed deer diets in southeast Alaska. Western hemlock is a nutritionally marginal forage, but it is commonly eaten in winter (Hanley and McKendrick 1985, Parker et al. 1999), and it is a very important competitor with other understory species in young-growth forests (Deal and Farr 1994). We conducted the experiments separately for each species, subjecting them to three intensities of clipping and three intensities of light. The clipping intensities were 0, 50, and 100 percent removal of aboveground current year's growth (leaves and current year's twigs of shrubs and hemlock, all aboveground tissue of bunchberry and foamflower), except for western hemlock, where clipping intensities were 0, 50, and 75 percent removal because we thought 100 percent removal would have caused death every time. Clipping treatments were

imposed twice (at the end of the first and second growing seasons) over the three-growing-season timeframe.[1] The light intensities were full sunlight (100 percent unobstructed incident light) and much-reduced light intensities under the same forest canopies of red alder (about 20 percent) and young-growth western hemlock–Sitka spruce (about 2 percent) used in the Hanley et al. (2013) light and soil experiments conducted a year earlier. The alder and conifer stands were natural stands, 25 to 33 years old, one of each type, and were chosen simply to provide two widely different light intensities typical of young-growth forests of the region. Because the alder and conifer stands were not replicated (several stands of each), they cannot be considered representative of "red alder" or "conifer" overstories generally.[2]

Each plant species was represented by 24 individual plants allocated to each of the three clipping by three light treatments (nine treatments total), for a total of 216 plants per species. Each light treatment was spatially replicated twice within each stand, with 12 plants of each species (each plant being a subsample) in each of the two replicates. Although for statistical power it would have been preferable to have more replicates and fewer subsamples (for the same number of plants), we needed a relatively large number of subsamples per replicate for quantifying survival (percentage remaining alive). Clipping treatments were assigned randomly to each plant within each replication of each light treatment and remained constant for both clipping times. All of the 18 treatment areas (nine treatments × two replications) were fenced with hardware cloth, 1.5-m high, to protect them from herbivory by mammals.

All plants were obtained from a commercial nursery as seedlings in excess of the number needed, and were sorted to select the 216 most similarly sized plants within each species for the experiments. The 216 plants of each species were transferred to 3.8-liter grow pots filled with horticultural-grade soil mixes (peat-based with vermiculite and lime added). Individually potted plants were then randomly assigned to each of the 18 replicated treatments (two replicates times three light by

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[1] Note that the clipping treatments were not intended to exactly replicate browsing by deer, in that the intensities of clipping (0, 50, 75 or 100 percent), the plant tissues removed (current annual growth), and the timing of clipping (end of growing season) were fixed for all species, not directed at species-specific plant parts or seasons. We wanted to be able to compare the six species in their responses to removal of current annual growth.

[2] Ideally, we would have replicated our experimental design with several alder and several conifer stands and considered the stands as replicates (instead of the spatial replication **within** each stand); then we could generalize our results to "alder" and "conifer" canopy types. However, only one stand of each was available to us for this work, so we must restrict our conclusions to only those two stands (i.e., a "case study" as far as canopy type goes). On the other hand, the two stands provided sharp contrasts in their light environments, which allowed us to test the species' responses to light and clipping within light treatments, which was our principal objective.

three clipping) with 12 plants in each replicate and were placed in the field within the second week of May of the first season. Fertilizing and watering were kept to a minimum throughout the experiments, once per season (general purpose fertilizer) and only as necessary (water), and then applied equally to all treatments. All plants were covered with straw during winter to protect them from hard frost.

In late August before leaf-fall in the first and second year, plants were subjected to the clipping treatment to which they had been assigned, visually estimating the percentage of biomass removed. At the end of the third growing season (same time in late August), survivorship (number of plants alive) was determined for all treatments and replicates, the experiments were terminated, and all plants were returned to the lab in their pots instead of being clipped. In the lab, each surviving plant was gently removed from its pot and all soil was washed from its roots. The total biomass (both above- and belowground) of each plant was then ovendried (100 °C for 24 hours) and weighed (to 0.01 gram) to provide a relative measure of its growth throughout the experiment. This was a relative (not absolute) measure of growth, because it was impossible to weigh each plant at the beginning of the experiment.

Ambient light was measured with a sunfleck PAR (photosynthetically active radiation—i.e., the wavelengths of light that plants are able to use in the process of photosynthesis) ceptometer (Decagon Devices, Inc.,[3] Pullman, Wash.) at 30 cm aboveground in the alder and conifer stands and adjacent opening at midday throughout each growing season. The mean light level within each of the two stands, expressed as a percentage of full sunlight in the open area, provided a measure of relative differences between the overstory types.

The survival and biomass data were tested for statistical significance in a 3 by 3 factorial analysis of variance with the Mixed Procedure of SAS (SAS Institute, Inc. 2004). Survival (mean percentage of original plants remaining alive) and biomass (mean ovendry weight per surviving plant, grams) were analyzed separately and independently for each species. Survival data (percentage) were transformed with the natural log transformation; biomass data (grams) were not transformed. We used the Tukey multiple comparisons test for determining significant differences among means when main effects or interactions were significant. Because statistical power was relatively weak with only two replicates per treatment, all tests of

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statistical significance were conducted at an α level of 0.10, and the multiple comparisons tests of main effects were one-tailed: we expected both survival and biomass to decrease with decreasing light and increasing clipping levels.

Results

Midday light intensities within the alder and conifer understories averaged 17.03 (± 1.07 SE) and 1.69 (± 0.62 SE) percent, respectively, of that in the open (711.4 µmol m^{-2} sec^{-1}). Those are virtually the same as the values reported for the same two stands in the Hanley et al. (2014) experiments conducted there 1 year earlier (19.5 and 1.7 percent, respectively, of 789 µmol m^{-2} sec^{-1} in the open).

Although we had been surprised at the high survival rates of potted plants under the conifer canopy in the earlier one-season study of light and soils (Hanley et al. 2014), the low light intensity under the conifer canopy took a fairly heavy toll on survival of several species after three seasons in this study (table 1; fig. 1). Survival of bunchberry, foamflower, and devilsclub was not affected by light intensities (table 1; no statistically significant differences), but survival of blueberry, salmonberry, and western hemlock was lowest under the conifer canopy and ranged from only 1.3 to 28.2 percent. Surprisingly, clipping had a statistically significant effect on survival of only salmonberry, and that was also the only species that exhibited a significant interaction effect between light and clipping (table 1): salmonberry survival was virtually nil under the conifer canopy and was nil in the 100 percent clipping treatment regardless of canopy type (fig. 1). Although survival of all species was unaffected by canopy differences during the first growing season (before clipping treatments were applied), differences in survival started becoming apparent after the second growing season, especially under the conifer canopy and regardless of clipping treatment (app. 1; data not analyzed statistically), and progressed further in year 3 (fig. 1). The strong effect of light, therefore, seems to compound with time in its effect on the survival of the more light-sensitive species, regardless of the potential effects of herbivory. And, at least in terms of survival, clipping was not a strong factor, either per se or in its interaction with light.

On the other hand, in contrast to survival, the effects of both light and clipping were much more pronounced on plant size (mean biomass per surviving plant, table 2 and fig. 2). All species exhibited statistically significant differences in the main effect of light; all but devilsclub exhibited significant differences in the main effect of clipping; and three species (bunchberry, blueberry, and salmonberry) had statistically significant interaction effects (table 2) with the combination of low light

Table 1—Mean survival (percentage of original plants surviving to end of experiment) within each of the main effects of the light by clipping factorial experiment and statistical significance of the interaction effect for each of the six species

	Light			Clipping (percentage)			Interaction Significance
Species	Open	Alder	Conifer	0	50	100	(Pr > F)
Bunchberry	100.00[a]	94.10[a]	49.77[a]	84.15[a]	83.40[a]	76.32[a]	0.895
Foamflower	94.02[a]	91.55[a]	71.47[a]	93.82[a]	90.34[a]	72.85[a]	0.506
Blueberry	79.10[a]	44.42[a,b]	28.20[b]	56.03[a]	56.75[a]	38.93[a]	0.877
Devilsclub	90.18[a]	53.07[a]	41.95[a]	72.60[a]	62.77[a]	51.83[a]	0.375
Salmonberry	16.95[a]	24.17[a]	1.27[b]	27.02[a]	15.37[a]	0[b]	0.027*
Western hemlock	100.00[a]	98.83[a]	8.68[b]	72.17[a]	67.77[a]	67.58[a]	0.984

Note: The maximum clipping treatment for western hemlock was 75 percent, not 100 percent.

Values with the same superscript within treatments within rows do not differ significantly. Statistical significance of the interaction effect is indicated by the probability of the null hypothesis (no interaction) being greater than the calculated F value ("Pr > F"), with significance indicated with an asterisk. All tests of statistical significance were at the $\alpha = 0.10$ level (i.e., Pr > F less than 0.10).

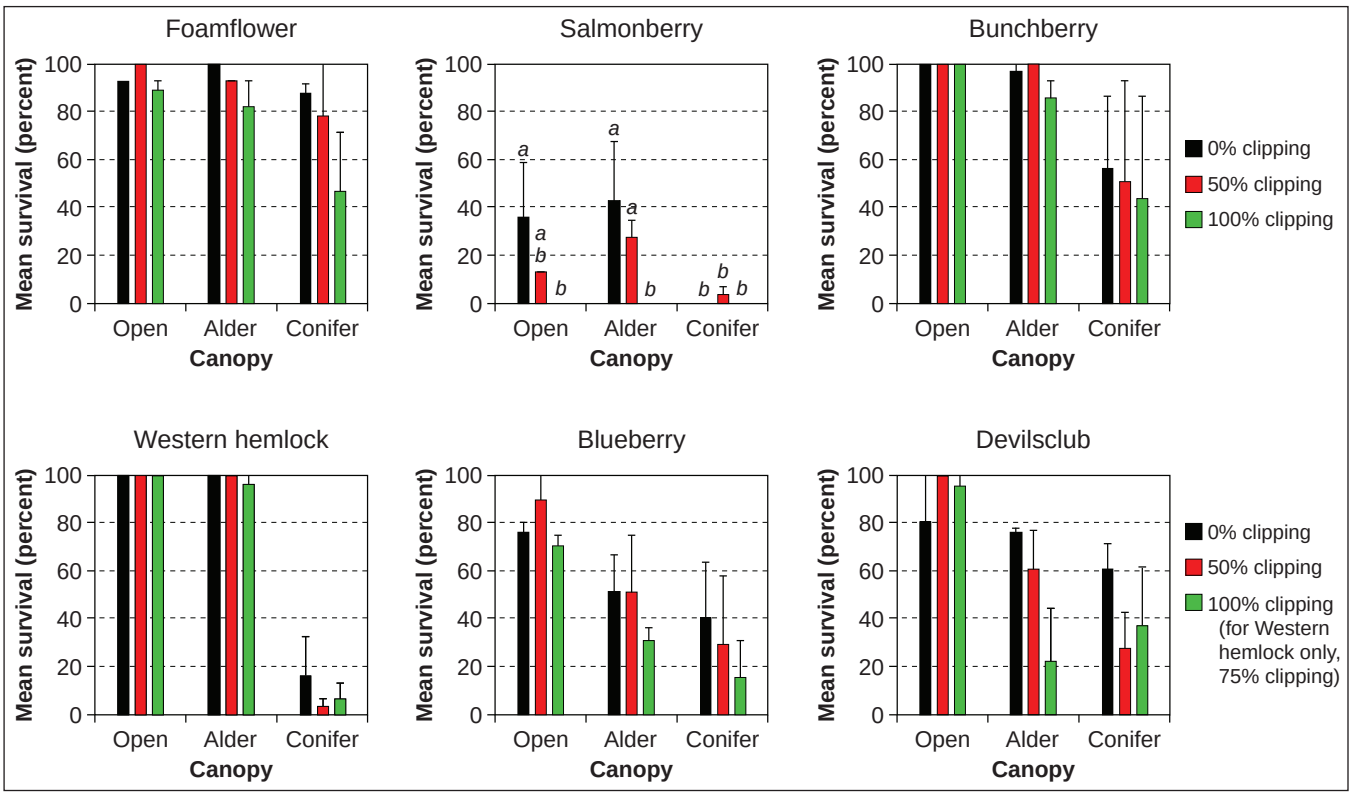

Figure 1—Mean (+ standard error) survival (percentage of original plants remaining alive) at the end of the experiment in year 3, after 2 successive years of clipping treatments at the end of the first and second growing seasons. See table 1 for statistically significant main effects. Statistically significant interactions are indicated here with alphabetic labels over each bar (canopy-clipping treatment); bars with same letter do not differ at the $\alpha = 0.10$ level (one-tailed; Tukey multiple comparisons test). Although survival data were natural log-transformed for analysis, they have been plotted without transformation, and standard errors are those calculated directly for each treatment combination rather than the pooled values from the analysis of variance to better show the actual means (untransformed) and the variation within each treatment.

Table 2—Mean total biomass (ovendry grams) per surviving plant within each of the main effects of the light by clipping factorial experiment and statistical significance of the interaction effect for each of the six species

	Light			Clipping (percentage)			Interaction significance
Species	**Open**	**Alder**	**Conifer**	**0**	**50**	**100**	**(Pr > F)**
Bunchberry	6.31^{a}	1.90^{b}	0.22^{c}	4.24^{a}	2.66^{b}	1.54^{c}	0.001*
Foamflower	8.28^{a}	3.98^{b}	0.71^{c}	6.85^{a}	$4.06^{a,b}$	2.07^{b}	0.326
Blueberry	2.79^{a}	0.37^{b}	0.09^{b}	1.35^{a}	1.33^{a}	0.58^{b}	0.090*
Devilsclub	48.02^{a}	34.92^{a}	6.49^{b}	37.78^{a}	29.82^{a}	21.84^{a}	0.193
Salmonberry	12.56^{a}	10.84^{a}	0.47^{b}	12.22^{a}	11.65^{a}	0^{b}	0.021*
Western hemlock	27.97^{a}	15.28^{b}	1.65^{c}	19.89^{a}	13.46^{b}	11.55^{b}	0.164

Note: The maximum clipping treatment for western hemlock was 75 percent, not 100 percent.

Values with the same superscript within treatments within rows do not differ significantly. Statistical significance of the interaction effect is indicated by the probability of the null hypothesis (no interaction) being greater than the calculated F value ("Pr > F"), with significance indicated with an asterisk. All tests of statistical significance were at the $\alpha = 0.10$ level (i.e., Pr > F less than 0.10).

intensity and high clipping intensity resulting in strongly reduced plant sizes (fig. 2). Therefore, even the most shade-tolerant species in terms of survival (bunchberry, foamflower, and devilsclub) were strongly affected in size by light, and the size of virtually all species (except devilsclub) was affected by clipping, too—light providing the basis for accumulating biomass, and clipping removing biomass and reducing subsequent growth.

We are able to assess the combined effects of survival and growth for each species by analyzing the total biomass of all surviving plants (combined) of that species within each replicate of the experimental treatments. That measure of total biomass effectively quantifies what one would see visually or measure in field-sampling biomass per unit area 3 years after the same initial starting conditions for each treatment, except that our data included belowground biomass. Those results are fairly similar to the effects on plant size for both light and clipping: significant main effect of light for all species; significant main effect of clipping for all species except devilsclub; and significant light-clipping interaction for bunchberry and blueberry (table 3). The overall pattern of response to treatments was similar to that for plant size in all species except salmonberry (compare figs. 2 and 3), where the relatively low survival rates greatly depressed total biomass per replication in both the open and alder light treatments, too (compare figs. 1 and 3). Thus, the total quantity of plant biomass growing within light and clipping treatments was most strongly affected by differences in plant size, which was strongly affected by both amount of light and intensity of clipping, but usually (four of the six species) in only an additive manner (i.e., light and clipping effects were mostly additive rather than strongly interactive).

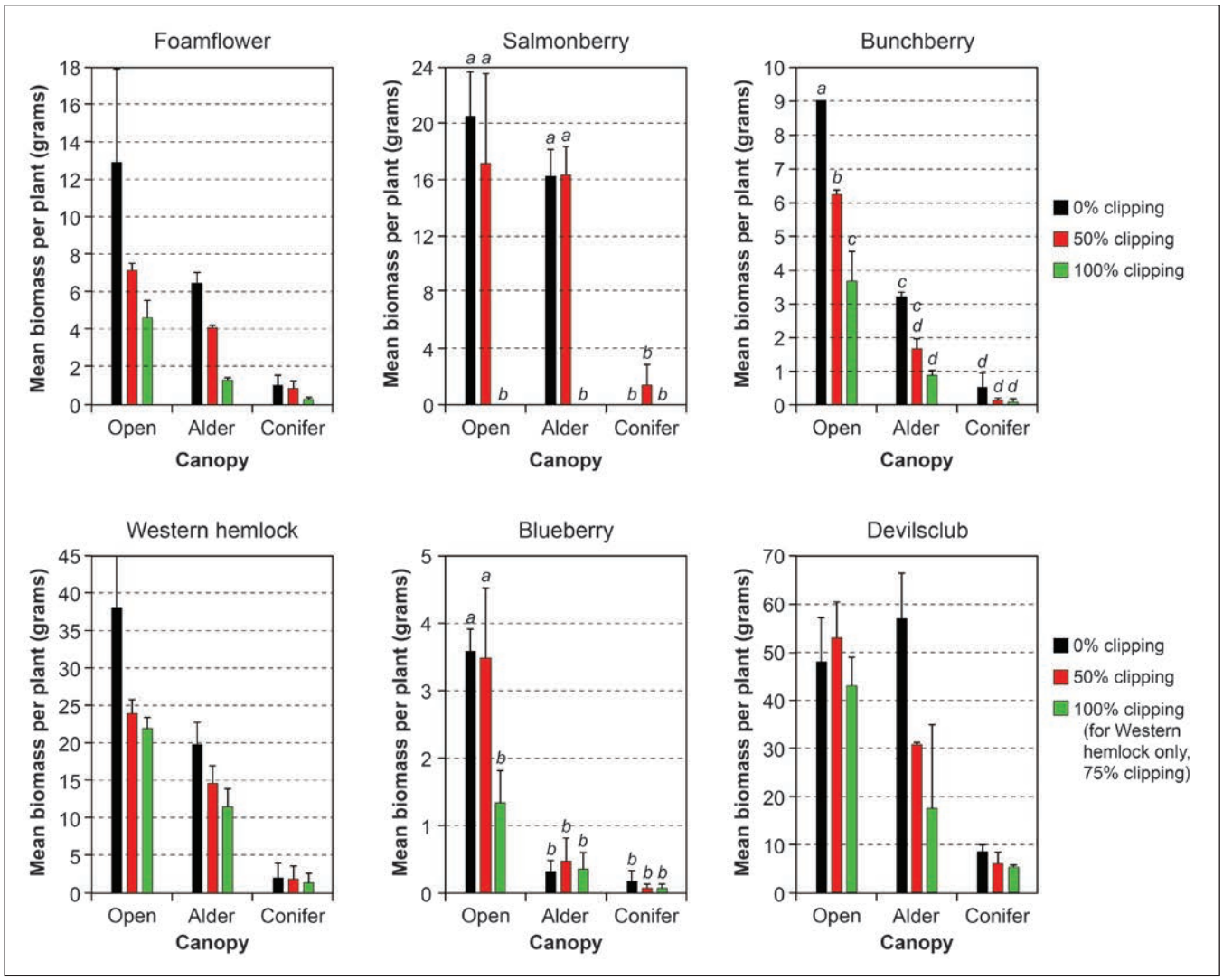

Figure 2—Mean (+ standard error) biomass (ovendry weight, grams) per surviving plant at the end of the experiment in year 3, after 2 successive years of clipping treatments at the end of the first and second growing seasons. Biomass is entire plant weight, both above- and belowground parts. See table 2 for statistically significant main effects. Statistically significant interactions are indicated here with alphabetic labels over each bar (canopy-clipping treatment); bars with same letter do not differ at the $\alpha = 0.10$ level (one-tailed; Tukey multiple comparisons test).

Discussion

Our results were both consistent with and contradictory to our expectations regarding the roles of light and clipping on understory vegetation. They were consistent with our expectation that both light and clipping would be strong factors affecting plant growth (biomass), but were contradictory to our expectations that both light and clipping would also be strong factors affecting plant survival and, especially, that the interaction of light and clipping intensities would have a strong effect on virtually all measures of plant performance. Differences in these relations, of

course, existed among species, but overall we were surprised how light and plant size tended to predominate over clipping and survival and that light-clipping interaction effects did not predominate over all.

Western hemlock was the most shade-intolerant species, and bunchberry was the most shade-tolerant species at low levels of light in the earlier 1-year study in these same stands (Hanley et al. 2014). These were important findings, because western hemlock seedlings can be strong competitors with other understory vegetation (Alaback and Herman 1988, Deal and Farr 1994, Doerr and Sandburg 1986), and bunchberry is one of the most important yet difficult species to maintain in young-growth forests of the region (Hanley 1993, 2005). In this 3-year study, however, those differences in species responses were evident in survival (table 1) but not in plant size (table 2) or total biomass per replicate (table 3). Survival, size, and total biomass were strongly suppressed in western hemlock under the conifer canopy, but low light intensity also strongly suppressed size and total biomass of bunchberry. Clipping had relatively little effect on survival in both species (table 1), but both size and total biomass of both species were strongly affected by clipping (tables 2 and 3), with bunchberry showing significant interaction effects of light and clipping treatments (figs. 2 and 3). The other species were mostly intermediate in their responses to both light and clipping, although salmonberry was especially sensitive to both, devilsclub was least sensitive to clipping, and foamflower (a species not studied in the Hanley et al. 2014 study) was an especially strong survivor under both treatments (figs. 1 through 3).

Table 3—Mean total biomass (ovendry grams) per replicate (sum of all surviving plants within a replicate) within each of the main effects of the light by clipping factorial experiment and statistical significance of the interaction effect for each of the six species

	Light			Clipping (percentage)			Interaction significance
Species	**Open**	**Alder**	**Conifer**	**0**	**50**	**100**	**(Pr > F)**
Bunchberry	75.75[a]	21.84[b]	2.25[c]	50.14[a]	31.75[b]	17.95[c]	0.001*
Foamflower	94.42[a]	45.69[b]	7.36[c]	78.73[a]	47.06[b]	21.69[b]	0.275
Blueberry	32.26[a]	2.61[a]	0.61[b]	14.79[a]	15.42[a]	5.27[b]	0.054*
Devilsclub	525.90[a]	377.30[b]	36.23[c]	343.10[a,b]	392.57[b]	203.75[a]	0.123
Salmonberry	38.53[a]	48.43[a]	0.47[b]	57.79[a]	29.60[a,b]	0.00[b]	0.409
Western hemlock	339.53[a]	185.43[b]	3.62[c]	233.73[a]	156.94[b]	137.91[b]	0.156

Note: The maximum clipping treatment for western hemlock was 75 percent, not 100 percent.
Values with the same superscript within treatments within rows do not differ significantly. Statistical significance of the interaction effect is indicated by the probability of the null hypothesis (no interaction) being greater than the calculated F value ("Pr > F"), with significance indicated with an asterisk. All tests of statistical significance were at the $\alpha = 0.10$ level (i.e., Pr > F less than 0.10).

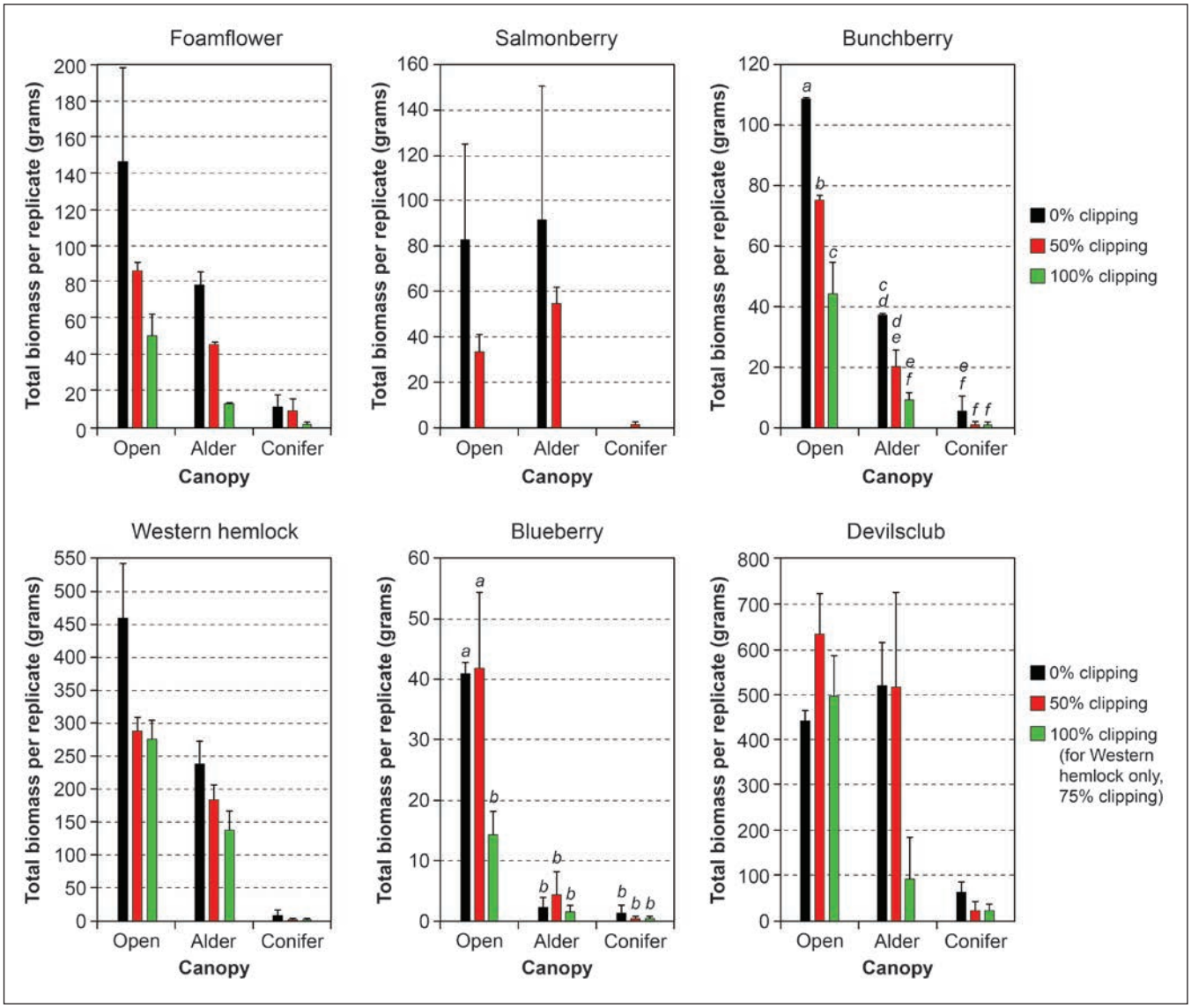

Figure 3—Mean (+ standard error) total biomass (ovendry weight, grams) per replicate (all surviving plants combined within a replicate) at the end of the experiment in year 3, after 2 successive years of clipping treatments at the end of the first and second growing seasons. Biomass is entire plant weight, both above- and belowground parts. See table 3 for statistically significant main effects. Statistically significant interactions are indicated here with alphabetic labels over each bar (canopy-clipping treatment); bars with same letter do not differ at the $\alpha = 0.10$ level (one-tailed; Tukey multiple comparisons test). This measure of biomass per replicate combines the effects of both survival (fig. 1) and biomass of surviving plants (fig. 2) into one measure of standing crop.

Clipping was intended to roughly simulate herbivory by a large herbivore like deer. However, the relatively extreme responses of salmonberry and devilsclub were probably related to an unrealistic way our clipping treatment (removal of current annual growth, both leaves and twigs) affected them. Both those species are eaten by deer only in summer, and leaves are virtually the only part eaten; deer eat very little, if at all, of the twigs of those two species (Parker et al. 1999). Thus, our clipping treatments of salmonberry were more severe than salmonberry would likely

experience under herbivory; and devilsclub twig growth was minor, so clipping mainly removed the leaf, which would have fallen relatively soon thereafter, anyway, as the deciduous plant went dormant at end of the growing season. Devilsclub biomass was strongly affected by light but not by clipping (tables 2 and 3).

These 3-year results (for all species) emphasize the importance of time in autecological field studies. Although studies of only one growing season can highlight important differences among species and major environmental factors, they cannot include effects that accumulate or compound with time. Our data for survival illustrate that most clearly, where survival was 100 percent for all species and habitats at the end of the first growing season (at which time the clipping treatments were then imposed), but began to decrease with the light effect (regardless of clipping) by the end of the second season (app. 1) and were pronounced by the end of the third season (fig. 1). We don't have time-sequence data for biomass, but the relative difference in bunchberry response to one year (Hanley et al. 2014) versus 3 years of light treatment (figs. 2 and 3 for 0 percent clipping) indicates a strong compounding effect over time. Furthermore, there is no reason to assume that the compounding had reached a culmination after 3 years; it may be that none of our species could persist under our dense conifer canopy indefinitely.

The overriding importance of light in both this study and the earlier one (Hanley et al. 2014) indicates that variation in overstory canopy must be especially important in forests of southeast Alaska, especially in the dark, closed-canopy forests of young-growth stands (with typically <2 percent of unobstructed incident light—Rose 1990, Tappeiner and Alaback 1989). Greenhouse light-gradient trials with these same species indicated approximate thresholds of about 4 mol m^{-2} day^{-1} below which western hemlock does more poorly than the other species and about 15 mol m^{-2} day^{-1} above which it does much better than the other species in terms of growth (Hanley et al. 2014). Using data from table 1 of Hanley et al. (2014), the corresponding mid-day light intensities would be about 100 and 400 µmol m^{-2} sec^{-1}, which would be approximately 13 and 53 percent, respectively, of an average 750 µmol m^{-2} sec^{-1} intensity of unobstructed incident light (average of the two studies for light in the open—see opening paragraph of "Results" section[4]). Therefore, the

[4] For perspective, measured average daily July irradiance (including effects of cloud cover) in southeast Alaska understory forests have ranged from <10 µmol m^{-2} sec^{-1} in closed-canopy young-growth forests, to 10 to 50 µmol m^{-2} sec^{-1} in dense-canopied old growth, to 50 to 300 µmol m^{-2} sec^{-1} in more open-canopy old growth and low-volume timber stands, and a maximum of 400 to 700 µmol m^{-2} sec^{-1} in open clearings (Rose 1990 and C.L. Rose unpublished data). Those values are about half of the maximum values measured on cloud-free days (Hanley et al. 2014, Rose 1990, Tappeiner and Alaback 1989).

low-light "window of opportunity" (Hanley et al. 2014) favoring understory species other than hemlock would be somewhat less than that under our alder canopy (17 percent), and the zone of relatively similar competitive abilities would range to much greater than that under our alder. These calculations are very simplistic, but they illustrate that a wide range of canopy variation within young-growth forests could be highly beneficial to understory species without necessarily tipping the competitive advantage to western hemlock seedlings. Even small canopy gaps and sunflecks could be a big improvement over the mean low light penetration in young-growth forests (Chazdon 1988).

High natural heterogeneity in site and disturbance is the norm for natural stands of forest in southeast Alaska, where major variation in soils commonly occurs at the scale of only a few (e.g., 20) square meters (Bowers 1987) and wind and disease are continuously at play (Harris and Farr 1974). Young-growth stands are much more homogeneous than old-growth stands in the region (Alaback 1984), but they nevertheless include substantial variation in tree spacing and size, overstory canopy coverage, and understory vegetation, especially at the entire stand scale (in contrast to small research plots) (Hanley 2005). That variation in stand structure provides variation in the understory light environment and results in strong effects on variation in understory species composition and biomass (Hanley and Barnard 1998). Our results from this study indicate that even small patterns of variation within a densely canopied young-growth forest would result in heterogeneous spatial patterns in survival, size, and biomass of understory species. Such heterogeneity is probably key to long-term persistence of understory species in young-growth forests of the region.

Spatial pattern, size, and biomass also are important factors affecting the foraging efficiency of herbivores the size of deer (Gross et al. 1993, Spalinger and Hobbs 1992), with clumping of forages (concentrated patches), large leaf size, and high biomass increasing foraging efficiency (net energy or nutrient intake per unit time spent feeding—i.e., time spent searching for, biting, chewing, and swallowing food), which has strong effects on net energy balance, body growth, and productivity (Parker et al. 1996, 1999). Of the three variables, however, biomass is the least important (Shipley and Spalinger 1992), and leaf size (equals bite size) is most important (Spalinger et al. 1988), although clumping certainly interacts with leaf size (Shipley and Spalinger 1992). Reasons are that time spent traveling between plants and time spent biting instead of chewing is lost, while the most profitable foraging time is spent chewing and swallowing, which is maximized by eating large

bites of plants in close proximity. Therefore, the effects of herbivory by deer, especially in combination with those of light intensity in relatively closed-canopy forest, create a self-dampening feedback loop where herbivory results in decreased plant size of most species and decreased survival (distribution) in many species, which in turn decreases foraging efficiency. The relative attractiveness of the browsed patch decreases as foraging efficiency decreases (Kohlmann and Risenhoover 1994, Langvatn and Hanley 1992, Roese et al. 1991), so herbivory decreases as foraging time decreases. This, of course, is all at the scale of habitat patches or stands of forest; patterns of habitat use can shift only when alternative patches exist.

Canopy gaps, especially in dense young-growth forest where understory vegetation is otherwise sparse, should be attractive to large foragers like deer, because understory plants there should be relatively abundant, large, and clumped, making the gaps especially favorable places for foraging. Deer should be expected to focus attention on such gaps until foraging efficiency is reduced by reduction in plant size and survival (the self-dampening feedback loop) to levels similar to alternative habitats. If light intensity is high enough to give a competitive advantage to conifers, and if the conifers are less palatable to deer than the other understory species, then the herbivory should hasten understory dominance by conifers (Hanley and Taber 1980), possibly even resulting in local exclusion of the palatable species.

Management Implications

To date, there have been few studies of the autecology of understory species in southeast Alaska forests, but all those that have been conducted implicate light intensity as the primary limiting factor in virtually all stages (except germination) of plant life histories, especially under low light intensities of densely canopied forests: Once seedlings germinate, their success at becoming established is directly related to the light intensity of their microenvironment (Tappeiner and Alaback 1989) and so is their subsequent rate of growth (Hanley et al. 2014, Rose 1990, Tappeiner and Alaback 1989, this study), vegetative reproduction (Tappeiner and Alaback 1989), and sexual maturation (in the case of blueberry, Alaback and Tappeiner 1991). Given that flowering, seed, and fruit production are carbon- and energy-intensive processes, it is highly likely that they, too, would be driven by light intensity, at least as threshold responses (Rose 1990, Waring and Schlesinger 1985). Thus, forest managers, especially silviculturists, who are concerned about understory plant communities and production need to think about the understory light environment not only at both stand and landscape scales but also even at microsite scales (i.e., within-stand heterogeneity), and not only at the present time but also in

terms of dynamics within seasons and future years. Hanley et al. (2014) identified two thresholds of light intensity where non-conifer understory species are favored at low intensities and western hemlock seedlings are favored at high intensities. We estimated those thresholds to be about 13 and 53 percent, respectively, of canopy-unobstructed incident light by very simplistic calculations (see "Discussion" section above). The exact values are not important; both are only very rough estimates. What is important is that they indicate a fairly wide range of latitude in managing light environments for understory vegetation before favoring western hemlock too strongly. However, when ground-layer plants such as evergreen forbs are of special concern (e.g., Hanley 1993), then shading effects of the shrub layer also come into play. The naturally high degree of site and canopy heterogeneity and the high-frequency, low-magnitude disturbance regimes of old-growth forests provide a naturally diverse, dynamic, and mid-intensity light environment for understory vegetation. Artificially creating and maintaining such rich light environments in young-growth forests might not be economically feasible, but the ecological principles are still the same and need to be considered throughout.

Our clipping treatments, to simulate removal of biomass by herbivory, were relatively moderate (50 percent removal) and severe (100 percent removal; 75 percent for hemlock). The 50-percent removal is comparable to the old adage of "take half, leave half" in range management (Stoddart et al. 1975) for species lacking more precise "proper-use factors," whereas the 100-percent removal would be considered severe under any possible criterion. The clipping treatments imposed a significant effect on most species (except devilsclub) for growth but not survival (yet). Although the most severe treatment resulted in the smallest sized plants in all six species, it was significantly different from the moderate treatment in only half of the species (table 2). We suspect that the difference in treatment effects must compound with time, however, and that two clipping episodes (each at the end of a growing season) combined with the experimental error associated with variation between replicates was simply not enough to yield statistically significant differences yet. But the most important result from our clipping data was the finding that the clipping effect was only additive instead of interactive with light for four of the six species (table 3), meaning that clipping affected light-stressed plants in the same way that it affected open-grown plants.

Now we can see how these understory plants interact with light and herbivory (both important environmental factors) in southeast Alaska forests: light predominates in determining virtually all life-history events, and understories of old-growth forests are so much more productive than those of dense-canopied young-growth

forests because they have much more light at the critical low-end of light intensities where growth rates are nonlinear and most sensitive to light (Hanley et al. 2014, light-gradient trials). On the other hand, light intensities in closed-canopy young-growth forests are so low that even small variation in canopy structure (gaps, sunflecks) can make the difference of species' persistence (survival) over time. Herbivory exerts a cost on the browsed plant, which even though only additive can be sustained much more easily in high-light environments than low-light environments simply because the growth margin is so much lower in low-light environments. Thus, for any given density of deer on a landscape, open environments (especially, productive, fast-growing recent clearcuts) should be able to sustain relatively high levels of herbivory (when measured as kilograms of forage removed per hectare), while dark, young-growth forests will be especially sensitive. The negative feedback loop between herbivory and foraging efficiency should provide some buffer for forage-poor understories, but if they occur as small patches within otherwise productive landscapes, they may experience a high level of herbivory disproportionate to their relative value as habitat simply because of the overall high density of deer in the general area (e.g., use by deer while traveling through the patch). Similarly, small patches of highly productive forage in an otherwise unproductive landscape (e.g., small gaps within a large area of closed-canopy young-growth forest) should be especially attractive to deer and therefore suffer high levels of herbivory and decreased growth rates disproportionate to what would be expected on the basis of their light environment and the overall low density of deer on the landscape (i.e., deer will actively seek them). Deer population densities, however, are in constant flux with annual variation in weather (e.g., especially winter snow), changing vegetation patterns with disturbance, and lag effects in population dynamics (body condition, fertility, natality, fawn survival, and demographic structure). Where deer population densities have remained high for extended periods of time (e.g., Coronation Island), herbivory can reach levels high enough to significantly reduce forage plant production in even the most productive and open habitats and affect plant community structure landscape-wide (Klein 1965, Lewis 1992). Over most of southeast Alaska, however, deer population densities have been low enough to not exert such a profound influence, and effects of herbivory have probably been most pronounced at the scale of small patches (forest stands or less) and deep-shade environments (Hanley 1987).

The "interesting" examples of potential consequences of herbivory mentioned in the "Introduction" can now be understood more clearly: (1) the high survival of our experimental plants in the dense young-growth forest (Hanley et al. 2014) was observed because we were seeing only the first year of treatment, and one year

alone is insufficient to judge the prospects for long-term survival; and (2) the high productivity of vegetation inside the deer exclosure at Pybus Bay indicates that the light intensity within that stand must surely have been greater than the light intensity under our conifer canopy in this experiment. The sharp contrast between inside and outside the Pybus Bay exclosure, however, illustrates the strong effect that herbivory can exert on a small stand of young-growth forest when deer population density is relatively high in the larger surrounding landscape (the Pybus Bay exclosure was in deer winter range on Admiralty Island, long known for its excellent deer habitat).

Finally, we offer the following points specifically for silviculturists who are developing plans and prescriptions that include consideration of deer habitat in southeast Alaska:

- Light is the most critical environmental factor in these forests, especially at the low intensities common in closed-canopy young-growth forests.
- Variation in canopy structure, and therefore light patterns within the understory, should be very important for maintaining and producing understory vegetation, including diversity in species composition.
- Beware of creating small, productive patches within otherwise marginal, forage-poor deer habitat, because herbivory focused there can negate the desired understory effects. This is a caution about "canopy gap" silviculture treatments for deer habitat on conifer-suitable soils (despite Alaback's recent favorable report for gap treatments[5])—the overall density of deer is the especially critical factor. Also beware of investing limited resources in silviculture treatments to improve relatively small young-growth stands that occur within a larger landscape of relatively high deer densities, because the disproportionately high levels of herbivory (disproportionate to the foraging value of the stands) in those stands may negate the efforts to improve their light environments.
- All considerations of potential effects of herbivory within a silviculture context must be made at a landscape scale, considering the overall suitability of habitat and deer densities, because the level of herbivory experienced within any given stand will be strongly influenced by its larger, landscape

[5] Alaback, Paul. 2010. 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. 32 p. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5404637.pdf.

context. In other words, deer herbivory is an important environmental factor affecting understory plants, but it is not a factor that can be evaluated and manipulated at the stand scale alone. When local deer densities have been monitored and are relatively well understood, that information will be especially useful. In the more usual case where deer data are few and relative density is judged on the basis of sign (abundance of fecal pellets, evidence of browsing), a suitable habitat evaluation model (e.g., FRESH-Deer, Hanley et al. 2012, especially its geographic information system application) could be a very useful complement.

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English Equivalents

When you know:	Multiply by:	To find:
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Liters (L)	.265	Gallons
Grams (g)	.0352	Ounces
Kilograms (kg)	2.205	Pounds
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

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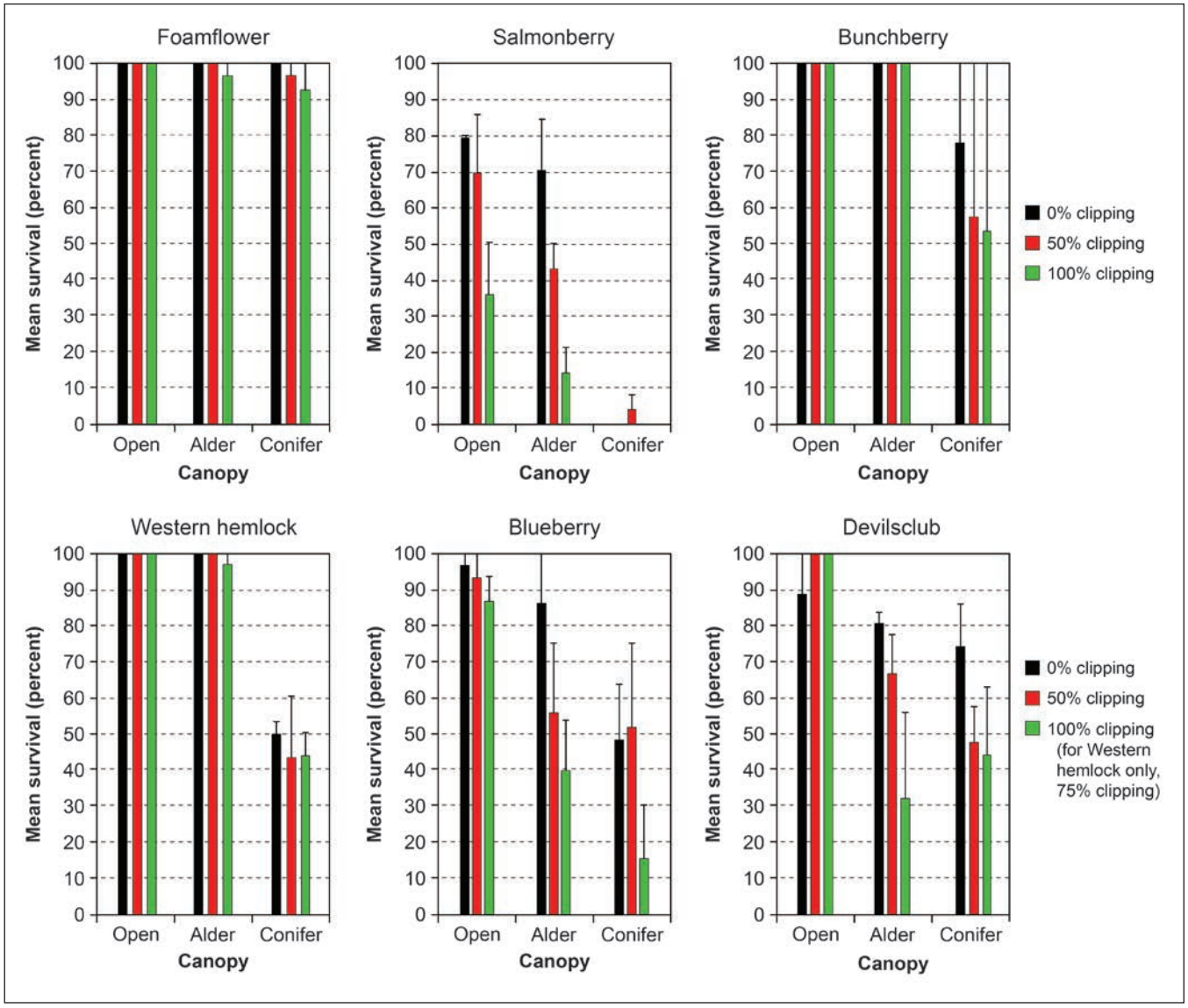
Appendix 1

Mean (+ standard error) survival (percentage of original plants remaining alive) at end of the second growing season, one year after clipping treatments were applied at end of first growing season. These data were not analyzed statistically.



Appendix 2: About the Experimental Design

As explained in footnote 2, our experimental design lacked replication of the alder and conifer light treatments because we had only one stand of each available to us for this work. Therefore, although the two canopies provided very different light intensities for testing our hypotheses about light and its interaction with clipping, our analysis cannot say anything about differences between "alder" and "conifer" canopies per se. Also, we must acknowledge that, from a strictly technical point of view, our light-intensity treatment can be viewed as a case of "pseudoreplication" instead of true replication, because with only one stand of each overstory there was not spatial intermixing of the light treatments. It could be argued that some other, unspecified environmental factor may have varied spatially with canopy, too, and effects of that unknown factor would not be distinguishable from the effects of light.

However, from a practical and much more realistic point of view, we point out that the difference in light intensities between the two overstories was a full order of magnitude, and the two stands were adjacent to one another and both on near-level ground (i.e., no difference in elevation, slope, exposure, etc.). Light intensity in the open area was nearly 6 times that of the alder understory and 60 times that of the conifer understory. Any other factor that we can think of (e.g., light wavelengths, relative humidity, air temperature) would have been independent of spatial replication and therefore not affected by "true replication" (keep in mind that all our plants were in pots, and truly replicated environments would have been similar among replicates). Therefore, unless one argues the potential existence of some unknown factor that depended on spatial location rather than overstory canopy, we argue that the case for bias from pseudoreplication is exceptionally weak here—far too weak to outweigh the insights from the factorial analysis of the data.

Problems from correlation among potential factors independent of true replication (e.g., light, relative humidity, and air temperature all varying together with stand type) are inherent in field experiments. They can't be controlled by replication—they require a laboratory setting (e.g., growth chambers), but that makes the experiment even more removed from the natural environment. Our experiments, using replicated clipping treatments within pseudoreplicated light treatments were a compromise between the natural environment and a more rigorously controlled experiment. Our conclusions and implications must be evaluated accordingly.

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