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Landscape and Urban Planning 72 (2005) 95–112

LANDSCAPE AND URBAN PLANNING

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Potential management of young-growth stands for understory vegetation and wildlife habitat in southeastern Alaska

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Abstract

I review the current state of knowledge about dynamics of understory vegetation in postlogging succession and responses to silviculture treatments in southeastern Alaska, and I derive implications for future research and development. The classic Alaback [Ecology 63 (1982) 1932] model of postlogging succession has dominated ecological thinking in the region for the past two decades. Understory vegetation is believed to increase dramatically immediately after logging but decrease to near-zero levels as the young stands attain conifer canopy closure. Depauperate understories are believed to persist for >100 years. Early studies indicated that understory response to thinning of even-aged stands is mainly by dominant shrubs and is short-lived; response by herbs, especially forbs, is slight. Western hemlock (*Tsuga heterophylla*) was identified as a potential long-lived, second layer, understory dominant in stands thinned to wide spacing. Recent studies, however, indicate three important deviations from conventional wisdom: (1) Red alder (*Alnus rubra*)–conifer, even-aged stands produce species-rich and high-biomass understories comparable to those of old-growth forests and much greater than similar-aged pure conifer stands. (2) "Commercial thinning" of older, even-aged stands may result in much greater understory biomass, including forbs, than previously thought, but time requirements might be longer than previously thought. (3) Extrapolation of data from small scales of research plots to large scales of timber-management stands tends to greatly overestimate stand homogeneity and underestimate understory biomass of even-aged conifer stands. The new findings provide a basis for renewed research into even-aged stand management in southeastern Alaska. I suggest a two-pronged approach emphasizing autecological studies of light and soil requirements of major understory species coupled with an "engineering" approach to designing optimal understory environments through silviculture. New silviculture prescriptions can be designed for specific understory objectives. Testing and application of new prescriptions is recommended at the scale of timber-management stands through adaptive management studies in collaboration between the Pacific Northwest Research Station and the Tongass National Forest.
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Keywords: Silviculture; Forest management; Even-aged forests; Clearcutting; *Picea sitchensis*; *Tsuga heterophylla*

1. Introduction

Clearcut logging has been the predominant timber-management practice in southeastern Alaska since the advent of large-scale logging in the 1950s. It is a

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doi:10.1016/j.landurbplan.2004.09.015

preferred harvest method for a number of silvicultural reasons (Ruth and Harris, 1979): (1) The old-growth western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) forests have much defective timber (dead or dying trunks) that is best removed from the new stand. (2) Maximum opening of the forest canopy provides maximum light and soil temperature for regenerating trees. (3) The more commercially valuable Sitka spruce is less shade tolerant than is western hemlock. (4) Physical damage of residual trees, eventually leading to disease, is minimized in the regenerating stand. (5) Logging costs per unit of timber harvested are least with the clearcut method. However, natural overstocking of the regenerating stand is a common silvicultural problem following clearcutting of the hemlock–spruce forests (Harris and Farr, 1974).

Even-aged forests resulting from clearcutting are widespread in southeastern Alaska, and clearcutting is expected to continue as a harvest technique. At the close of year 2000, there were over 160,000 ha of Tongass National Forest and about 85,000 ha of Alaska Native corporation forests in an even-aged condition (Eugene DeGayner et al., USDA Forest Service, Alaska Region, Juneau, AK, unpublished report based on data in Forest Service files). The record of decision on the 1997 Tongass Land and Resource Management Plan projected an additional 35,000 ha harvested per decade, with 80% of that harvest by clearcutting. About 100,000 ha of Alaska Native Corporation forests not yet harvested will likely be harvested by clearcutting.

Although clearcut logging is a highly preferred timber-management practice, it is recognized as having negative consequences for wildlife habitat in southeastern Alaska, primarily because of its effects on understory vegetation in the regenerating stand (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). Understory vegetation is very important as food for herbivores and as cover for ground-nesting and ground-foraging birds and small mammals. Silvicultural thinnings of young stands have shown few encouraging results for long-term maintenance of a diverse and productive understory (Alaback and Tappeiner in Hanley et al., 1989, pp. 5–6; Deal and Farr, 1994). Recent observations, however, indicate new potentials for young-growth management along two lines of approach very different from earlier thinking: (1) inclusion of red alder (*Alnus rubra*) in the regenerating stand, leading to an alternative pathway of secondary succession (Hanley and Barnard, 1998); and (2) commercial thinning of older, even-aged conifer stands (Zaborske et al., 2002).

The purpose of this paper is to review the evolution of knowledge about even-aged stand management for understory vegetation in southeastern Alaska, to examine potentials for new approaches based on the most recent findings, and to suggest implications for the future for both research and application.

2. Empirical evidence and theoretical considerations

The 1982 *Ecology* paper by Paul Alaback (Alaback, 1982), based on his Ph.D. research of understory response to postlogging succession, became a classic in the ecological literature for southeastern Alaska. It described the pattern of understory biomass and production along a chronosequence of 60 stands ranging from 3 to >550 years of age, with greatest emphasis on stands <100 years old. The pattern observed by Alaback was clear and dramatic: understory production, especially shrubs, increased strongly within the first decade or two after removal of the forest overstory, but within 25–30 years, understory became overtopped by young conifers and was quickly shaded almost out of existence, and that condition persisted through at least 150 years stand age (Fig. 1). With an anticipated rotation age of about 100 years, even-aged stands 30 years to rotation age appeared very poor as wildlife habitat.

The use of silvicultural thinnings to increase and maintain understory in even-aged stands has not been encouraging. In 1984, Alaback and Tappeiner (P.B. Alaback and J.C. Tappeiner II, Oregon State University, Corvallis, OR, unpublished report) measured understory biomass in twenty-nine 0.4 ha even-aged stands that had been thinned 5–7 years earlier at three levels of between-tree spacing. All stands were a mixture of western hemlock and Sitka spruce and ranged in age from 20 to 72 years when measured by Alaback and Tappeiner. The stands were distributed throughout southeastern Alaska as part of a mensurational study of effects of stand density on tree growth and yield

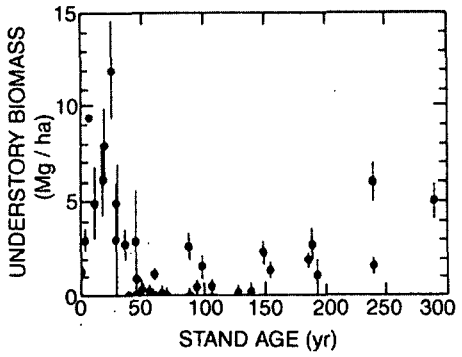

Fig. 1. Total biomass of vascular understory as a function of stand age; the classic paradigm of postlogging succession in southeastern Alaska (Fig. 3 from Alaback, 1982). Dots are mean values of individual stands; bars are 95% confidence intervals.

(DeMars, 2000). Although Alaback and Tappeiner's results were never published independently, they were summarized by Hanley et al. (1989, pp. 5–6; Fig. 2). The results indicated a high degree of variation between stands within the same treatment (thinning intensity) in both young (20–30 years) and older stands (39–72 years). The young thinned stands had 5–10 times more understory biomass than did the older stands. The proportion of biomass in shrubs, forbs, ferns, and trees, however, was relatively constant across stand ages and thinning intensities for both young and old stands. Shrubs (especially *Vaccinium ovalifolium* on better drained sites and *Rubus spectabilis* on wetter sites) composed about 76–92% of the total vascular understory biomass, young conifers composed about 7–23%, and forbs and ferns together composed <1–4%. Hanley et al. (1989) concluded the following:

"These results indicate three potentially important problems with thinning to maintain understory throughout a rotation. First, understory is slow to respond to thinning of older stands that have not been thinned before. Second, the understory that results from thinning is likely to be strongly dominated by two species and to consist almost entirely of woody shrubs

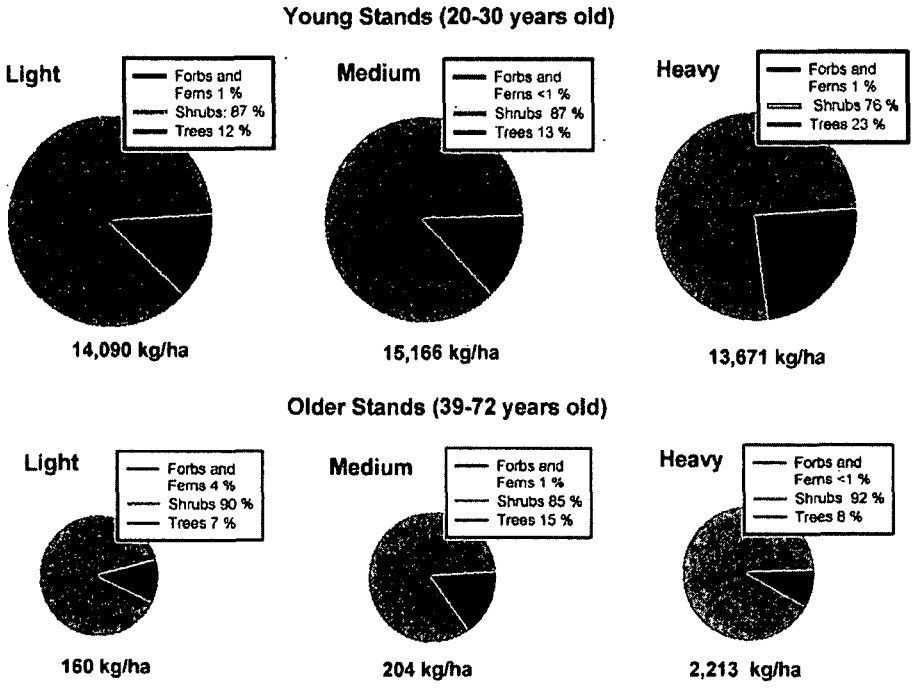

Fig. 2. Biomass of vascular understory of hemlock–spruce stands 5–7 years after thinning at three levels of intensity (light, medium, heavy). Total understory biomass is indicated beneath each circle. (Data are from P.B. Alaback and J.C. Tappeiner II, as reported in Fig. 4 of Hanley et al., 1989.)

and trees, rather than the more balanced distribution of shrubs, trees, forbs, and ferns typical of old-growth forests. And third, as the stand matures, subsequent periodic thinnings will be necessary, and the understory is likely to become increasingly dominated by western hemlock to the eventual exclusion of even the shrubs. Maintaining a floristically diverse and productive understory through a rotation appears to be a more difficult problem than was first thought."

Although few data have been published concerning understory response to silvicultural thinnings in southeastern Alaska, widespread observations of large-scale treatments applied by Forest Service Ranger Districts have been consistent with the results found by Alaback and Tappeiner (Doerr and Sandburg, 1986; DellaSala et al., 1994). Corroborating evidence also came from Deal and Farr (1994) in a study of conifer regeneration in the stands thinned for mensurational study (some of the same stands used by Alaback and Tappeiner). Deal and Farr found that conifer regeneration, especially western hemlock, dominated the understory of both young (<30 years old at thinning) and old stands (31–98 years old at thinning) when visited 9–14 years postthinning. Although the dominant understory conifers in the young stands were about the same age as the overstory trees, the understory of the older stands was dominated by dense, new regeneration that germinated 2–3 years after thinning. The amount of regeneration increased in both age groups with increasing intensity of thinning. Deal and Farr concluded that heavy thinning would likely produce dense understory of conifers, eventually leading to a two-layered conifer stand with very little understory. Similar results and a similar prediction had been reported earlier by Doerr and Sandburg (1986) based on their study of a 34-year-old stand 18 years postthinning. Alaback and Herman (1988) also reported similar results and implications from even-aged Sitka spruce stands along the Oregon coast.

In contrast to the above, forbs typically compose 3–9% of the biomass of old-growth understories, and ferns typically compose another 3–7% (see Table 1 for summary of old-growth forest understory biomass). *Vaccinium ovalifolium* and *Menziesia ferruginea* typically dominate the shrub component of old-growth forest understories, and *Cornus canadensis*, *Rubus pedatus*, and *Lysichiton americanum* are common herb dominants (see Table 2 for summary of old-growth forest species composition).

Theoretical considerations of the mechanisms involved in overstory–understory dynamics of southeastern Alaskan forests primarily centered on the role of disturbance regime. The natural disturbance regime responsible for all-aged, old-growth forests in the region was described as "low magnitude, high frequency" on the basis of predominant patterns of wind disturbance and disease, overstory age structure, and principal modes of reproduction by understory species (Brady and Hanley, 1984). The resulting "gap phase" (Bray, 1956) successional pattern contrasts markedly with the large-scale stand-replacement pattern described by Alaback (1982) following clearcutting.

In addition to the disturbance pattern, however, differential time lags in species responses to canopy gaps also were believed to play a major role in maintaining the high diversity of species and growth forms characteristic of old-growth forests of the region (Hanley, 1991). Although most plants become established early after a canopy gap, they differ in their growth rates and timing of response to the gap. Forbs and ferns respond quickly to a new canopy gap; shrubs require 2 or 3 more years; and conifers need several years beyond the shrub response (Tappeiner and Alaback, 1989). A constantly shifting light environment with high spatial heterogeneity at a relatively small scale (e.g., gaps the size of individual trees or small groups of trees), as in the old-growth forest, combined with time-lag differences in species responses to light, creates a dynamic environment where no single species or growth form attains widespread dominance in the understory.

The high-magnitude, low-frequency disturbance regime of clearcut logging, on the other hand, creates a large-scale, spatially uniform environment, where dominant species replace each other through the pattern described by Alaback (1982). The more that silvicultural thinnings are similar to high-magnitude, low-frequency disturbance regimes, the more likely they will fail to create and maintain a productive and diverse understory. Silvicultural thinnings involving high-frequency, low-magnitude disturbance in young-growth stands (i.e., frequent, individual-tree removal), however, would be very expensive and intensive management.

Table 1
Understory biomass (kg/ha, oven-dry weight) in old-growth stands of southeastern Alaska

	Alaback (1982)	Alaback and Juday (1989)	Hanley and Hoel (1996)	Hanley and Brady (1997)
Number of stands	6[a]	7	4	36
Understory biomass (kg/ha)				
Forbs[b]	97 ± 24	94 ± 18	144 ± 72	161 ± 14
Ferns	157 ± 53	118 ± 49	136 ± 81	53 ± 13
Shrubs	2147 ± 1010[c]	2117 ± 621	3280 ± 402	1637 ± 257[d]
Conifers	–[e]	747 ± 411	–[e]	37 ± 11
Total	2400 ± 1025	3076 ± 494	3562 ± 221	1890 ± 99

Values are mean ± S.E.
[a] Stands ≥250 years old.
[b] Includes minor amount of graminoids (<1 kg/ha total).
[c] Only current year's growth (leaves and twigs) was reported. Total shrub biomass (including stems) shown here was calculated by difference: total biomass − (forbs + ferns biomass), for each stand.
[d] Only current year's growth (leaves and twigs) was reported. Total shrub biomass (including stems) shown here was estimated for each species by applying that species' stem:leaf ratio from Hanley and Hoel (1996).
[e] Conifer biomass was not reported. Conifer seedlings were analyzed by density and height class.

3. Red alder as an alternative pathway of secondary succession

The Alaback (1982) pattern of secondary succession formed virtually the only model of postlogging succession in southeastern Alaska for more than a decade after being published. In the mid 1990s, however, wildlife, silviculture, and stream researchers, working independently, took notice of highly productive, species-rich understories in red alder stands of age classes that would be very depauperate in the Alaback model. Hanley and Hoel (1996) found that understories of 40-year-old, riparian red alder stands (previously clearcut) did not differ significantly from those of adjacent old-growth forests in either species richness or total biomass (Table 3). They differed in species composition from adjacent upland old-growth stands but did not differ from adjacent riparian old-growth stands. Similarly, Deal (1997) reported that understories of mixed red alder–conifer stands had more than twice the number of species and >10 times the canopy coverage of the understory of an adjacent predominantly spruce stand. All stands were even-aged and riparian; the mixed alder–conifer stands were 45 years old, and the spruce stand was 26 years old. Wipfli (1997) found significantly greater abundance of terrestrial-derived invertebrates in stream water from even-aged 31-year-old alder forests than from old-growth hemlock–spruce forests. He attributed the greater invertebrate abundance to the deciduous overstory and to an understory that was both more species-rich and more "dense" in the alder than in the old-growth forests.

All three of those studies highlighted the fact that there exists more than one potential postclearcutting successional pathway in southeastern Alaska, at least within riparian forests. General observations of upland forests quickly lead to extending the alder successional pathway to uplands as well. When large-scale clearcutting began in the 1950s, most logging was done with bulldozers, tractors, and "A-frame" yarding systems (methods of dragging logs to a central site) and resulted in much soil disturbance. Red alder quickly became established on such heavily disturbed sites, and many even-aged stands from the 1950s are mixtures of alder and conifer (western hemlock and Sitka spruce) today. With the advent of high-lead yarding systems in the 1960s, however, soil disturbance was minimized, and red alder did not become a significant component of even-aged stands, except along roads and landings. Thus, there exists an extensive red alder component in upland, even-aged stands throughout the Tongass National Forest, but it is largely limited to a narrow range of stand ages. Alaback (1982) purposely excluded red alder when selecting his stands for study, because he was interested in future implications of postlogging succession, and logging practices by then had virtually excluded red alder from the successional pathway.

Table 2
Understory species composition (production of current annual growth, kg/ha) of two major community associations within upland, old-growth forests of southeastern Alaska[a]

	Blueberry/Goldthread association[b]	Blueberry/Skunkcabbage association[c]
Forbs		
Coptis asplenifolia	4.5 ± 1.4	5.6 ± 2.6
*Cornus canadensis**	23.9 ± 5.0	41.6 ± 6.3
Listera cordata	0.2 ± 0.1	1.3 ± 0.6
*Lysichiton americanum**	0 ± 0	107.2 ± 29.9
Lycopodium spp.	0.4 ± 0.4	6.4 ± 5.5
Maianthemum dilatatum	5.4 ± 3.6	4.1 ± 1.2
Moneses uniflora	6.1 ± 1.6	5.9 ± 1.2
Rubus pedatus	14.7 ± 1.5	13.9 ± 1.6
Streptopus amplexifolius	0.2 ± 0.1	0 ± 0
Streptopus spp.*	0.5 ± 0.1	0.2 ± 0.1
Tiarella trifoliata	4.0 ± 1.8	1.8 ± 0.8
Viola glabella	0.1 ± 0.1	0.5 ± 0.3
Ferns		
Athyrium filix-femina	4.3 ± 2.3	2.6 ± 1.9
Blechnum spicant	12.8 ± 6.4	19.3 ± 10.9
*Dryopteris dilatata**	7.7 ± 2.8	0.1 ± 0.1
Gymnocarpium dryopteris	10.6 ± 3.6	3.9 ± 1.6
Graminoids		
Carex spp.	0 ± 0	0.9 ± 0.6
Shrubs		
Gaultheria shallon	0.3 ± 0.3	6.1 ± 3.5
Menziesia ferruginea	15.6 ± 7.5	73.9 ± 14.6
Oplopanax horridum	6.2 ± 4.8	2.2 ± 1.3
Rubus spectabilis	7.3 ± 4.1	6.6 ± 6.6
Vaccinium ovalifolium[d]	97.4 ± 13.3	128.5 ± 21.3
Vaccinium parvifolium	0.4 ± 0.3	0.8 ± 0.6
Vaccinium spp.[e]	10.5 ± 2.9	8.7 ± 3.4
Conifers (seedlings)		
Picea sitchensis	10.5 ± 9.9	1.6 ± 1.6
Thuja plicata	2.3 ± 1.6	0.1 ± 0.1
Tsuga heterophylla	26.2 ± 9.7	35.8 ± 22.5

Values are mean ± S.E.
* Species that differ statistically ($P < 0.05$) between the two associations.
[a] Data from Hanley and Brady (1997). All values are oven-dry weight. Only species with >1.0 kg/ha in any stand are included.
[b] $N = 19$ stands, Admiralty and Prince of Wales Islands.
[c] $N = 12$ stands, Admiralty and Prince of Wales Islands.
[d] Includes *V. alaskensis*.
[e] Immature, decumbent, evergreen form of *V. ovalifolium*, *V. alaskensis*, and *V. parvifolium*.

Hanley and Barnard (1998) followed up the initial riparian observations with a study of understory composition and biomass in 16 even-aged, mixed alder–conifer stands on upland sites. The stands were 28–39 years old when studied and ranged in size from 10 to 100 ha. Hanley and Barnard used within-stand, microsite (80 m^2) variation to compare understory species composition and biomass under predominantly alder, mixed, and conifer overstories (microsites). They found that biomass of forbs and ferns were significantly greatest under alder overstory, least under conifer overstory, and intermediate under mixed overstory (Table 4). Species composition of alder microsites, however, tended to be more similar to wet or riparian sites than to species more characteristic of upland sites. For example, *Rubus spectabilis*, *Cir-*

Table 3
Biomass (kg/ha, oven-dry weight) of understory species in three forest types[a]

Class/species	Red alder riparian	Old-growth riparian	Old-growth upland
Forbs			
Actaea rubra	2 ± 1	*t* ± *t*	0 ± 0
Circaea alpina	19 ± 2 b	15 ± 1 b	1 ± 1 a
Coptis asplenifolia	0 ± 0	0 ± 0	6 ± 4
Cornus canadensis	0 ± 0	0 ± 0	15 ± 6
Galium kamtschaticum	*t* ± *t*	2 ± 1	0 ± 0
Heracleum lanatum	4 ± 4	3 ± 3	0 ± 0
Impatiens noli-tangere	3 ± 3	0 ± 0	0 ± 0
Lysichiton americanum	25 ± 25	0 ± 0	185 ± 135
Maianthemum dilatatum	13 ± 7	5 ± 3	9 ± 2
Moneses uniflora	*t* ± *t* a	*t* ± *t* a	3 ± 1 b
Osmorhiza spp.	4 ± 1 b	*t* ± *t* a	0 ± 0 a
Streptopus amplexifolius	3 ± 1	6 ± 3	1 ± t
Streptopus streptopoides	0 ± 0	*t* ± *t*	1 ± 1
Tiarella trifoliata	21 ± 7	30 ± 6	3 ± 3
Viola glabella	5 ± 1	5 ± 3	1 ± 1
Total forbs	97 ± 2	64 ± 12	224 ± 136
Ferns			
Athyrium filix-femina	196 ± 112	122 ± 41	3 ± 3
Dryopteris dilatata	31 ± 11	11 ± 5	4 ± 3
Gymnocarpium dryopteris	37 ± 7	108 ± 28	8 ± 4
Polystichum braunii	10 ± 10	21 ± 16	0 ± 0
Thelypteris phegopteris	4 ± 2	0 ± 0	0 ± 0
Total ferns	277 ± 97	261 ± 89	15 ± 4
Shrubs			
Menziesia ferruginea	*t* ± *t*	0 ± 0	475 ± 345
Oplopanax horridum	920 ± 150 ab	2365 ± 35 b	*t* ± *t* a
Ribes bracteosum	1165 ± 275	1445 ± 555	100 ± 100
Rubus spectabilis	83 ± 78	0 ± 0	50 ± 0
Vaccinium alaskensis	0 ± 0 a	0 ± 0 a	965 ± 185 b
Vaccinium ovalifolium	0 ± 0 a	0 ± 0 a	1125 ± 95 b
Total shrubs	2225 ± 165	3845 ± 555	2715 ± 155
Total vascular biomass	2599 ± 67	4170 ± 655	2953 ± 23

Values are mean ± S.E. $N = 2$ stands of each forest type. Values with different alphabetic letters within a row differ at the alpha level of 0.05. *t* = trace = <0.5 kg/ha.

[a] Data from Hanley and Hoel (1996). Conifer seedling biomass was not reported. Only shrubs with ≥20 kg/ha and herbs with ≥2 kg/ha within a stand are listed. See Hanley and Hoel (1996) for other species.

caea alpina, *Galium triflorum*, *Tiarella trifoliata*, *Viola glabella*, *Athyrium filix-femina*, *Gymnocarpium dryopteris*, and *Thelypteris phegopteris* all are species more characteristic of riparian forests than of upland forests (compare with Table 3).

The species-rich and productive understory of red alder and mixed alder–conifer stands has important implications for wildlife. Hanley and Barnard (1999a, 1999b) studied food resources, diet composition, and population dynamics of Keen's mouse (*Peromyscus keeni*) in even-aged red alder riparian, old-growth riparian, beaver-pond floodplain, and old-growth upland forests and found only minor differences in diet composition and no significant differences in population dynamics between habitats. Species of food resources differed between habitats, and abundance of food re-

Table 4
Understory biomass (kg/ha, oven-dry weight) of "alder", "conifer", and "mixed" microsite types across sixteen 28–39-year-old red alder–conifer stands in Tenakee Inlet, Alaska[a]

Class/species	Alder	Conifer	Mixed
Forbs			
Actaea rubra	0.4 ± 0.3	0 ± 0	0 ± 0
Circaea alpina	9.5 ± 2.6 b	1.0 ± 0.5 a	2.9 ± 1.2 a
Coptis asplenifolia	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Cornus canadensis	0.1 ± 0.1	0.5 ± 0.3	0.1 ± 0.1
Galium triflorum	0.4 ± 0.2 b	*t* ± *t* a	*t* ± *t* ab
Heracleum lanatum	8.9 ± 4.3	0 ± 0	4.8 ± 3.0
Lysichiton americanum	1.0 ± 1.0	1.7 ± 1.3	0.1 ± 0.1
Maianthemum dilatatum	4.1 ± 1.4	1.4 ± 0.2	2.5 ± 0.6
Mitella pentandra	0.1 ± 0.1	0 ± 0	0.1 ± 0.1
Prenantheses alata	0.2 ± 0.1	0 ± 0	0 ± 0
Rubus pedatus	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Streptopus amplexifolius	4.7 ± 1.9	4.3 ± 1.5	11.0 ± 4.5
Stellaria crispa	0.2 ± 0.2	0 ± 0	0 ± 0
Tiarella trifoliata	12.2 ± 2.8 b	2.9 ± 0.6 a	5.2 ± 1.4 a
Viola glabella	0.8 ± 0.2 c	*t* ± *t* a	0.1 ± 0.1 b
Total forbs	42.9 ± 5.7 c	12.4 ± 2.5 a	27.1 ± 5.3 b
Ferns			
Adiantum pedatum	0.4 ± 0.3	0 ± 0	0 ± 0
Athyrium filix-femina	56.5 ± 9.0 b	7.5 ± 5.6 a	24.8 ± 7.8 ab
Blechnum spicant	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.3
Dryopteris austriaca	13.0 ± 1.9	10.6 ± 2.0	18.5 ± 3.5
Gymnocarpium dryopteris	40.7 ± 5.5 c	7.5 ± 1.1 a	21.9 ± 3.8 b
Thelypteris phegopteris	8.1 ± 2.3 c	0.9 ± 0.5 a	1.0 ± 0.4 b
Total ferns	118.8 ± 11.8 c	26.5 ± 7.9 a	66.6 ± 11.1 b
Graminoids			
Carex mertensii	0.1 ± 0.1	0 ± 0	0 ± 0
Luzula parviflora	0.1 ± 0.1	0.2 ± 0.2	0 ± 0
Trisetum cernuum	0.5 ± 0.4	*t* ± *t*	0 ± 0
Total graminoids	0.7 ± 0.4	0.2 ± 0.2	0 ± 0
Shrubs			
Menziesia ferruginea	*t* ± *t*	6.8 ± 6.8	0.5 ± 0.4
Oplopanax horridum	236.9 ± 94.7	212.7 ± 133.1	33.7 ± 30.7
Ribes bracteosum	22.1 ± 11.5	2.4 ± 2.3	0.2 ± 0.2
Rubus spectabilis	86.1 ± 36.5 b	62.7 ± 24.5 b	8.8 ± 3.9 a
Sambucus racemosa	7.7 ± 6.7	0.5 ± 0.5	29.0 ± 27.2
Vaccinium ovalifolium	14.8 ± 12.5	70.8 ± 44.7	8.6 ± 5.4
Total shrubs	367.5 ± 105.7 b	355.9 ± 147.8 b	80.8 ± 44.5 a
Conifer seedlings			
Picea sitchensis	20.3 ± 10.8	0 ± 0	0 ± 0
Tsuga heterophylla	19.8 ± 19.8	3.2 ± 3.1	0 ± 0
Total conifers	40.1 ± 21.2	3.2 ± 3.1	0 ± 0
Total vascular biomass	570.0 ± 111.0 b	398.3 ± 147.7 ab	175.4 ± 54.6 a

Values are mean ± S.E. Values with different alphabetic letters within a row differ at the alpha level of 0.05. *t* = trace = <0.05 kg/ha.
[a] Data from Hanley and Barnard (1998).

sources, diet composition, and population dynamics differed greatly between years, but red alder forests were consistently similar to the other habitats in quality for mice.

Similarly, when Hanley (1996) compared small-mammal species composition, densities, body weights, age, and sex ratios in upland even-aged mixed alder–conifer stands (31–36 years old) with adjacent old-growth stands, he found only minor differences: significant differences between forest types occurred only in that the density of common shrews (*Sorex cinereus*) and body weights of juvenile Keen's mice were greater in mixed alder–conifer stands than in old-growth stands. Long-tailed voles (*Microtus longicaudus*) were more commonly associated with alder than conifer patches within the mixed alder–conifer stands, and mice densities were significantly correlated with estimated total understory biomass across all stands.

Hanley and Barnard (1998) used their data (Table 4) to illustrate the importance of plant species composition as well as total biomass in food resources for wildlife. Using a nutritionally based deer-habitat model (Hanley and Rogers, 1989) to convert understory biomass to deer-days use (number of deer days that can be supported at maintenance levels by a given food supply while meeting a specified level of nutrition), they calculated summer carrying capacities (deer-days use per hectare) of their three microsite types. Alder microsites yielded 202 deer-days use per hectare, mixed microsites 73, and conifer microsites 45. The greater nutritional value of forbs compared to shrubs, combined with the greater biomass of forbs in the mixed microsites compared to conifer microsites, resulted in the mixed sites having greater carrying capacity than conifer sites despite their lesser total understory biomass.

Potential use of the red alder successional pathway as a mitigating factor for both wildlife and fish habitat following clearcut logging has recently been studied in a broad, interdisciplinary study of tree growth and yield, bird and fish habitat, invertebrate ecology, geomorphic processes, and disease and decomposition processes in trees (Wipfli et al., 2002). Preliminary results for understory vegetation are consistent with results reviewed above (Deal and Orlikowska, 2002). Moreover, results for invertebrates and bird habitat, are consistent with the hypothesis that mixed alder–conifer stands are significantly better habitat than are pure conifer stands of similar age in southeastern Alaska (Johnson et al., 2002).

Most evidence to date is that greater benefit for wildlife might be accomplished by including red alder when regenerating clearcuts at the time of logging than can be accomplished by silvicultural treatment once even-aged conifer stands are fully established. Another, long-term consideration is that as red alder is eventually overtopped by conifers and dies, the resulting conifer stand will likely be much more structurally diverse than what is usually associated with even-aged conifer stands. Structural diversity of overstory is another factor believed to be important in maintaining understory in coastal coniferous forests (Franklin et al., 1981; Spies and Franklin, 1991).

Red alder might be included in even-aged stands by simply incorporating a certain amount of soil disturbance into the logging operation (Ruth and Harris, 1979). However, very much remains to be learned about the role of red alder in the understory patterns observed to date. For example, it currently is not known if alder has a cause-and-effect relation with these understory patterns, or if alder is simply correlated with the understory in its response to site disturbance. Much more needs to be learned about ecological interactions between red alder, site factors, soil disturbance, and understory before we can design optimal silvicultural applications and prescriptions.

4. Commercial thinning of spruce–hemlock stands, 13–14 years posttreatment

Virtually all thinning in southeastern Alaska has been conducted in young stands (<30 years old) as "precommercial thinning", where cut trees have no commercial value and are left on site as slash. Costs of removing tree boles from older stands exceed the value of their wood, so true "commercial" thinning has not been done. Also, it has been reasoned that understory would more likely respond to precommercial thinning where an existing understory might be maintained, than to thinning of older stands where the understory already has been shaded out.

Thinning of commercial-sized timber, however, was conducted as part of a Forest Service (Alaska Region) demonstration study in 1984–1985 on Prince

of Wales and Kuiu Islands (Zaborske et al., 2002). Its purpose was to see what would happen if older, even-aged stands were thinned as "commercial thinnings" in a way that might be done sometime in the future. The stands were 42–95 years old when thinned in 1984–1985 and had very sparse understories typical of closed-canopy even-aged stands of that age. The Sitka spruce and western hemlock trees were thinned to a between-tree spacing of 6.1–7.6 m (20–25 ft). Much doubt existed about whether understory plants could reestablish themselves and grow significantly before lateral branch growth in the overstory closed the canopy again. Unfortunately, understory response was not measured until 1998, and results are available from only four sites. However, the results obtained in 1998 (Michael H. McClellan, USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, unpublished data) were striking enough to warrant discussion.

The Alaback and Tappeiner data for "heavily thinned, older stands" 5–7 years postthinning (Fig. 2) provide perspective for what might be expected in these commercially thinned stands 13–14 years postthinning. Alaback and Tappeiner found a large response to thinning, with a biomass in the heavily thinned stands about 14 times that in the lightly thinned stands. Almost all the understory, however, was shrubs (92% of total). A "second layer" of young western hemlock seedlings composed most of the remaining understory, with total forb and fern biomass composing <1% of the total understory. Projection of the Alaback and Tappeiner data was that the hemlock layer would increase and the shrub and herb layers would decrease with time. McClellan's data, however, indicate that although conifers composed 42% of the total understory biomass of thinnings after 13–14 years, the herb component was 11% of the total. The relatively large herb component is important, because it is the most difficult component to favor in young-growth stands. Several important results are evident from the McClellan data (Table 5).

First, total understory biomass in the thinned treatments was about 10 times that in the untreated stands. Between-stand variation, however, was great, ranging from a high of 1780 kg/ha in the Shaheen thinning to 839 kg/ha in the Gravelly Creek thinning. Nevertheless, even the Gravelly Creek thinning had more understory biomass than the greatest biomass of any untreated stand (191 kg/ha, also at Gravelly Creek). Total understory biomass of untreated stands ranged from 99 kg/ha (Camden Bay) to 191 kg/ha (Gravelly Creek).

Table 5
Understory biomass (kg/ha, oven-dry weight) and its value as food for black-tailed deer (deer-days use) in thinned and unthinned stands of 56–109-year-old even-aged forests[a]

	Unthinned	Thinned
Understory biomass (kg/ha)		
Forbs	10.5 ± 7.1	27.6 ± 12.6
Ferns	50.6 ± 17.1	145.3 ± 56.6
Graminoids	0 ± 0	0.9 ± 0.1
Shrub leaves	11.3 ± 5.3	106.8 ± 46.1
Shrub twigs	9.0 ± 4.0	70.1 ± 30.3
Shrub stems	36.3 ± 16.1	526.1 ± 287.7
Conifers	26.5 ± 19.6	644.6 ± 345.2
Total biomass	144.4 ± 24.0	1521.4 ± 309.6
Deer-days use (per hectare)[b]		
Maintenance	68.1 ± 17.4	337.6 ± 53.3
Reproduction	16.6 ± 9.9	85.0 ± 31.9

Values are mean ± S.E.

[a] Data are from Michael H. McClellan (USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, unpublished). $N = 4$ sites (Kuiu Island, Camden Bay, Gravelly Creek, and Shaheen). Stands were "commercially thinned" at 20–25-ft spacing in 1984–1985 when 42–95 years old. Understory was measured in August 1998, 13–14 years postthinning.

[b] "Deer-days use" is the number of deer days (one deer day = one adult deer for 1 day) that can be supported by the food resources at a specified daily metabolic requirement. Deer-days use has been calculated for adult, female, black-tailed deer, assuming a summer body weight of 42 kg, under two sets of metabolic requirements: maintenance only and reproduction (maintenance plus peak lactation costs for one fawn). Values for "maintenance only" are as follows: metabolizable energy requirement = 2350 kcal/day; digestible protein requirement = 58.6 g/day; dry matter intake = 1220 g/day. Values for "reproduction" are as follows: metabolizable energy requirement = 3100 kcal/day; digestible protein requirement = 147.0 g/day; dry matter intake = 1470 g/day. See Hanley and Rogers (1989) for details of the model and calculations, Parker et al. (1999) for details of metabolic requirements, and Zaborske et al. (2002) for field and laboratory methods. All values are for summer only.

Second, conifer biomass (mostly western hemlock) was a very substantial component of the biomass in thinning treatments, composing on average 42% of the total biomass. At 645 kg/ha in thinned treatments, it was 24 times that in the untreated stands. However, between-stand variation was great in the thinnings, ranging from 234 kg/ha (Kuiu Island and Gravelly Creek) to 1670 kg/ha (Shaheen). Both amount and variation in conifer biomass were low in the untreated stands, ranging from 0 kg/ha (Camden Bay) to 84 kg/ha

(Shaheen). The Shaheen site was clearly dominated by a conifer understory, both in the thinned stand (94% of total was conifers) and untreated stand (78% of total was conifers). Conifers played a much smaller role at the other three sites, ranging from 19% (Kuiu Island) to 28% (Gravelly Creek) in the thinnings and from 0% (Camden Bay) to 11% (Kuiu Island) in the untreated stands. The Shaheen results demonstrate that western hemlock response can be strongly determined by a site effect, whether thinned or not.

Third, the shrub component showed the second strongest response to thinning, composing 46% of the total understory biomass and with biomass in the thinnings (703 kg/ha) averaging more than 12 times that in the untreated stands (57 kg/ha). Although between-stand variation in biomass was great, the species composition was mostly *Rubus spectabilis* at all four sites. *Vaccinium ovalifolium* also was abundant at all four sites, while *Ribes laxiflorum* was the second-most abundant shrub at the Gravelly Creek site. Other species of shrubs (e.g., *Oplopanax horridum*, *Menziesia ferruginea*), although relatively common, did not dominate any of the understories.

Fourth, biomass of the herb component (forbs, ferns, and graminoids) composed 11% of the total biomass in the thinnings (174 kg/ha) and was almost three times that of the untreated stands (61 kg/ha). It was mostly ferns in both cases (84% of herbs in thinnings, 83% of herbs in untreated stands). Dominant fern species were *Dryopteris dilatata* and *Gymnocarpium dryopteris*, and dominant forb species were *Rubus pedatus*, *Tiarella trifoliata*, and *Cornus canadensis*. All dominant herb species were common in both the thinnings and the untreated stands. The major effect of thinning was to increase the abundance of herbs rather than change species composition strongly. At 174 kg/ha, the herb component of the thinned stands was less than that of most old-growth stands (c.f., Table 1). However, it was much stronger than that of the stands studied by Alaback and Tappeiner (c.f., Fig. 2).

Finally, when the understory biomass and species composition are evaluated on the basis of their food value to black-tailed deer (*Odocoileus hemionus*) (deer-days use per hectare), it is apparent that the thinnings could support about five times the number of deer that could be supported by the untreated stands. The calculation of deer-days use combines the effects of both biomass and nutritional value of all species and plant parts (leaf, twig) into one measure of food value (Hanley and Rogers, 1989). The value at "maintenance level" (see Table 5 for explanation) in the thinnings (338 deer-days use/ha) exceeded that in the red alder understories (202 deer-days use/ha) studied by Hanley and Barnard (1998). In comparison to upland old-growth, even-aged young-growth, and red alder–conifer forests more generally (Fig. 3), the commercially thinned stands provided relatively high food value for deer at maintenance requirements and intermediate value at reproductive requirements. The greater amount of forbs in the red alder–conifer forests than the commercially thinned stands resulted in their

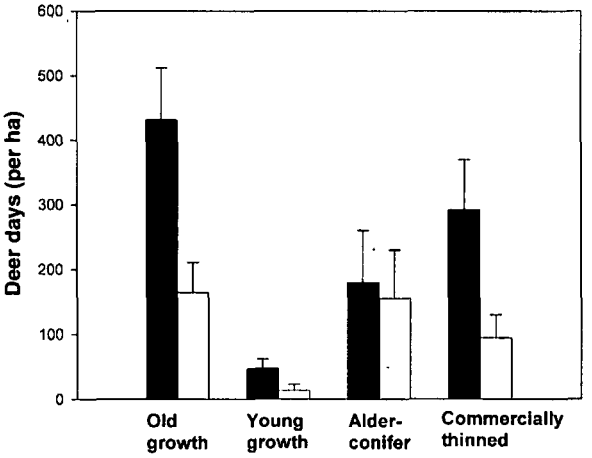

Fig. 3. Potential black-tailed deer carrying capacities (deer-days use; see footnote b of Table 5) of major forest types during summer, based on understory biomass and species-specific values of digestible energy and digestible protein (Thomas A. Hanley, USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, unpublished regional database). Solid bars are for maintenance requirements only; open bars include reproductive requirements. Values are means (±S.E.) of calculations from understory data sets: upland old-growth forests ($N=5$: Hanley and Hoel, 1996; Hanley and Brady, 1997); even-aged young-growth forests ($N=6$: Hanley and Barnard, 1998; Michael H. McClellan, USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, unpublished data; Robert L. Deal, USDA Forest Service, Pacific Northwest Research Station, Portland, OR, unpublished data); red alder–conifer forests ($N=10$: Hanley and Hoel, 1996; Hanley and Barnard, 1998; Robert L. Deal, USDA Forest Service, Pacific Northwest Research Station, Portland, OR, unpublished data); commercially thinned even-aged forests ($N=4$: Michael H. McClellan, USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, unpublished data). Note, data sets range from individual stands to means of up to 19 stands; standard errors provide only a general indication of variation among data sets.

greater value to deer at reproductive requirements. On the other hand, no values have been calculated for winter food supplies, but the commercial thinnings should provide much greater snow interception than that of red alder overstory, so winter food availability would likely be greater in the thinnings than the alder.

Although these commercial thinning results are interesting and encouraging, they also are very few (only four sites), highly variable from site to site, and strictly descriptive. They are consistent with the Alaback and Tappeiner data (Fig. 2) in demonstrating a strong response by conifer seedlings over time and shrub dominance by only two species (*Rubus spectabilis* and *Vaccinium ovalifolium*). However, they demonstrate that the conifer response is highly site specific, also that the herb response might be much greater than expected from a projection of the Alaback and Tappeiner data. The temporal dynamics of conifer seedlings (especially western hemlock) are very important yet remain very unclear now. The McClellan data are too limited to provide guidance for silviculture, but they are encouraging for further research into cause-and-effect mechanisms and temporal dynamics in understory response to thinning older, even-aged stands.

5. Role of landscape heterogeneity

"Landscape heterogeneity" is most commonly thought of as the variation in distribution of habitat patches across the landscape. As such, it can play an important role in providing a variety of habitats to organisms with home ranges larger than the scale of the patches (Kie et al., 2002). Additionally, "edge" habitats result in heterogeneity and unique conditions where two or more habitats abut one another. Habitat heterogeneity at the landscape level has been shown to be important for black-tailed deer in southeastern Alaska by providing variety in structural features (e.g., canopy influence on snow interception) and food resources (Parker et al., 1999). This concept of habitat heterogeneity also underlies the reasoning behind small "gap" clearcuts (several hectares) and residual patches of forest left within larger clearcuts at the smaller scale of stand-level treatment. In southeastern Alaska, however, the benefits of such within-stand cutting regimes remain speculative. In some cases, edge habitats are detrimental (e.g., increased predation on songbird nests; DeSanto and Willson, 2001). Empirical results demonstrating a benefit of within-stand clearcut gaps and residual patches do not yet exist, except at the smallest scale of individual-tree selective cutting (Kirchhoff and Thomson, 1998; Deal, 2001), which is a form of uneven-age management.

Another important consideration of landscape heterogeneity in even-age management does exist at the level of individual stands: variation in topographic relief, soils, and soil drainage patterns results in much site variation within stands in southeastern Alaska, especially when stands are delimited on the scale of tens or hundreds of hectares, which is the usual case. This has important implications for extrapolating empirical results from research plots (usually measured at the scale of 1.0 ha or less) to entire stands. Research plots are small, compared to timber-management stands, and their selection is usually based on maximizing homogeneity relative to the factors under study. Entire stands are not nearly so uniform. Extrapolation of results from research plots to entire stands greatly underestimates the variation that occurs within the stands.

A classic example of the importance of this can be seen in the widespread extrapolation of the Alaback (1982) postlogging successional model to entire stands and landscapes. Alaback's study plots ranged in size from 0.09 to 0.50 ha each and were chosen for being relatively *homogeneous* and representative of site conditions. Features such as red alder, for example (noted earlier), were intentionally excluded; so were low-productivity soils, rocky outcrops, areas of poor conifer regeneration, etc. However, those features and other forms of variability are important components of landscape heterogeneity within stands, and they are completely excluded from the picture portrayed by extrapolating the Alaback results to entire stands.

Alaback's study plots were entirely appropriate for the purposes of his study (comparison of variation *between* stands of different ages), but are not appropriate for describing either variation within stands or mean stand conditions. An example of the implications of this can be seen in Hanley and Barnard's (1998) study of understory in mixed alder–conifer, even-aged stands (Table 4), where total shrub biomass in the conifer microsites was more than four times that in the mixed alder–conifer microsites. The Alaback successional model would have predicted that 28–39-year-old conifer patches would have extremely low biomass

of all understory and certainly not such high levels of shrub biomass (measured at 398 kg/ha total understory biomass; 356 kg/ha shrub biomass). Indeed, that was exactly the case for 9 of the 16 stands, which averaged only 55 kg/ha total understory biomass. However, the results from 7 of the 16 stands were strongly influenced by a few patches of poor tree regeneration, where shrubs were consequently very abundant. Those seven stands supported very high levels of biomass at the stand level (averaging 839 kg/ha total biomass), even though they certainly also had much near-zero-biomass habitat in their more "representative" and homogeneous areas. The poorly stocked inclusions in the stands were picked up by Hanley and Barnard only because they were sampling entire stands rather than small research plots. This is an important lesson to keep in mind when applying research results from studies conducted at one scale to applications at another scale.

When variation in logging disturbance combines with variation in site characteristics, individual timber-management stands can be highly heterogeneous indeed. Such heterogeneity greatly limits the information content of mean values of stand attributes (e.g., understory biomass). Animals do not use habitat uniformly, and rich patches within stands can contribute much more toward habitat quality than would be indicated by the mean values for the entire stand. Widespread sampling and measures of variation (e.g., standard deviation), therefore, are important factors to consider when evaluating even-aged stands. Similarly, timber management that includes within-stand variation in logging disturbance can increase the within-stand heterogeneity of even-aged stands beyond what might be expected from site variability alone.

6. Implications for research, development, and application

Although it appears that significant progress might be made in managing young-growth stands for understory vegetation as well as overstory production, the ideas discussed in this review need much work in research, development, and application. We are currently at the stage of initial observations and speculation about what might be accomplished with silviculture. We need a sound understanding of cause-and-effect relations between environment and plant responses in order to design silvicultural prescriptions to achieve specified objectives. Moreover, we need to field-test the applications of such prescriptions through large-scale adaptive management studies.

We currently suffer major limitations in our scientific knowledge of ecological factors controlling understory response to stand management in southeastern Alaska. For example, what is the ecological role of red alder in the "alternative successional pathway"? Does red alder have a cause-and-effect role in creating a desirable environment for understory vegetation, or are red alder and its associated understory species simply correlated with one another after responding similarly to soil disturbance (and exposed mineral-soil seedbeds) during logging operations? We need to learn the effect of red alder overstory on the light environment of the understory. How does it differ from that of pure conifer even-aged stands? We also need to learn the effects of red alder on soil structure and nutrients. We already know that red alder is a nitrogen fixer, and that its nitrogen-rich, cation-rich, deciduous leaves add significant quantities of nitrogen and organic matter to the soil (Hibbs et al., 1994), but we know little about rates and magnitudes of such change in the very wet, cool forest environments of southeastern Alaska. We also know little about understory species' responses to such changes in light and soil environments.

What about the role of time in understory response to thinning of pure conifer stands? An understanding of the temporal dynamics of understory response to thinning requires understanding a host of mechanisms controlling the response: (1) seed sources and reproductive ecology of major understory species, (2) seedling establishment, (3) growth and competition with other understory species, (4) the changing light environment postthinning and species differences in requirements for light.

6.1. Research and development

The list of needed information appears at first to be inexhaustible, but priorities can be identified through a process of model formulation and consideration of information needed for "engineering" understory objectives. Our current knowledge is strongly empirical, based on descriptions of understory communities in given environments. Experimental manipulations and controlled-environment studies are extremely few. We

need to formulate a theory of plant response to environment, aimed strongly at the level of individual plants first, and then build to the community as an aggregate of individuals and species. The theory should be able to explain the reasons underlying our empirical observations and, more importantly, enable us to predict responses to new silvicultural treatments.

6.1.1. A preliminary model

As a beginning, I offer the following simple model of plant response to understory environment in southeastern Alaska: (1) Light is the most important environmental factor limiting understory production. (2) Plant germination and early establishment is directly linked to light intensity, and plant species differ in their potential rates of response to changes in the light environment. (3) Plant species also differ in their minimum requirements for light and their growth rates in relation to light. (4) Many understory species may survive under low intensity of light common in even-aged, young-growth stands, but their production is minimal, and they are very susceptible to death from other environmental stresses (e.g., herbivory). Therefore, understory species composition, production, and dynamics are the result of: (1) differential time lags in species responses to light, (2) differential species productivity in relation to light, and (3) dynamics of change in the understory light environment. This is a highly simplistic model, but it is a starting point that can be elaborated as necessary.

Preliminary examination of life history characteristics of common understory species of southeastern Alaska (Brady and Hanley, 1984) indicates that evergreen growth form and vegetative reproduction are very common in the region. Both characteristics are consistent with a "stress-tolerant growth strategy" (Grime, 1979), where understory plants survive but grow very slowly in poor light environments. A sudden improvement in the light environment (through change in overstory) allows such species to respond with rapid growth relatively quickly, although species differ in their rates of response (Alaback and Tappeiner, 1991). When plants establish from seed, their establishment and survival are directly correlated with the amount of light they receive (Tappeiner and Alaback, 1989).

Once plants are established, their growth rates are strongly dependent on quantity of light, and species differ in their growth curves in relation to light (production of biomass as a function of quantity of light). Greenhouse experiments currently underway with five common species showed substantial differences in growth curves in relation to light. All four understory species (*Cornus canadensis*, *Vaccinium ovalifolium*, *Rubus spectabilis*, *Oplopanax horridum*) grew more than western hemlock at lowest intensities of light (<30% full greenhouse light), whereas western hemlock did best at high intensities of light (>60% full greenhouse light) (Bernard Bormann, Mark Nay, Thomas Hanley, Jeffrey Barnard, USDA Forest Service, Pacific Northwest Research Station, unpublished data). Relative growth rates among the understory species changed with light intensities, too: *Cornus canadensis* greatest at lowest light and *Vaccinium ovalifolium* greatest at intermediate to high light. In manipulation field experiments currently underway with the same five species, all species showed greater production under red alder canopy than under conifer canopy, but soil type (alder versus conifer) was important only for two species (*Vaccinium ovalifolium* and *Rubus spectabilis*, both doing better in organic soil than mineral soil) (Thomas Hanley, Jeffrey Barnard, Bernard Bormann, Mark Nay, unpublished data). Light intensity under the alder canopy averaged about 18% of full sunlight, whereas that under the conifer canopy averaged about 2% (Jeffrey Barnard and Mark Nay, unpublished data). In other words, understory light intensity was low in both forest types but under alder was about nine times that under conifers.

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 from mammalian herbivores with fencing. A similar understory response to fencing was observed by Hanley (1987) in an examination of understory response to deer exclosures in southeastern Alaska: the one exclosure that occurred in an even-aged stand (~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% of the biomass within the 21-year-old exclosure was western hemlock seedlings, 309 kg/ha was shrubs and herbs. The low biomass of understory outside the exclosure was typical of that expected from the Alaback (1982) secondary succession model, yet the exclosure demonstrated that

herbivory by deer had played a major role in the understory vegetation at the Pybus Bay site. The combination of recent (current field experiments) 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, there have been no experimental tests of this idea.

6.1.2. "Engineering" understory objectives

What sorts of information are needed to design silviculture prescriptions for specific understory objectives? First, recognizing that we cannot study the autecology of all species, it is important to select a few major understory species for intensive study and rely on empirical relations for responses by associated, lesser species. Western hemlock is perhaps the single most important species, given its potential effect of forming a dense, second layer of canopy within understories (Deal and Farr, 1994). Among the shrubs, *Vaccinium ovalifolium* and *Rubus spectabilis* certainly appear to be major species in silvicultural thinnings (P.B. Alaback and J.C. Tappeiner II, Oregon State University, Corvallis, OR, unpublished; M. McClellan, USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, unpublished); *Oplopanax horridum* is a major species in the red alder successional pathway (Hanley and Barnard, 1998). *Gymnocarpium dryopteris* is about the most abundant and common fern in both thinnings and red alder stands, and major forbs are *Cornus canadensis*, *Tiarella trifoliata*, and *Rubus pedatus* (P.B. Alaback and J.C. Tappeiner II, Oregon State University, Corvallis, OR, unpublished; M. McClellan, USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, unpublished). In addition to those eight species, others could be added as resources permit.

Second, we need to understand light, temperature, and soil requirements for germination and establishment. We already know that all of the species above, except western hemlock, reproduce vegetatively, but we know little of their requirements for establishment from seed or their rates of response in vegetative reproduction as a function of environment.

Third, we need to know each species' requirements for light and nutrients for growth and reproduction—e.g., growth curves in relation to light, factorial experiments testing interaction of light and nutrients. Is the role of light, at intensities normally experienced in southeast Alaskan forests, so overwhelmingly important that we can focus our attention primarily on light? Or must we include soil factors as well?

Fourth, we need to understand how various silviculture treatments change the understory light and soil environments, and how those changes vary with time after treatment. In other words, we must understand both the environmental consequences (light, nutrients) of silviculture treatments and the dynamics of the understory environment through time. By developing quantitative relations (e.g., regression models) between-stand attributes and understory environment, we can design silviculture treatments to create desired environmental conditions.

The engineering of silviculture for understory objectives combines all of the above information by first specifying the desired environmental conditions (e.g., light levels) and their changes through time, and then designing the silviculture prescription to create those conditions. For example: (1) If forbs respond most quickly to increased light, and western hemlock responds most slowly, we might want a silviculture prescription that begins with a relatively light-starved environment and then opens the overstory canopy abruptly. (2) If western hemlock requires more light for growth than do forbs, then we might want the overstory canopy to fill in before the western hemlock seedlings can begin shading out the forbs. (3) Once our desired understory is established, we would want to maintain a light environment that would be sufficient for the forbs but insufficient for the western hemlock. This hypothetical example might be exactly what happened in the "commercial thinning" trials discussed earlier. However, without sufficient knowledge of the autecology of major species, we do not know whether such an explanation is plausible, whether western hemlock is likely to increase or decrease in abundance in those stands, or how we might design even better treatments for specific objectives.

6.2. Application

Application of research provides its ultimate test. The most valuable application would be through large-scale adaptive management studies coordinated between the Tongass National Forest and the Pacific

Northwest Research Station. Adaptive management studies can test predictions from theory while also determining practical limitations to silviculture prescriptions. Although research focused on relatively small experimental plots can yield our best understanding of cause-and-effect relations necessary for developing predictive theory, the application of that theory is best tested at large scales under conditions typical of "real world" operations. Large-scale tests would include within-stand landscape heterogeneity, and they could be applied over wide-ranging geographic distribution within the Tongass National Forest. Statistically significant results of such large-scale experiments would have important implications for future land management.

The major requirements of adaptive management studies include the following: (1) large scale: the same scale as would be applicable for land management; (2) replication: multiple trials of the same treatment, preferably over a large geographic area; (3) untreated controls providing a reference for comparison of the effects of the silviculture treatments; and (4) randomization in the assignment of treatments (including controls) to stands. Ideally, one replicate of each treatment (and control) would be identified within clusters of stands scattered widely throughout the region. All treatments (and control) would occur within each cluster. Which treatment (and the control) would be assigned to which stand within a cluster would be determined entirely randomly. The more clusters (replicates) in the design, the better. Each cluster also would act to statistically "block" the effects of geographic variation. Although this might describe the ideal large-scale study design, other variations might be more appropriate for specific purposes.

Adaptive management studies could be designed to test predicted outcomes from specific silviculture prescriptions, or they could be designed to develop an empirical database of stand response to given treatments (in the absence of specific predictions). In either case, silviculture studies require many years, especially if temporal dynamics are of interest. Logistical problems of coordination of personnel and contractors, routine data collection, and database management certainly are not minor or easily resolved. However, the rewards from conducting a carefully selected set of adaptive management studies would pay large dividends in future management. Consider how much more we already would know today, if even a very small proportion of the thinned stands to date had been incorporated into a study design.

7. Conclusions

Early investigations of the dynamics of understory vegetation during postlogging succession and its response to silvicultural thinnings indicated significant problems in maintaining a species-rich and productive understory. However, reliable, quantitative data were few, and published scientific reports were even fewer. Early investigations focused on treatments applied evenly within relatively homogeneous, small areas within even-aged, spruce–hemlock stands. Stand management practices at that time (1980s) emphasized large scale, uniform treatment and even-aged stands (e.g., clearcutting, precommercial thinning to uniform spacing). In retrospect, it is not surprising that understory response to thinning was dominated by one or two shrub species and was short-lived at best. Today, we have a much greater appreciation for the importance of within-stand heterogeneity in site characteristics and, especially, timing and magnitude of disturbance. Recent studies indicate that soil disturbance during clearcutting can profoundly alter the course of postlogging succession, depending on whether the regenerating stand becomes pure spruce–hemlock or becomes mixed red alder–conifer. Furthermore, we have recently seen some encouraging results in understory response to thinning of older, "commercial"-aged stands. Recent studies provide encouragement that silvicultural solutions to conflicting demands in multiple use management might yet be found for the forests of southeastern Alaska. They also highlight the importance of learning more about the ecology of major understory species and how silviculture treatments affect their environment.

Almost all research to date, for silviculture in southeastern Alaska, has been descriptive. Research of understory ecology has been conducted there for little more than two decades, and widespread, intensive management of young-growth stands has been underway for even less time than that. Nevertheless, it is time now for research to begin focusing on cause-and-effect relations controlling understory response to stand management, and it is time for timber management to exper-

iment with innovative techniques within an adaptive-management framework. Description is the beginning of scientific process; experimentation is the basis for predictive theory. Predictive theory is what is needed for designing silviculture and management plans of the future.

The studies and results reviewed in this report are only the beginning of understanding the ecology of understory vegetation in young-growth stands of southeastern Alaska. Need for greater understanding and new silviculture prescriptions is huge, as more than 200,000 ha of even-aged stands already are in early stages of postlogging succession, and many more will be in the foreseeable future. Although the challenges of maintaining understory vegetation within young-growth, even-aged stands are substantial, the rewards will be seen in significantly improved wildlife habitat throughout southeastern Alaska and significantly reduced conflict between resources in a paradigm of sustained, multiple use within an ecosystem-management context.

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