Red Alder, *Alnus rubra*, as a Potential Mitigating Factor for Wildlife Habitat Following Clearcut Logging in Southeastern Alaska

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Within-stand variation in understory species composition and biomass was studied in 16 even-aged stands of mixed Red Alder - Sitka Spruce - Western Hemlock *(Alnus rubra - Picea sitchensis - Tsuga heterophylla)* forest. The sites were upland sites, and the stands were 28-39 years old. We compared understory within three categories of microsite types: Red Alder-dominated, conifer-dominated, and mixed alder-conifer. Biomass of forbs and ferns differed significantly (P < 0.05) between microsite types, being greatest in alder microsites, least in conifer microsites, and intermediate in mixed alder-conifer microsites for all of the following: *Circaea alpina, Galium triflorum, Tiarella trifoliata, Viola glabella, Athyrium filix-femina, Gymnocarpium dryopteris, Thelypteris phegopteris,* total forbs, total ferns, and total herbs. Shrub biomass also was greatest in alder microsites but was least in mixed microsites and intermediate in conifer microsites (P < 0.05 for *Rubus spectabilis* leaves and total shrub leaves). The greater shrub biomass in conifer than mixed microsites resulted from several large patches of poor tree regeneration within 7 of the 16 stands; the other 9 stands had very low understory biomass in their conifer microsites, which is consistent with published studies of understory dynamics in even-aged stands of the region. The results illustrate two important conclusions regarding current understanding of secondary succession following clearcutting in southeastern Alaska: (1) inclusion of Red Alder in the regenerating stand may result in much greater understory biomass than occurs in pure conifer stands; and (2) extrapolation of data from small, uniform, fully-stocked research stands to the landscape level may underestimate understory biomass from poorly stocked patches. Both conclusions have important implications for wildlife habitat in terms of understory vegetation for food and cover. The potential of Red Alder as a mitigating factor for wildlife habitat following clearcutting in the region needs additional study of disturbance-site-understory interactions. Our results, however, indicate that an understory-exclusionary stage of secondary succession is not necessarily the only successional pathway following clearcutting in southeastern Alaska.

Key Words: Red Alder, *Alnus rubra,* Sitka Spruce, *Picea sitchensis,* Western Hemlock, *Tsuga heterophylla,* secondary succession, understory, biomass, forests.

Land-management practices for timber production and for wildlife habitat often are in conflict in southeastern Alaska. Timber managers prefer clearcut logging as the timber harvest technique for a variety of silvicultural reasons (Ruth and Harris 1979): (1) the old-growth Western Hemlock-Sitka Spruce *(Tsuga heterophylla - Picea sitchensis)* forests have much timber "defect" (dead or dying trunks and limbs) that is best removed from the new stand; (2) maximum opening of the forest canopy provides maximum light and soil temperatures for maximum productivity of regenerating trees; (3) the more commercially valuable Sitka Spruce is less shade tolerant than is the less valuable Western Hemlock; (4) physical damage of the residual or regenerating stand, eventually leading to disease, is minimized; and (5) logging costs per unit of timber harvested are least with the clearcut method. Natural overstocking of the regenerating stand is a common silvicultural problem (Harris and Farr 1974).

Clearcut logging, however, is recognized as having broadly negative consequences for wildlife habitat in southeastern Alaska (Wallmo and Schoen 1980; Schoen et al. 1981, 1988; Samson et al. 1989; Hanley 1993). Dense conifer regeneration and canopy closure result in a very depauperate understory from about 25-150 years stand age (Alaback 1982, 1984a, 1984b). Silvicultural thinnings of the regenerating stand promote tree growth but have insignificant effects on understory, with widely spaced thinnings resulting in a second layer of Western Hemlock regeneration (Deal and Farr 1994). Recent concern about such negative effects on understory and wildlife habitat have prompted new research into selective logging systems (uneven-aged management) with helicopters. Helicopter logging is very expensive, however, and is not likely to be cost-effective on all sites. Selective logging without helicopters is prohibitively costly in the steep, wet terrain, where roading costs are high and damage to residual trees by cable yarding is great.

In a study of riparian forests, Hanley and Hoel (1996) recently reported that understory biomass and species richness of 40-year-old Red Alder *(Alnus rubra)* stands did not differ from that of either old-growth Sitka Spruce riparian stands or old-growth Western Hemlock-Sitka Spruce upland stands. Such productive and diverse understory was contrary to expectations based on stand age-understory relations in the region (also see Deal 1997). Hanley (1996)

subsequently studied small mammal densities and body weights in upland, even-aged, Red Alder -conifer forests in comparison to upland, old-growth forests and found very few significant differences: Densities of Common Shrew *(Sorex cinereus)* and body weights of Sitka Mouse *(Peromyscus keeni sitkensis)* were greater in the even-aged than oldgrowth stands during the second of two trapping periods; and Long-tailed Vole *(Microtus longicaudus)* was more commonly associated with Red Alder microsites than with conifer microsites within the even-aged stands.

The purpose of our study was to describe quantitatively the understories of upland, even-aged, Red Alder - conifer forests to gain a better understanding of their biomass and species composition. Such stands apparently differ significantly from expectations based on stand-age relations in the region (Alaback 1982), and may offer greater prospect for wildlife habitat than has heretofore been recognized. Alaback (1982, 1984a, 1984b) deliberately excluded Red Alder patches from his chronosequence studies, because modern logging methods (high-lead cable yarding) minimize soil disturbance and the subsequent presence of Red Alder. Although Red Alder is a common tree along active channel courses in riparian forests, its presence in upland forests of the region is very minimal without extensive soil disturbance from log skidding or road construction.

We were especially interested in within-stand variation between conifer-dominated microsites (the "typical" successional sequence) and Red Alder-dominated microsites.

Methods

We sampled 16 Red Alder - conifer, even-aged stands scattered throughout Tenakee Inlet on Chichagof Island, Alaska (57° 45' N, 135-136° W) within 500 meters of the beach. Such stands regenerated in the early years of clearcutting shortly after the construction of pulp mills in Sitka and Ketchikan in the 1950s. Large amounts of Red Alder resulted from high degrees of soil disturbance in the early logging methods involving tractor skidding and Aframe yarding of logs (Ruth and Harris 1979). Red Alder establishment was greatly reduced when logging methods changed to high-lead yarding of logs with minimal soil disturbance. Consequently, stands with an extensive Red Alder component tend to be concentrated within a relatively narrow range of ages in southeastern Alaska. Our stands ranged in age from 28-39 years and in size from 10-100 ha.

Field reconnaissance was conducted during June 1997, and included site selection for sampling, aging of each stand by counting growth rings from cores of 10 Red Alders taken at near-ground level, and understory plant collections for species identification and preliminary size-weight estimates. Sampling was

conducted throughout July and August, when understory biomass is at its peak and relatively constant in amount (Hanley and McKendrick 1985). We sampled both understory and overstory on the same transects within each stand: 10 parallel transects, each 200 m long and running perpendicular to the beach, spaced 15 m apart (providing a sample area of about 3 ha per stand).

Understory biomass was sampled at 10-m intervals along each transect (200 stations per stand) within a 0.1-m² quadrat (0.2 X 0.5 m). We chose to sample many small quadrats rather than fewer large quadrats (e.g., 1.0-m²) to obtain a large number of samples and to spread those samples over a large area. We sampled only vascular species and did not include mosses, lichens, and liverworts. Species-specific biomass of all herbs and shrub leaves within each quadrat was estimated by the plant-unit method (Parker et al. 1993): regression equations were developed between oven-dry weight (100°C) and estimated weight for each species; accuracy and precision were checked frequently throughout the twomonth sampling period (the total data base consisting of 982 paired measures). Shrub stems were clipped at ground level, stripped of leaves, and weighed in the field with Pesola spring scales; representative samples were oven-dried for dry-matter coefficients. Tree seedlings (< 2.5 cm diameter at breast height) were harvested, oven-dried, and weighed. An overstory category type ("conifer," "alder," or "mixed") was assigned to each quadrat on the basis of overstory within a 5-m radius of the quadrat center: canopy coverage ≥ 70% relative composition was required for categorizing as predominately "conifer" or "alder," while anything less was "mixed." Mean values for all variables were calculated for each stand for each of the three overstory types.

Every fourth quadrat was used as a point center for the point-center-quarter method (Cottam and Curtis 1956) of sampling forest overstory (50 points per stand) for density, basal area, and species composition. These data were used for descriptive purposes only and were not used in analysis of the understory data.

Statistical analysis of the understory data consisted of species-specific comparisons of "conifer," "alder," and "mixed" microsites across all 16 stands in randomized-block analysis of variance tests (Zar 1974) with stands as blocks and microsites as treatments. Multiple comparisons were tested for significance with Sheffe's test (Wilkinson et al. 1992). An alpha level of 0.05 was the criterion of statistical significance in all analyses.

Results and Discussion

The stands were predominately conifer with a substantial Red Alder component: 35 percent Sitka

Spruce, 21 percent Western Hemlock, and 44 percent Red Alder, on a basal area basis (Table 1). Variation across all 16 stands was relatively low with standard errors ranging from 3-19 percent of their means (dbh of Red Alder, and basal area of Sitka Spruce, respectively). The differences between microsite types, however, were great: the alder sites were 68 percent Red Alder (basal area), while the conifer sites were 60 percent Sitka Spruce and 29 percent Western Hemlock. Conifer basal area within the conifer microsites was similar to that of evenaged conifer stands of similar age throughout southeastern Alaska (Deal and Farr 1994).

Major differences between microsite types occurred in understory biomass, especially among the herbs (Table 2). All of the following had greatest biomass in the alder microsites and least biomass in the conifer microsites: Enchanter's Nightshade *(Circaea alpina),* Sweet-scented Bedstraw *(Galium triflorum),* Foamflower *(Tiarella trifoliata),* Stream Violet *(Viola glabella),* Lady Fern *(Athyrium filix-femina),* Oak Fern *(Gymnocarpium dryopteris),* Beech Fern *(Thelypteris phegopteris),* total forbs, total ferns, and total herbs. It is the herb component that is most difficult to maintain through secondary succession of even-aged stands following clearcutting in southeastern Alaska (Alaback 1982; Hanley 1993).

The shrub component also differed between microsite types (Table 2), but its pattern was not the same as that of the herbs: While biomass was greatest in alder microsites, it was least in mixed, rather than conifer microsites, and statistically significant differences occurred only for Salmonberry *(Rubes spectabilis)* leaves and total shrub leaves. Because the shrub component far outweighed the herb component, the pattern for total understory biomass followed the shrub pattern rather than the herb pattern.

The strong showing of shrubs in the conifer microsite type was surprising. We had expected the mixed type to form a transition between alder and conifer. Closer inspection of the within-stand data, however, revealed that the conifer-type means were strongly influenced by a few patches of poor tree regeneration, where the shrubs were consequently very abundant. Such patches occurred in 7 of the 16 stands; mean total understory biomass of the conifer type in the other 9 stands was 5.46 ± 1.42 (SE) g/m², which is similar to published values for similar aged conifer stands in the region (Alaback 1982).

Current understanding of vegetation dynamics during secondary succession following clearcutting in southeastern Alaska is based on results from research plots that were carefully selected to be relatively homogeneous and representative of site conditions (e.g., Alaback 1982; Deal and Farr 1994). Minimizing within-stand variance is an important and necessary objective of studies of between-stand differences. However, our study illustrates two very important consequences of extrapolating such data to the landscape level: (1) the exclusion of Red Alder patches from the chronosequence yields a very different pattern of secondary succession than is necessarily the case; and (2) the exclusion of patches of poor regeneration within even-aged conifer stands yields a pattern of understory biomass more depauperate than may be the case over a larger area (e.g., the entire stand).

Both of those considerations have important consequences for understory vegetation and wildlife habitat. Although our stands were still relatively young, the understory differences between alder and conifer microsites should be expected to persist for some additional time into the future. Furthermore, we expect that as the Red Alder eventually dies and is replaced by conifers, the resulting conifer stand

TABLE 1. Overstory characteristics of 16 Red Alder-conifer stands in Tenakee Inlet, Alaska (mean ± standard error, range).

Grouping/species	Density (stems/ha)	DBH[a] (cm)	Basal Area (m²/ha)
Entire stands			
Red Alder	426 ± 57, 135-1029	23.0 ± 0.7, 18-28	19.0 ± 2.2, 6-36
Sitka Spruce	365 ± 32, 123-645	18.4 ± 1.3, 15-26	15.0 ± 2.8, 2-39
Western Hemlock	267 ± 45, 39-752	16.8 ± 1.0, 11-24	9.1 ± 1.6, 1-25
Alder Microsites			
Red Alder	799 ± 78, 354-1619	22.5 ± 0.8, 17-29	31.5 ± 1.9, 15-47
Sitka Spruce	141 ± 25, 69-489	15.8 ± 0.9, 9-22	6.0 ± 1.2, 1-20
Western Hemlock	55 ± 18, 9-285	15.0 ± 1.2, 9-22	8.6 ± 4.5, 1-42
Conifer Microsites			
Red Alder	106 ± 13, 0-174	21.5 ± 1.0,17-29	4.9 ± 0.8, 0-11
Sitka Spruce	598 ± 56, 315-1111	20.9 ± 0.8, 12-32	27.3 ± 4.1, 12-77
Western Hemlock	547 ± 105, 160-1793	17.6 ± 1.4, 10-24	13.1 ± 1.9, 4-31
Mixed Microsites			
Red Alder	390 ± 38, 116-645	25.4 ± 1.0, 18-35	20.9 ± 1.9, 8-32
Sitka Spruce	356 ± 33, 71-1072	18.7 ± 1.3, 7-28	12.6 ± 3.0, 1-49
Western Hemlock	201 ± 57, 7-570	16.5 ± 1.8, 6-30	6.2 ± 2.1, 0-32

[a]Diameter at breast height

TABLE 2. Understory biomass (g/m^2, mean ± standard error) of "alder," "conifer," and "mixed" microsite types across 16 Red Alder-conifer stands in Tenakee Inlet, Alaska. Values with different superscripts within a row differ at the alpha level of 0.05, randomized block analysis of variance followed by Sheffm's multiple comparison test. t = trace = < 0.005. Total number of 0.1-m^2 quadrats sampled in each of the microsite types: alder 1283, conifer 1281, mixed 636. L = leaves; S = stems.

Class/species	Alder	Conifer	Mixed
Forbs			
Baneberry *Actaea rubra*	0.04 ± 0.03	0 ± 0	0 ± 0
Enchanter's Nightshade *Circaea alpina*	0.95 ± 0.26[b]	0.10 ± 0.05[a]	0.29 ± 0.12[a]
Fern-leaf Goldthread *Coptis asplenifolia*	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Bunchberry *Cornus canadensis*	0.01 ± 0.01	0.05 ± 0.03	0.01 ± 0.01
Sweet-scented Bedstraw *Galium triflorum*	0.04 ± 0.02[b]	t ± t[a]	t + t[ab]
Cow Parsnip *Heracleum lanatum*	0.89 ± 0.43	0 ± 0	0.48 ± 0.30
Skunkcabbage *Lysichiton americanum*	0.10 ± 0.10	0.17 ± 0.13	0.01 ± 0.01
False Lily-of-the-valley *Maianthemum dilatatum*	0.41 ± 0.14	0.14 ± 0.02	0.25 ± 0.06
Five-stemmed Mitrewort *Mitella pentandra*	0.01 ± 0.01	0 ± 0	0.01 ± 0.01
Rattlesnake-root *Prenanthes alata*	0.02 ± 0.01	0 ± 0	0 ± 0
Five-leaved Bramble *Rubus pedatus*	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Clasping Twisted-stalk *Streptopus amplexifolius*	0.47 ± 0.19	0.43 ± 0.15	1.10 ± 0.45
Crisp Sandwort *Stellaria crispa*	0.02 ± 0.02	0 ± 0	0 ± 0
Foamflower *Tiarella trifoliata*	1.22 ± 0.28[b]	0.29 ± 0.06[a]	0.52 ± 0.14[a]
Stream Violet *Viola glabella*	0.08 ± 0.02[c]	t ± t[a]	0.01 ± 0.01[b]
Total Forbs	4.29 ± 0.57[c]	1.24 ± 0.25[a]	2.71 ± 0.53[b]
Ferns			
Maidenhair Fern *Adiantum pedatum*	0.04 ± 0.03	0 ± 0	0 ± 0
Lady Fern *Athyrium filix-femina*	5.65 ± 0.90[b]	0.75 ± 0.56[a]	2.48 ± 0.78[ab]
Deer Fern *Blechnum spicant*	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.03
Shield Fern *Dryopteris austriaca*	1.30 ± 0.19	1.06 ± 0.20	1.85 ± 0.35
Oak Fern *Gymnocarpium dryopteris*	4.07 ± 0.55[c]	0.75 ± 0.11[a]	2.19 ± 0.38[b]
Beech Fern *Thelypteris phegopteris*	0.81 ± 0.23[c]	0.09 ± 0.05[a]	0.10 ± 0.04[b]
Total Ferns	11.88 ± 1.18[c]	2.65 ± 0.79[a]	6.66 ± 1.11[b]
Graminoids			
Merten's Sedge *Carex mertensii*	0.01 ± 0.01	0 ± 0	0 ± 0
Small-flowered Woodrush *Luzula parviflora*	0.01 ± 0.01	0.02 ± 0.02	0 ± 0
Nodding Trisetum *Trisetum cernuum*	0.05 ± 0.04	t ± t	0 ± 0
Total Graminoids	0.07 ± 0.04	0.02 ± 0.02	0 ± 0
Total Herbs	16.23 ± 1.35[c]	3.91 ± 0.83[a]	9.37 ± 1.38[b]
Shrubs			
Rusty Menziesia *Menziesia ferruginea* (L)	t ± t	0.07 ± 0.07	t ± t
Menziesia ferruginea (S)	t ± t	0.61 ± 0.61	0.05 ± 0.04
Devilsclub *Oplopanax horridum* (L)	4.37 ± 1.81	1.82 ± 1.41	0.52 ± 0.42
Oplopanax horridum (S)	19.32 ± 7.66	19.45 ± 11.90	2.85 ± 2.65
Stink Current *Ribes bracteosum* (L)	0.54 ± 0.23	0.10 ± 0.10	0.01 ± 0.01
Ribes bracteosum (S)	1.67 ± 0.92	0.14 ± 0.13	0.01 ± 0.01
Salmonberry *Rubus spectabilis* (L)	2.23 ± 0.91[b]	0.85 ± 0.34[ab]	0.27 ± 0.12[a]
Rubus spectabilis (S)	6.38 ± 2.74	5.42 ± 2.11	0.61 ± 0.27
Red Elderberry *Sambucus racemosa* (L)	0.23 ± 0.20	0.02 ± 0.02	0.53 ± 0.43
Sambucus racemosa (S)	0.54 ± 0.47	0.03 ± 0.03	2.37 ± 2.29
Early Blueberry *Vaccinium ovalifolium* (L)	0.50 ± 0.40	1.31 ± 0.99	0.16 ± 0.09
Vaccinium ovalifolium (S)	0.98 ± 0.85	5.77 ± 3.48	0.70 ± 0.45
Total Shrub Leaf	7.87 ± 2.19[b]	4.18 ± 1.60[ab]	1.49 ± 0.64a
Total Shrub Stem	28.88 ± 8.38	31.41 ± 13.18	6.59 ± 3.81

Continued

TABLE 2. *Concluded*

Class/species	Alder	Conifer	Mixed
Tree Seedlings			
Sitka Spruce *Picea sitchensis* (L)	0.69 ± 0.34	0 ± 0	0 ± 0
Picea sitchensis (S)	1.34 ± 0.74	0 ± 0	0 ± 0
Western Hemlock *Tsuga heterophylla* (L)	0.73 ± 0.73	0.11 ± 0.11	0 ± 0
Tsuga heterophylla (S)	1.25 ± 1.25	0.21 ± 0.20	0 ± 0
Total Tree Seedlings	4.01 ± 2.12	0.33 ± 0.31	0 ± 0
Total Vascular Biomass	57.00 ± 11.10[b]	39.83 ± 14.77[ab]	17.54 ± 5.46[a]

will have a much more structurally diverse character than that normally associated with even-aged conifer stands. Structural diversity of the overstory is one of the factors believed to be important in maintaining understory in coastal coniferous forests (Franklin et al. 1981; Spies and Franklin 1991). Equally important for wildlife is the strong herb component of the alder microsites. Finally, the patches of poor tree regeneration result in delayed timing of the conifer chronosequence and add to the total understory biomass of the site as a whole.

The significance of these patterns in herb composition and total understory biomass is evident in the presence of abundant and productive populations of Common Shrew, Sitka Mouse, and Long-tailed Vole in mixed Red Alder - conifer stands of southeastern Alaska (Hanley 1996), as well as those of many other species of small mammals and birds reported elsewhere (McComb 1994). Both the abundance of understory (biomass) and its nutritional quality are important. This can be illustrated by a simple conversion of understory biomass to the number of adult, female, Black-tailed Deer *(Odocoileus hemionus sitkensis)* that could be supported at maintenance levels by the food bases of the microsite types (Hanley and Rogers 1989). For simplicity, we base the calculations on digestible energy and assume the following digestible dry-matter values, calculated at the forage-class level from species-specific data for plants collected in August (Hanley and McKendrick 1983): Forbs and ferns, 61.7%; graminoids, 52.8%; shrub leaves, 48.0%; conifer leaves, 29.9%. The resulting summer carrying capacities (deer days use per hectare) from the Hanley and Rogers (1989) algorithm follow: alder microsites, 202; mixed microsites, 73; conifer microsites (all 16 stands), 45; and conifer microsites excluding the seven stands with large patches of poor regeneration, 7. The greater nutritional value of forbs than shrubs, combined with the greater biomass of forbs in the mixed than conifer microsites, results in the greater carrying capacity of mixed than conifer sites despite their lesser total understory biomass.

We believe that these results are important in highlighting a potential value of Red Alder as a miti-gating factor for wildlife habitat following clearcut logging in southeastern Alaska. Red Alder has been considered a weed species by timber managers concerned about its competition with conifers in regenerating stands (Ruth and Harris 1979), yet it might be viewed quite differently if it can help reduce the loss of wildlife habitat now associated with clearcutting in the region. Red Alder can be included in even-aged stands perhaps as simply as by incorporating a certain amount of soil disturbance into the logging operation (Ruth and Harris 1979). However, the necessity for including Red Alder *per se* is not yet clear: Is Red Alder a causative factor in the environment for the understory vegetation; or is its presence simply correlated with that of the understory as a consequence of the initial site disturbance? Much more needs to be learned about ecological interactions between Red Alder, site factors (including disturbance), and understory vegetation before we can design optimal silvicultural applications and prescriptions. That will require additional research into both alder-understory relations and alder-conifer relations (Newton and Cole 1994). Our study is simply a first step that indicates that the potential is there and that an understory-exclusionary stage of secondary succession is not necessarily the only successional pathway following clearcutting in southeastern Alaska.

Literature Cited

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. Ecology 63: 1932-1948.

Alaback, P. B. 1984a. A comparison of old-growth foreststructure in the western hemlock-Sitka spruce forests of Southeast Alaska. Pages 219-226 *in* Fish and Wildlife Relationships in Old-growth Forests: Proceedings of a Symposium, 12-15 April 1982, Juneau, Alaska. *Edited* by W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Alaback, P. B. 1984b. Plant succession following logging in the Sitka spruce-western hemlock forests of Southeast Alaska: implications for management. General Technical Report PNW-173. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 26 pages.

Cottam, G., and **J. T. Curtis.** 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451-460.

Deal, R. L. 1997. Understory plant diversity in riparian alder-conifer stands after logging in Southeast Alaska. Research Note PNW-RN-523. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 8 pages.

Deal, R. L., and **W. A. Farr.** 1994. Composition and development of conifer regeneration in thinned and unthinned natural stands of western hemlock and Sitka spruce in Southeast Alaska. Canadian Journal of Forest Research 24: 976-984.

Franklin, J. F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and **G. Juday.** 1981. Ecological characteristics of old-growth Douglas-fir forests. General Technical Report PNW118. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 48 pages.

Hanley, T. A. 1993. Balancing economic development, biological conservation, and human culture: the Sitka black-tailed deer *Odocoileus hemionus sitkensis* as an ecological indicator. Biological Conservation 66: 61-67.

Hanley, T. A. 1996. Small mammals of even-aged, red alder-conifer forests in southeastern Alaska. Canadian Field-Naturalist 110: 626-629.

Hanley, T. A., and **T. Hoel.** 1996. Species composition of old-growth and riparian Sitka spruce-western hemlock forests in southeastern Alaska. Canadian Journal of Forest Research 26: 1703-1708.

Hanley, T. A., and **J. D. McKendrick.** 1983. Seasonal changes in chemical composition and nutritive value of native forages in a spruce-hemlock forest, southeastern Alaska. Research Paper PNW-312. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 41 pages.

Hanley, T. A., and **J. D. McKendrick.** 1985. Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, southeastern Alaska. Journal of Wildlife Management 49: 103-114.

Hanley, T. A., and **J. J. Rogers.** 1989. Estimating carrying capacity with simultaneous nutritional constraints. Research Note PNW-RN-485. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 29 pages.

Harris, A. S., and **W. A. Farr.** 1974. The forest ecosystem of Southeast Alaska. 7. Forest ecology and timber management. General Technical Report PNW-25. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 109 pages.

McComb, W. C. 1994. Red alder: interactions with wildlife. Pages 131-138 *in* The Biology and Management of Red Alder. *Edited by* D. E. Hibbs, D. S. DeBell, and R. F. Tarrant. Oregon State University Press, Corvallis.

Newton, M., and **E. C. Cole.** 1994. Stand development and successional implications: pure and mixed stands. Pages 106-115 *in* The Biology and Management of Red Alder. *Edited by* D. E. Hibbs, D. S. DeBell, and R. F. Tarrant. Oregon State University Press, Corvallis.

Parker, K. L., M. P. Gillingham, and **T. A. Hanley.** 1993. An accurate technique for estimating forage intake of tractable animals. Canadian Journal of Zoology 71:1462-1465.

Ruth, R. H., and **A. S. Harris.** 1979. Management of western hemlock-Sitka spruce forests for timber production. General Technical Report PNW-8. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon. 197 pages.

Samson, F. B. *[and Committee]* 1989. Conservation of rain forests in Southeast Alaska: report of a working group. Transactions of the North American Wildlife and Natural Resources Conference 54: 121-133.

Schoen, J. W., O. C. Wallmo, and **M. D. Kirchhoff.** 1981. Wildlife-forest relationships: is a reevaluation of old growth necessary? Transactions of the North American Wildlife and Natural Resources Conference 46: 531-544.

Schoen, J. W., M. D. Kirchhoff, and **J. H. Hughes.** 1988. Wildlife and old-growth forests in southeastern Alaska. Natural Areas Journal 8: 138-145.

Spies, T. A., and **J. F. Franklin.** 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-109 *in* Wildlife and vegetation of unmanaged Douglas-fir forests. *Edited by* L. F. Ruggiero, K. A. Aubry, A. B. Carey, and M. H. Huff. General Technical Report PNW285. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Wallmo, O. C., and **J. W. Schoen.** 1980. Response of deer to secondary forest succession in Southeast Alaska. Forest Science 26: 448-462.

Wilkinson, L., M. Hill, J. P. Welna, and **G. K. Birkenbeuel.** 1992. SYSTAT for Windows: Statistics, version 5 edition. SYSTAT, Evanston, Illinois. 750 pages.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey. 620 pages.