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Plant Succession Following Logging in the Sitka Spruce-Western Hemlock Forests of Southeast Alaska: Implications for Management

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EDITOR'S
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Abstract

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Preliminary information on general landscape patterns in southeast Alaska suggests that two major, compositionally distinct vegetation zones can be defined for the closed-forest type: western hemlock-Sitka spruce/Alaska huckleberry/bunchberry on the uplands, and Sitka spruce/devils club-salmonberry on alluvial flats and terraces.

Recent clearcuts (0 to 30 years old) produce the most shrubby vegetation of any age class in the forest succession. Even-aged forests (30 to 150 years old) produce the least understory vegetation. Uneven aged, old-growth forests sustain the most structurally diverse understory vegetation. Forests with open, patchy canopies tend to produce the most understory vegetation. More data is needed before forest management techniques can be successfully used to improve the quality of habitat for wildlife over that presently found in unmanaged old-growth forests.

Keywords: Succession (secondary), biomass, understory layer, logging effects, logging (-wildlife, old-growth stands, wildlife management, Alaska (southeast), western hemlock, Sitka spruce.

Summary

Preliminary information from several studies of vegetation dynamics in southeast Alaska suggests that silvicultural thinning may enhance understory productivity in young even-aged (<100-year-old) stands, yet there are no data at this time to suggest that silvicultural thinnings or timber rotations less than 200 years will measurably increase either the diversity or productivity of understory vegetation over that typically found in old-growth forests. Repeated thinnings may be necessary to maintain a high rate of understory productivity in second-growth stands. More data are needed before forest management techniques can be successful in improving the quality of habitat for wildlife over that presently found in unmanaged old-growth forests.

Increased understory growth tends to be associated with environmental factors that are related to decreased canopy density, low stocking, and reduced tree vigor. Thin, rocky soils and alluvial terraces tend to have the most productive understory vegetation and the least dense overstory canopy. Windthrown stands have highly variable understories, depending on the frequency and intensity of disturbance.

The same general pattern of successional development has been documented over a range of site conditions, although sites on alluvial flats or terraces dominated by Sitka spruce tend to develop a productive understory in the earliest stages of stand development and have a rate of successional development more variable than most upland sites. Prior to closure of the overstory canopy, stands with high site indices (>120) have significantly greater understory productivity than stands with low site indices (<110). Site index is not significantly related to understory productivity over the range of post-canopy closure sites that have been sampled.

To evaluate long-term management alternatives, we need to better define the relationships of site conditions, forest canopy structure and understory growth so that more realistic predictions of understory responses to management can be made. Changes in forest nutrient cycling, snow interception, and overall microclimate that result from management have yet to be studied in southeast Alaska. The value of intensively managed forests to wildlife throughout a forest rotation remains a key topic for future research.

Contents

Introduction

Populations of wildlife in Alaska are often limited by the availability of suitable habitat (Klein 1965, Van Horn 1981, 1982, Wallmo and Schoen 1980, Wolff 1980). The relafionship of habitat to animal density has been the focus of numerous studies in wildlife ecology but is still poorly understood.

Wildlife habitat has three basic components: forage, cover, and microclimate. Each species of wildlife has requirements that vary with genetic and behavioral plasticity, time of day, season of year, competition, and climate. Habitat require-. ments may also vary with geographic location. The value of specific sites also depends on the interactions of snow accumulation, habitat diversity, travel corridors, predators, and diseases.

The availability of nutritious understory herbs and shrubs, in snow-free environments, is generally considered the key habitat factor that limits Sitka black-tailed deer in Alaska (Bloom 1978, Schoen and Wallmo 1979, Wallmo and Schoen 1980). For forest bird populations, the abundance of understory plant species and their vertical stratification and diversity are key habitat factors in Alaska and the Pacific Northwest' (Meslow 1978, Meslow and others 1981). Changes in populations of mammals have also been related to changes in understory structure (Harris and others 1982, Van Horn 1981, 1982).

In view of the importance of understory vegetation to many wildlife species, the response of understory vegetation to management should be a key factor in management decisions. To evaluate the potential of forest sites for wildlife habitat it is necessary to predict the response of understory plant species to natural and human-caused disturbances. The accuracy of predicting management impacts on wildlife populations is limited by a lack of information on both the habitat requirements of wildlife species and the response of vegetation to perturbation.

This study had three primary objectives:

1. To summarize knowledge about the response of forest vegetation to natural and human disturbance in the Sitka spruce-western hemlock forests of southeast Alaska.

2. To illustrate how site characteristics and management activities affect the productivity and composition of understory vegetation.

3. To outline research needs and directions on the relationship of stand characteristics to understory vegetation growth and abundance.

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[1] Kessler, Winifred, B. Bird population responses to clearcutting in the Tongass National Forest of southeast Alaska. Juneau, AK: U.S. Department of Agriculture, Forest Service, Alaska Region; 1979; Rep. 71. 22 p.

Forest Plant Communities of Southeast Alaska

The response of understory vegetation to disturbance varies with the environmental characteristics and history of sites. Environmental characteristics are reflected by the plant community that characterized the site before disturbance. A statewide hierarchical vegetation classification has been proposed to define these plant communities for Alaska (Viereck and Dyrness 1980). This classification is most nearly complete for interior and northern Alaska. Detailed information on plant community patterns in southeastern Alaska is lacking. Vegetation studies in southeast Alaska have focused on broad landscape patterns and corresponding environmental gradients. The transition between muskeg and the forest vegetation in southeast Alaska was the subject of one major study, but it did not include data relevant to development of a community classification (Neiland 1971). A life-form classification for the vegetation of the Glacier Bay area was the subject of another study, but it did not include information on specific-plant communities within each of the physiognomic vegetation units (forest, subforest, spruce parkland, deciduous shrublands).[2]

A classification system has been developed for southeast Alaska which divides forested land into classes based on soil morphology.[3] The classification was designed to relate soil types to forest productivity classes (site index of dominant Sitka spruce at 100 years of age). Although the classification relates well to broad site-productivity classes, each type encompasses a broad range of forest types (and site indexes) and is not closely related to plant communities.

The only vegetation-based land classification that has been proposed for southeast Alaska is a broad-based, zone-level classification.[4] As with the soils classification, this scheme is insufficient for stratifying the response of vegetation to disturbance. Two forest community types, for example, cover most of the commercial forest land on the Tongass National Forest: Sitka spruce and western hemlock-Sitka spruce (table 1).

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[2]Worley, I. A. Plant community analysis. In: Dixon Harbor Biological Survey, Final Report on the summer phase of 1975 research. Juneau, AK: U.S. Department of the Interior, Park Service; 1977; p. 126-239.

[3]Stephens, F. R.; Gass, C. R.; Billings, R. F.; Paulson, D. E. Soils and site index in southeast Alaska. Juneau, AK: U.S. Department of Agriculture, Forest Service, Alaska Region. 1969. 67 p.

[4]Alaback, Paul B. Provisional plant community types of southeastern Alaska. Fairbanks, AK: U.S. Department of Agriculture, Forest Service, Institute of Northern Forestry. 1979.

Table 1—Closed forest types of southeast Alaska[1]

Type	General location
Closed conifer forest:	
1. Sitka spruce	Alluvial floodplains or terraces and shorelines
2. Sitka spruce-western hemlock	Extensive below 1500 feet; transition between types 1 and 3
3. Western hemlock-Sitka spruce	Extensive below 1500 feet; more widespread than type 2
4. Western hemlock-western redcedar	South of Frederick Strait; on average to poorly drained sites
5. Pacific silver fir	Localized east and south of Ketchikan; on well drained slopes protected from salt spray; below 2000 feet
6. Mountain hemlock	Near timberline, generally above 1500 to 2000 feet; where winter snow-pack persists and saturated organic soils occur
7. Mountain hemlock-western hemlock	Transition to mountain hemlock from type 3; 0 to 2500 feet but generally above 1000 feet, with a longer snowpack than type 3
8. Subalpine fir	Isolated pockets on Prince of Wales and Kosciusko Islands and other locales; associated with mountain and western hemlock
Closed hardwood forest:	
11. Red alder	Riparian, often on wet and disturbed sites; generally below 2000 feet; seral to types 1 through 4
12. Black cottonwood	Recently deglaciated terrain with thin, rocky soils; also on and along streams; seral to types 1 through 4

[1]Adapted from Viereck and Dyrness 1980.

Forest Development Following Disturbance

Ecologists initially conceptualized plant succession as a unidirectional progression of plant species that results in a "climax" or self-perpetuating community. Studies of forest succession have consistently indicated that the process is far more complex. In their review of more than 100 years of the world literature on plant succession, Drury and Nisbet (1971) conclude that initial conditions, combined with disturbance during the successional sequence, exert a major influence on patterns of forest development. In southeast Alaska the type and intensity of disturbance also plays an important role in determining the course of plant successional development.

Primary Succession

Plant succession that involves colonization of rock or soil that has been completely denuded of vegetation is generally referred to as "primary succession" (Whittaker 1975). Under the austere microclimatic conditions characteristic of seedbeds that undergo primary succession, forest development proceeds slowly and involves many stages, as defined by changes in dominant plant species. Shallow soils, low in moisture-holding capacity and suboptimal in nutrient availability are the most likely cause of slow and variable vegetative response during primary succession[5] (Crocker and Major 1955).

Primary succession has been studied in Alaska for more than five decades. Plant succession at Glacier Bay following deglaciation has been documented by information on glacial retreat and remeasurement of a series of permanent plots (Cooper 1923, 1939, Lawrence 1958, Reiners and others 1971). Four general stages of plant community development are recognized: (1) pioneer, (2) willow-alder, (3) spruce forest, and **(4)** climax spruce-hemlock (Cooper 1923, Reiners and others 1971).

The most variable rate of plant colonization and growth occurs in the pioneer stage of primary succession, in which mosses and lichens (such as *Rhacomitrium* and *Stereocaulon*)[6] are the most common species. **As** soil development proceeds, herbs adapted to disturbed areas, such as fireweed, *Dryas,* and horsetail begin to colonize. Prostrate shrubs such as willow and bearberry may also occur during this stage.

The willow-alder stage is characterized by the dominance of woody shrubs and tree saplings. Sitka alder, black cottonwood, Sitka willow, and Alaska willow are the most common species during this stage. Sitka spruce colonizes the thickets, eventually forming a continuous canopy over the shrubs and giving rise to the third stage of the succession (Cooper 1923).

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[5] Ugolini, F. C. Soils. In: Soil development and ecological succession in a deglaciated area of Muir Inlet, southeast Alaska. Rep. 20. Columbus, OH: Ohio State University Institute of Polar Studies. 1966: 29-72.

[6] Scientific and common names of plants are listed in the appendix.

Invasion by western hemlock and the development of a dynamic equilibrium of tree growth and decay lead to the final climax stage. Western hemlock is generally dominant in both overstory and understory and maintains dominance unless large gaps in the canopy are created by windthrow, fire, or disease. When such gaps are formed, Sitka spruce, red alder, and other species less tolerant of shade may colonize the site. Despite the youthfulness of these soils, the species composition and vegetation structure of climax forests are usually comparable to those of forests growing on older soils (Lawrence 1958, Reiners and others 1971).

The development of forest vegetation following landslides or mudflows—a type of primary succession important to forest management—remains largely unstudied in southeast Alaska. Physical factors relating to the incidence and form of mass wasting have been the subject of more than two decades of research (Bishop and Stevens 1964, Swanston 1970, Swanston and Swanson 1976). But additional information is needed on plant colonization of landslides under differing microclimatic and edaphic conditions before we can predict the course and timing of forest development.

Secondary Succession

Plant succession following a disturbance that does not entirely eliminate the original vegetation is termed "secondary succession" (Whittaker 1975). Most forest management activities in southeast Alaska involve sites undergoing secondary succession.

After a site is clearcut, vegetation develops in predictable stages, defined by plant community composition and structure (Alaback 1982a, 1982b, Harris and Farr 1974, Taylor 1932a). At any stage, species composition may differ according to environmental characteristics peculiar to the site, but the overall pattern of understory productivity over time is similar for all sites studied in the region (fig. 1).

Seedling-sapling and understory colonization stage: 1 to 25 years.—Within three growing seasons after a site has been logged, shrubs such as Alaska blueberry and red huckleberry vigorously sprout from underground stems or establish new seedlings and dramatically increase in productivity over growth sustained in undisturbed old-growth forests (fig. 1). The quickest response of understory shrubs to logging is in alluvial river bottoms or old terrace sites (Alaback 1980, Harris and Farr 1974). Herbs, such as bunchberry, and ferns, such as oakfern and spreading wood fern, also rapidly colonize logging sites but usually accumulate less biomass than woody shrubs (Alaback 1980) (table 2, fig. 2). Extensive soil disturbance caused by logging on moist sites often encourages colonization by shrubs such as salmonberry, trailing black currant, and red alder. Lady fern, spreading wood fern, and bunchberry tend to dominate moist microsites and areas where tree and shrub regeneration is sparse. It is during this stage that most of the colonizing tree and shrub seedlings become established.

Figure 1.—Accumulation of understory biomass following disturbance in southeast Alaska. Bars represent 95-percent confidence limits on estimates of mean biomass accumulation for each site (adapted from Alaback 1982b)

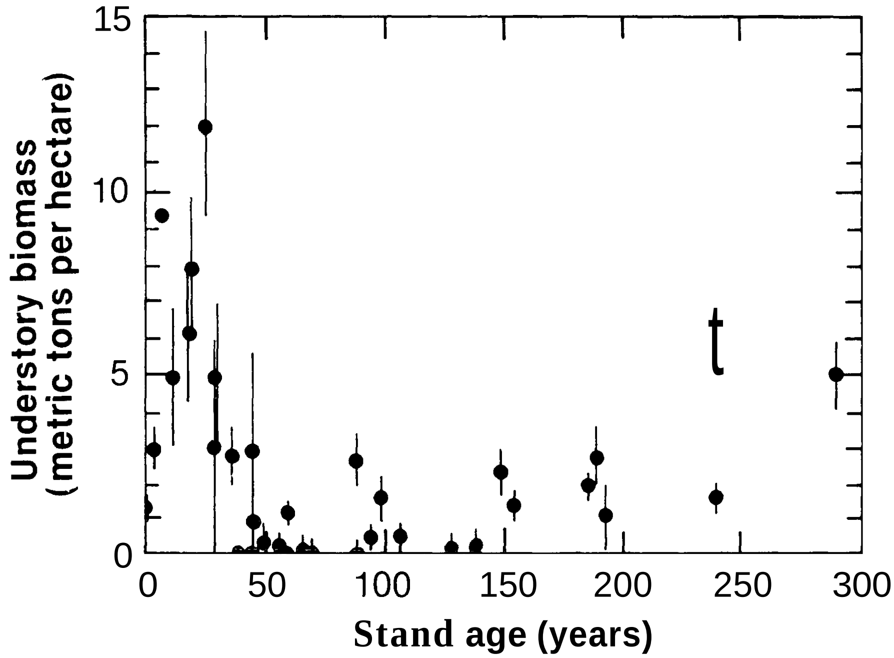

Table 2—Tree seedling and shrub biomass in 4 forest types in southeast Alaska'

Species	Forest type[2]			
	Clearcut	Dense, even-aged	Mature, even-aged	Old-growth
	Kilograms per hectare			
Shrubs:				
Rusty menziesia	125.7	4.7	27.4	36.5
Devils club	0	.1	5.4	3.3
Trailing currant	14.7	1.7	0	.2
Salmonberry	1,031.0	11.5	1.9	48.5
Alaska blueberry	829.3	16.4	69.2	378.0
Red huckleberry	170.7	19.6	52.8	24.0
Tree seedlings:				
Sitka spruce	1,574.3	16.7	2.8	10.2
Western redcedar	90.0	7.6	0	.1
Western hemlock	6,042.3	64.9	133.2	822.5

'Adapted from Alaback 1982b. Seedlings are trees with diameter at breast height less than 1 inch.

[2]Clearcuts include sites logged 0-30 years ago; dense, even-aged sites are 30-100 years old; mature, even-aged sites are 100-250 years old; and old-growth sites are more than 250 years old.

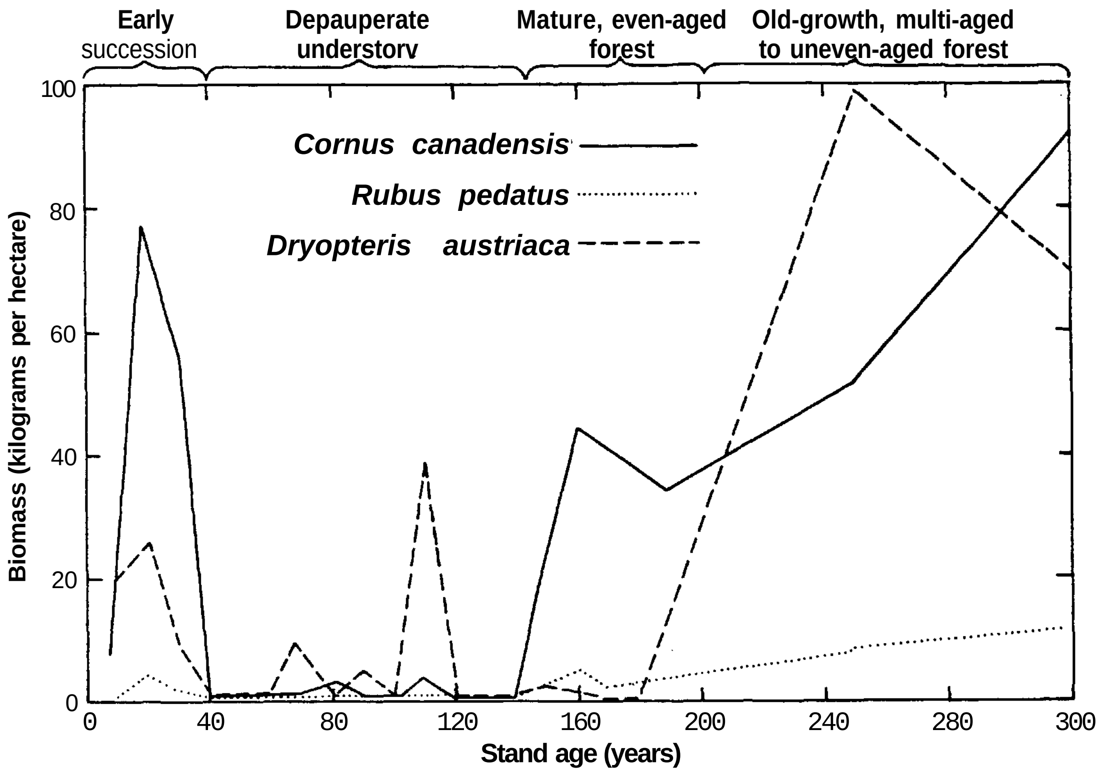

Figure 2.—Biomass accumulation of three common herbaceous species during stages of secondary succession in southeast Alaska (adapted from Alaback 1982a).

Dense, closed-forest and understory-exclusion stage: 26 to 150 years.—Canopy closure decreases the amount of light that reaches the forest floor and is associated with a rapid reduction in understory biomass (fig. 1). Low, herbaceous vegetation is usually less than one percent of the biomass it attains in the seedling-sapling stage (Alaback 1980).

Alaska blueberry is generally restricted to gaps in the canopy or other areas where direct sunlight reaches the understory. Semi-parasitic plants, such as single delight, and achlorophyllous plants, such as coralroot, are often the only herbaceous, flowering plants that persist. This stage has been termed the "stem exclusion stage" because few shrubs or tree seedlings can successfully colonize (Oliver 1981).

The dense, closed-forest stage includes pole-sized timber on overstocked sites or lower site class, normally stocked lands (site index less than 80) and young sawtimber on medium- to high-site lands (site index 90 and above; Taylor 1934). On understocked, poorly drained sites (F5 ecosystems; see footnote 3) the understory exclusion stage is least pronounced, because a continuous dense overstory canopy may be lacking or sustained for a shorter period than on well drained sites (Alaback 1980).

Mature, even-aged forest and understory-reinitiation stage: 150 to 250 years.—As even-aged forests reach stand age 150 to 200, shrub seedlings begin to recolonize the understory (Alaback 1982b). Alaska blueberry usually forms a low, highly branched layer in older, even-aged forests. Five-leaf bramble and other herbs may also be found scattered within these stands (Alaback 1980). The establishment of a productive understory is generally associated with a decline in moss and liverwort biomass, which probably improves seedbed conditions for further understory colonization (Minore 1972, Taylor 1935).

The mature, even-aged forest stage represents the peak in gross standing timber volume of the successional sequence (Alaback 1980, 1982a). Toward the end of this phase, wood decay and defect become more significant (Farr and others 1976) and the rate of woody biomass accumulation steadily declines (Alaback 1982a). These changes in the dynamics of the overstory are usually reflected in a more open overstory canopy. The transition from the stage of dense, closed forest and understory exclusion to the stage of mature, even-aged understory reinitiation is usually characterized by the opening and vertical stratification of the overstory canopy (Alaback 1982b, 1984, Franklin and others 1981).

Old-growth stage: 250 years and older.—The highest degree of variation and the most structurally diverse understory of any successional stage is found in old-growth forests. Patches of shrubs, tree saplings, and herbs alternate with patches dominated by moss and duff or ferns, making a complex, multilayered mosaic. The highest dominance by shrubby understory species and the highest frequency of herbs occur on understocked, poorly drained sites (Neiland 1971). In contrast, well-drained, well-stocked sites have less understory (Alaback 1980, 1982b). This pattern of understory growth in relation to site conditions reflects differences in overstory canopy structure. Stands with widely spaced trees and complex, multilayered canopies, allow more light, highly variable in intensity, to reach the forest floor than do stands with several canopy strata of dense western hemlock or western red cedar pole-sized trees (Alaback 1980, Logan and Peterson 1964).

The amount of understory vegetation varies considerably in old-growth forests. In many stands, there are pockets of trees less than 150 years old, under which shrubby or herbaceous understory is deficient. In open portions dominated by trees more than 250 years old, there is often a shrub stratum composed of red huckleberry, Alaska blueberry, and rusty menziesia[7] (Alaback 1982a; also see footnote 1).

Although woody shrubs dominate, old-growth forests have the greatest proportion of understory production contributed by herbs and low shrubs of any successional stage (Alaback 1982b, 1984) (fig. 3). Bunchberry, five-leaf bramble, fernleaf goldthread, and foamflower are particularly abundant (Alaback 1982a). At elevations less than 500 feet these herbs may be the most nutritious available forage for deer during the winter months (Schoen and Wallmo 1979).

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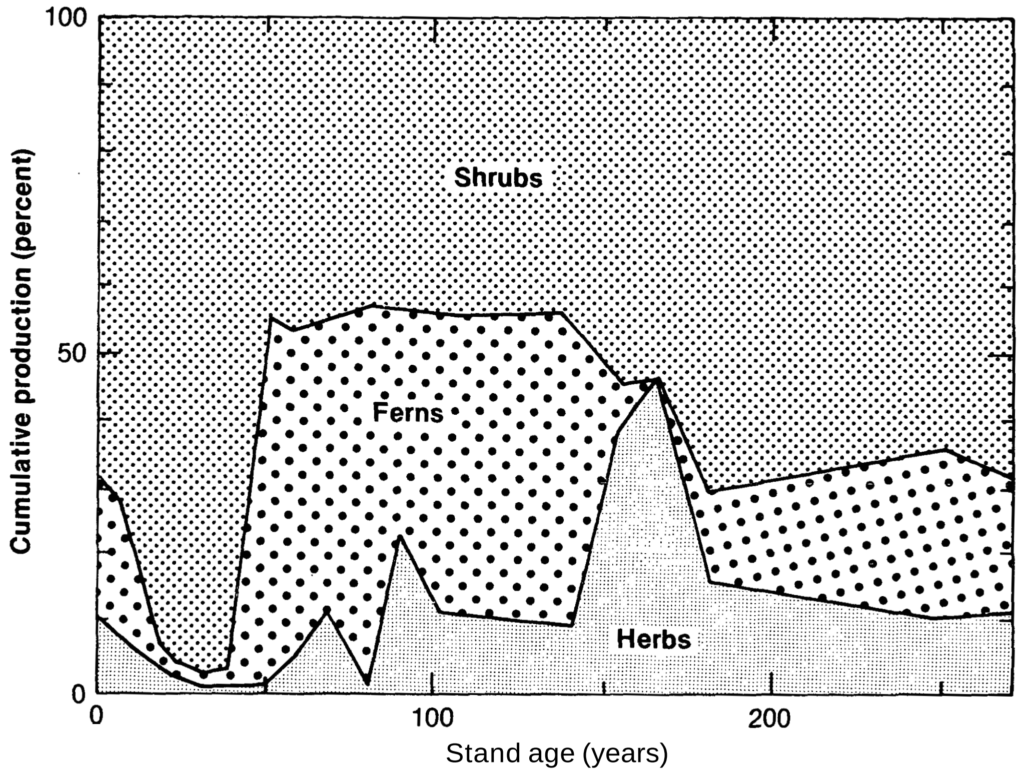
[7] Noble, R. E. Breeding bird populations in hemlock-spruce old-growth and clearcuts, Prince of Wales Island, Alaska. Ketchikan, AK: U.S. Department of Agriculture, Forest Service, Tongass National Forest, Ketchikan Area; 1979. 65 p.

Figure 3.—Changes in understory production during secondary succession in southeast Alaska (adapted from Alaback 1982b).



Understory compositional changes during successional development.—The herbaceous and shrubby vegetation of Sitka spruce-western hemlock forests of southeast Alaska is composed primarily of 20 to 30 species (table 3). In the 60 sites studied by Alaback (1980) 70 percent of the ground cover was provided by the 10 most abundant species, each of which was found on 90 percent or more of the sites. Subtle changes in the dominance of these plants can be significant both to wildlife and the course of plant succession.

Variations in the relative dominance of understory plants are associated with differing degrees of overstory canopy disturbance, disruption of the soil mantle, and site characteristics such as soil drainage, nutrient availability, and microclimate (Alaback 1980; also see footnote 4). If bare mineral soil is exposed and much of the organic layer is lost, early successional or even primary successional species will colonize the site. Early colonizers include horsetail, ***Dryas,*** lichens, mosses, and deciduous trees such as Sitka alder, red alder., black cottonwood, and willow species (Cooper 1923).

The most fundamental change in composition during post-logging succession is the elimination of most shrub and herb species during the period after canopies close and before they open again at stand age 150 to 200. During the later part of the depauperate-understory phase, a fern-dominated understory may form a compositionally distinct subphase in the succession (fig. 3).

Table 3—Relative abundance of understory plants on 60 study plots located throughout southeast Alaska'

Class and species	Cover[2]	Production[2]	Cover rank[3]	Constancy[4]
		Percent		
Bryophytes **and** lichens:				
Cladonia conioceraea	0.5	+	33	41
Dicranum fuscescens	1.8	.8	10	94
Foliose Lichens[5]	.8	+	26	77
Hookeria lucens	.2	+	40	26
Hylocomium splendens	11.4	7.7	2	97
Isothecium stoloniferum	.6	+	31	62
Jungermanniales spp.	3.3	.5	7	86
Marchantia polymorpha[6]	.6	.3	32	30
Plagiothecium undulatum	3.7	.6	5	97
Pogonatum macounii	.7	.1	27	68
Polytrichum spp.[7]	.5	+	34	44
Porella navicularis	1.8	+	13	86
Ptilium crista-castrensis	.9	.3	23	41
Rhizomnium glabrescens	7.0	2.8	4	92
Rhytidiadelphus Loreus	25.0	11.2	1	96
Sphagnum spp.[8]	1.6	1.2	14	61
Timmia austriaca	.2	+	41	23
Other **mosses**[9]	1.6	.5	15	70
Conifers:				
Picea sitchensis	.9	3.3	22	47
Thuja plicata	.2	.5	42	11
Tsuga heterophylla	2.9	18.0	9	89
Ferns:				
Athyrium felix-femina	1.2	.3	19	38
Blechnum spicant	.6	.1	29	26
Dryopteris austriaca	3.6	.8	6	85
Gymnocarpiurn dryopteris	3.0	.2	8	71
Lycopodium annotinum	.1	+	47	11
Thelypteris phaegopteris	.1	+	46	6
Shrubby flowering plants:				
Gaultheria shallon	.2	+	43	9
Menziesia ferroginea	.1	.8	21	55
Oplopanex horridum	.9	+	25	29
Ribes laxiflorum	.3	+	47	6
Rubus spectabilis	2.6	19.1	10	39
Sambucus canadensis	.1	+	45	11
Vaccinium alaskaense	8.4	5.0	3	88
Vaccinium parvifolium	1.2	1.9	20	91

See footnotes at end of table

Table 3—Relative abundance of understory plants on 60 study plots located throughout southeast Alaska' —continued

Class and species	Cover[2]	Production[2]	Cover rank[3]	Constancy[4]
		Percent		
Herbaceous flowering plants:				
Coptis asplenifolias	.9	+	24	38
Cornus canadensis	1.5	.5	16	61
Maianthemum dilatatum	.7	.1	28	46
Moneses uniflora	.6	+	30	61
Rubus pedatus	2.0	+	11	59
Streptopus amplexifolius	.4	+	36	30
S. roseus	.3	+	37	30
S. streptopodes	.5	.2	22	47
Tiarella trifoliata	.2	+	18	70
Viola glabella	.1	+	44	12

+ indicates <0.1 percent production.

'Source: Alaback 1982b.

[2]Mean percent of total vegetation.

[3]Rank from highest (1) to lowest (57) in percent ground cover.

[4]Percent of study sites for which the species was recorded.

[5]Primarily *Lobaria oregona* and *Peltigera canina*; Also *Sphaerophorus bulbosus* and *Hypnogymnia enteromorpha.*

[6]Also includes *Conocephalum commune.*

[7]*P. juniperinum* and *P. commune.*

[8]*S. squarrosus* and *S. girgensohnii.*

[9]*Plagiothecium elegans, Ptilium crista-castrensis,* and *Hypnum* spp.

Herbaceous annuals are less important in early succession in southeast Alaska than they are in other forest regions (Alaback 1982a, Hill 1979, Dyrness 1973, Kellman 1969, Long and Turner 1975). On sites with less soil disturbance from logging operations, Alaska blueberry and bunchberry are usually the most abundant. Salmonberry and trailing black currant are prolific on recently disturbed sites, particularly on alluvial river bottoms or terraces (Alaback 1980). Herbaceous colonizing plants (as opposed to resprouting woody residuals) are usually most abundant in sites that have been burned after logging (Dyrness 1973, Kellman 1969). Preliminary evidence also suggests that fire may encourage the colonization of herbaceous species in southeast Alaska.

The response of plant species to disturbance of varying severity can be predicted by ranking plants in order of shade tolerance. Percent of ground covered by vegetation under gaps in the canopy and under closed canopies can be used to define patterns of shade tolerance for these species (table **4).** On this basis, salmonberry is the most intolerant of shade, followed, in order, by bunchberry, fernleaf goldthread, Alaska blueberry, red huckleberry, five-leaf bramble, spreading wood fern and oakfern. Preliminary evidence suggests that oval-leaf huckleberry may be less shade-tolerant than Alaska huckleberry, because it is distributed in more open areas (Neiland 1971).

Species with the least shade tolerance, such as salmonberry, are more abundant on heavily disturbed sites where little forest canopy persists. Shade-tolerant species such as five-leaf bramble or fernleaf goldthread are more abundant in forests that have undergone the least amount of disturbance.

Little is known about the autecological requirements of the principal herbs and shrubs that colonize Sitka spruce-western hemlock forests. In Oregon and British Columbia, where similar species occur, distinct patterns of change in species composition have been documented in relation to microenvironment, forest productivity, soil morphology, and disturbance (Dyrness 1973, Kellman 1969, Zobel and others 1976).

The patterns of species abundance across environmental gradients are complex, partly because the growing season is mild and many understory species are able to grow in the widely contrasting ecosystems of bogs, forests, and alpine meadows (Jacques 1973, Neiland 1971; also see footnote 2). As a consequence, the presence or absence of a particular species often has little relation to microenvironment or site fertility. The presence or absence of some species, especially those with little annual seed production, may be limited by the efficiency of their propagule-dispersing mechanisms as well as their growth requirements.

Only two forest zones can be defined on the basis of species composition in the zonal vegetation classification for southeast Alaska (Viereck and Dyrness 1980; also see footnote **4).** These are (1) Sitka spruce and (2) Western hemlock-Sitka spruce. On fertile, wet alluvial, or bench sites of the Sitka spruce type, the understory usually includes foamflower, salmonberry, and devils club. Most upland forests are included in the western hemlock-Sitka spruce community and are characterized by poorly drained, lower tree-site indices and understories dominated by Alaska blueberry, five-leaf bramble and bunchberry[8] (Taylor 1932b). This gradient in site conditions is often poorly displayed by changes in understory composition caused by localized conditions and differing disturbance regimes (Alaback 1982b).

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[8] Schoen, John W.; Kirchoff, Matthew D.; Wallmo, O. C. VII Progress Report, Federal Aid in Wildlife Research, Project W-21-1. Seasonal distribution and habitat use by Sitka black-tailed deer in southeastern Alaska. Juneau, AK: Alaska Department of Fish and Game; 1981.

Table 4—Proportion of understory vegetation under canopy and under gaps in canopy in southeast Alaska[1]

Species	Mean average cover[2]				Proportion under gaps
	Under gaps[3]		Under canopy		
	Percent	*Standard error*	*Percent*	*Standard error*	*Percent*
Shrubs:					
Salmonberry	2.5	0.37	0	0	100.0
Alaska blueberry	8.5	1.35	3.6	.49	70.2
Red huckleberry	.4	.06	.20	.06	64.3
Total shrubs	11.39		3.8**		75.0
Herbs:					
Fern-leaf goldthread	1.16	.15	.43	.12*	73.0
Bunchberry	11.30	.35	.87	.28**	93.0
Spreading wood fern	3.71	.35	3.10	.78	54.5
Oakfern	2.70	.31	3.10	.80	46.6
Five-leaf bramble	2.42	.23	1.58	.37	60.5
Total herbs	21.29		9.08**		70.1

*Significantly different at P=0.95.

**Significantly different at P=0.99.

[1]Adapted from Alaback 1982a.

[2]Percent cover is the arithmetic mean for all microplots under gaps or under closed canopy.

[3]Subplots with less than 80-percent tree canopy cover in any quadrant.

Effects of Stand Disturbance on Understory

The frequency and intensity of disturbance of the forest canopy has an important influence on the productivity of understory vegetation. Stands of seedlings or saplings are most resilient to disturbance (Alaback 1980). Virtually any kind of disturbance will result in a prompt increase in shrub and herb production. Understory shrubs and herbs in dense, closed stands of poles or young sawtimber respond much less vigorously to disturbance than those in stands of seedlings or saplings.

When pole or sawtimber stands are subject to localized windthrow, and less than 40 percent of the canopy is destroyed, the increased growth of seedlings or saplings often results in the prompt reestablishment of a dense canopy. The resulting, multi-layered stand tends to have much less herbaceous and shrubby understory than undisturbed stands (Alaback 1980). Windthrow over more than one acre leads to a dramatic increase in understory productivity, setting portions of the stand back to earlier stages of succession (Alaback 1980, Whitmore 1982) (table 5).

The type of disturbance and the environmental characteristics of the site immediately following the disturbance, may significantly influence the pattern and course of forest development for decades (table 5). For example, a stand that develops following windthrow differs substantially from a stand that develops after logging. Following windthrow, overstory biomass accumulates more slowly, while levels of understory biomass are higher (Alaback 1982a). Large numbers of slowly decaying logs, which often characterize stands that develop in the wake of destruction by windthrow, may inhibit tree regeneration and lead to patchy, open canopies. Windthrow usually causes less disturbance to understory plants than logging and favors the growth of residual understory species such as Alaska blueberry and spreading wood fern (Alaback 1980).

Table 5—Time required for plant succession following disturbance in southeast Alaska, under average site conditions[1]

Disturbance type	Shrub colonization	Tree colonization	Spruce dominance
	Years		*Percent of basal area*
Glaciation or landslides	>10	>10	>50
Logging, infrequent	<2	<5	20-50
Windthrow, frequent	<1	<1	<10
Windthrow, (<1 acre)	NA	<1	<1

NA means not available.

[1] Does not include forest developing on alluvial-terrace or uplifted beach soils.

Relationships Between Forest Structure and Understory Development

In the natural pattern of post-logging succession, understory vegetation is eliminated for 60 to 70 years in stands with average to above average stocking (Taylor 1934). To find how the course of successional development can be altered to encourage the growth of understory vegetation over a longer period it is necessary to first understand the relationship between stand structure and understory growth.

The biomass of mosses, liverworts, and ferns is usually greatest on sites with heavy log cover and a closed overstory canopy. Variation in moss and liverwort biomass in second-growth stands is not clearly related to stand age, stand basal area, stand volume, or canopy cover as herb and shrub biomass are (Alaback 1980).

Shrub biomass is greater in second-growth stands with open overstory canopies, low tree-foliage biomass, low basal area, low stocking, and low tree volume. Herbaceous plants tend to be most productive in young clearcuts (3 to 15 years) prior to canopy closure (Alaback 1980, 1982a).

In old-growth and mature stands with average to above average stocking (30,000 to 100,000 board feet per acre), the relationship of understory strata to stand characteristics is fundamentally different (Alaback 1980). Shrubs are most abundant in old-growth stands with large mean diameters. Herb abundance on the more productive sites (F1 and F4 soil ecosystems; see footnote 3) is also strongly associated with large tree diameters, high stand volume, wide tree spacings and low tree density (Alaback 1982b). On sites that are understocked (less than 70 percent of normal), windthrown, or poorly drained, tree density is inversely proportional to abundance of understory (Alaback 1980, Neiland 1971).

In older stands, percent canopy cover does not have a significant relationship to understory abundance. This is most likely because of the difficulty in precisely measuring percent canopy cover in multilayered old-growth forests. In the deep, shade-tolerant canopies of western hemlock, relationships between light interception and canopy cover are highly variable. Multiple regression analysis showed that 79 percent of the variation in total understory production in mature and old-growth stands can be accounted for by stand age (average age of codominant overstory trees), mean stand diameter, and volume (Alaback 1982b). Thus for the stands sampled (30,000 to 100,000 board feet per acre) these three variables can be used to make reasonable predictions of understory productivity.

The change in structure from the dense, uniform canopies of even-aged, second-growth forest to the open canopies of uneven-aged, old-growth forests changes the understory environment by increasing the amount of canopy light and reducing rainfall interception (Anderson and others 1969, Franklin and others 1981, Pike and others 1977). Measures of canopy cover are not sufficiently precise to detect the subtleties of canopy structure. When precise and detailed data on overstory structure and the amounts of light they intercept become available, questions on overstory-understory interactions can be answered more fully.

Effects of Stocking and Site on Forest Succession

While the above-mentioned forest development pattern may apply generally to the low-elevation, well-drained sites most commonly managed for timber production, variations on the pattern and their causes are also of interest to forest and wildlife managers. In general, the more productive and well stocked the rotation-aged forest is, the less likely it is to support a high level of diverse and productive understory vegetation (Alaback 1982b).

The relationship of site quality to the course of plant succession is complex, often resulting in a different response for each developmental stage. Site index, for example, is not linearly related to the amount of understory biomass on a given site over the successional sequence. Prior to canopy closure, site index is positively related.to understory productivity. After canopy closure, differences in productivity of the understory on different site classes are not statistically significant (table 6).

A high-site stand (site index greater than 150) usually regenerates quickly, allowing for more rapid establishment of dominance among seedlings than on an average site of the same age. Thus on highly productive sites canopies usually close earlier than on sites with average productivity, and understory vegetation is eliminated. Later in the developmental sequence, the forest canopy develops more quickly in high-site stands, resulting in fewer trees and a more open canopy.

Table 6—Relationship between site index and understory productivity during the first 2 phases of postlogging succession

Successional phase and site index class[1]	Understory biomass	Standard error
	Kilograms/hectare	
Early postlogging succession (precanopy closure):		
100-110	4 400	1 700
111-120	12 000	—
121-130	21 000	11 000
Mature, even-aged forests (postcanopy closure):		
60-100	347	102
101-120	234	56
121-130	171	54
131-150	546	225

— Means not available.

[1]Site index is based on the mean height of dominant Sitka spruce 100 years old (Taylor 1934).

As a result, levels of understory biomass may be higher in high-site stands (site index exceeding 150) than is typical of sites with average productivity (site index 100 to 130) (Alaback 1980; also see table 6).

Tree density is usually related to the time understory vegetation requires to recolonize following canopy closure. Stands with high stocking (greater than that given by Taylor 1934) often lack measureable understory vegetation (less than 100 kilograms production per hectare). On the Chilcat Peninsula, a densely stocked stand (622 trees per acre, 150 years old), lacked any evidence of understory recolonization, even though most stands of this age have a well developed understory (Alaback 1980, 1982b). On steep, rocky slopes where stands are often subject to windthrow and may attain less than 80 percent of normal stocking (Taylor 1934) shrubby and herbaceous vegetation may persist throughout the successional sequence. The open canopy, characteristic of understocked stands (less than 80 percent of normal), is usually associated with more understory vegetation.

At higher elevations, especially on steep, unstable slopes where widely spaced, large diameter, residual trees provide an open patchy overstory canopy, a more productive and diverse understory tends to develop. In general the higher the elevation, and the less productive and more open the canopy, the more abundant the understory.

Effects of Thinning on Understory Vegetation

The Alaska Region of the Forest Service cites thinning as one of the most promising management tools for improving rotation-aged forests as wildlife habitat.[9] [10] No comprehensive studies of understory response to thinning in southeast Alaska have been completed. The only available data are from a case study of a 20-year-old stand on Prince of Wales Island (Tongass National Forest) (Alaback 1980), where, four years after thinning, a strong, positive response by shrubs and some herbs was noted. In an intensively thinned stand (16-foot spacing) salmonberry dominated the site, to the exclusion of most other species. The lightest level of thinning (12-foot spacing) resulted in the most diverse vegetation (fig. 4).

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[9]USDA Forest Service, Alaska Region. Alaska regional plan. Juneau, AK: **U.S.** Department of Agriculture; 1981.

[10]**Kessler**, Winifred, B. Wildlife and second-growth forests of southeast Alaska: Problems and potential for management. Administration Document 110, Wildlife and Fisheries Habitat Management Notes 4. **U.S.** Department of Agriculture, Forest Service, Alaska Region; 1982.

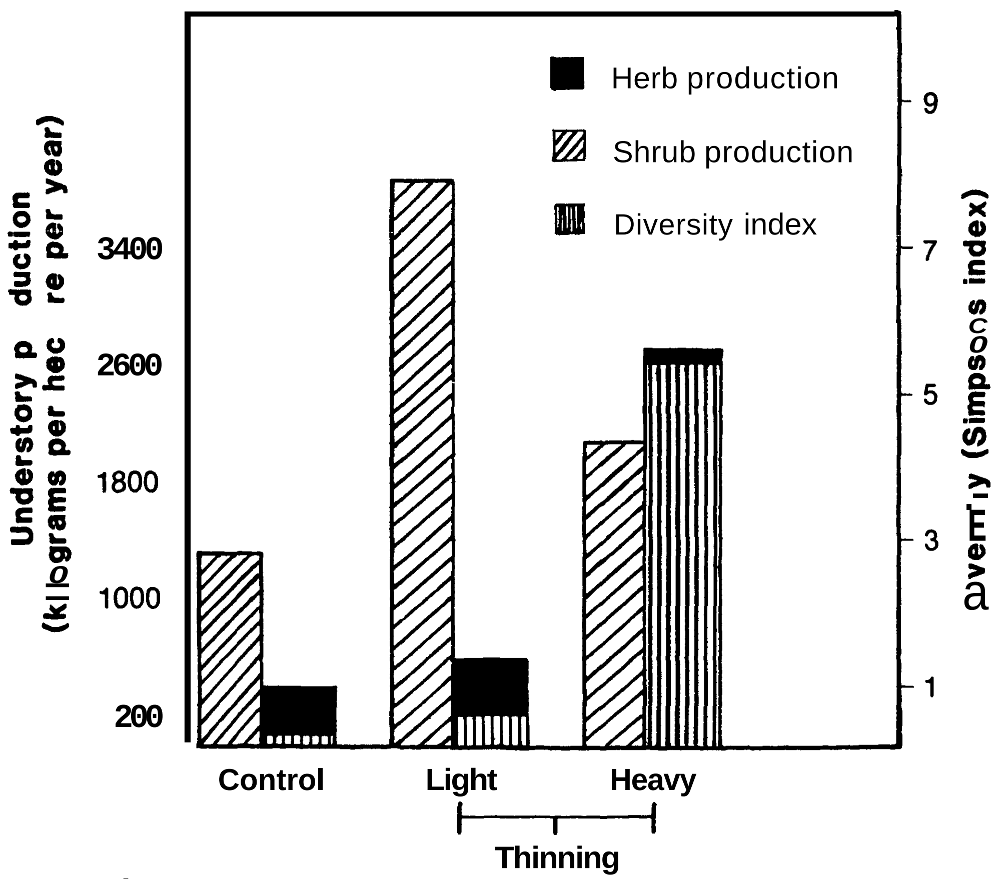

Figure 4.—Response of understory productivity to thinning in a 20-year-old stand. Diversity index is that developed by Simpson (1949).

Preliminary results of thinning experiments on other plots established throughout southeast Alaska[11] suggest that the response of understory vegetation to thinning following canopy closure at 25 to 35 years is much slower than in forests thinned prior to canopy closure. In general, stands that were thinned following canopy closure and elimination of understory vegetation have few shrub or herb species in the understory 5 years after thinning. At the widest spacings (16 feet for younger sites, 20 feet or more for the oldest sites) the principal understory species that respond to thinning are western hemlock and Alaska blueberry.[12] In heavily thinned stands opened up by subsequent windthrow—which is especially common in the older stand-age classes—western hemlock is the principal understory species to respond.

To objectively assess the effects of thinning on understory development, it is necessary to predict not only the short-term response but also the growth of understory plants over an entire rotation. At Cascade Head Experimental Forest in the Siuslaw National Forest on the Oregon coast, a series of Sitka spruce-western hemlock plots thinned 20 years ago provide one of the few opportunities to observe the longer term effects of precommercial thinning on understory vegetation. The greatest number of understory species was found on heavily thinned plots, yet none of the treatments had the continuous understory layer so characteristic of surrounding old-growth forests (see footnote 12). Under such conditions, the beneficial effects of thinning on understory growth would not be expected to last more than 20 years.

A one-time precommercial thinning only delays canopy closure and extends the period of understory persistence. Thinning alone would have little effect on understory growth during the latter half of a 100-year rotation (table 7). Repeated thinnings throughout the life of a stand may be necessary to maintain a highly productive understory (Witler 1975). The nutritive value to wildlife of an understory maintained by thinning remains a key topic for research.

[11] Farr, Wilbur A. Revised study plan. The effects of stand density upon growth and yield of hemlock-spruce stands in coastal Alaska. Juneau, AK: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, 1976; 24 p.

[12] Alaback, Paul A. Unpublished data on file at Forest Science Department, Oregon State University, Corvallis, Oregon.

Table 7—Management strategies and hypothesized time stands would be in 3 classes of understory productivity over 3 centuries of stand development

Strategy	Productivity class[1] Low	Medium	High	Period of medium or high productivity
		Years		
1OO-year rotation	210	0	90	90
100-year rotation with precomrnercial thinning[2]	180	0	120	120
300-year rotation	120	150	30	180
Old-growth reserve	0	300	0	300

[1] Low = 1 to 100 kilograms/hectare; medium = 100 to 1,000 kilograms/hectare; high = more than 1,000 kilograms/hectare.

[2] Assuming thinning delays canopy closure for 10 years.

Management Implications

Maintaining diverse and productive understory vegetation in the Sitka spruce-western hemlock forests of southeast Alaska requires the consideration of many site-specific factors. The importance of any one factor usually depends on the value of all other factors that influence the environmental characteristics of a site. For sites measured throughout southeast Alaska, 10 to 20 percent of the variation in productivity of understory vegetation was associated with soil type, after the variation associated with canopy cover and stand basal area was accounted for (Alaback 1980, 1982b).

The effect of soil characteristics on vegetation development is most pronounced during the earliest stages of succession, prior to canopy closure. On Prince of Wales Island, clearcuts studied attained only 20 percent of the average understory biomass for their age classes. All of the recent clearcuts with below average productivity were on somewhat poorly drained soils (Flc, F4c soil ecosystems; see footnote 3) which generally give rise to mixed western hemlock-western red cedar forests. Nearby forests on better drained sites (Fln, Flt soil ecosystems) had average to above average understory production for their ages (Alaback 1980).

By contrast, sites located on poorly developed, uplifted beach soils (Flb, F3b) tended to produce above average understory. For uplifted beach sites, tree basal area and sapling density were lower than the average for their age classes. The effect of soils on the understory was more likely an influence on overstory-understory competition than of direct soil interactions with the understory (Alaback 1980).

For older study sites in which tree canopies had closed, the influence of soils on understory productivity was more pronounced on thin, rocky soil types (F2n soil ecosystems; see footnote 3). Most stands on poorly developed soils had understory productivity significantly above average for their age classes. As in the case of poorly developed, uplifted beach soils, the increase in understory productivity on thin, rocky soils was also associated with a less productive and less dense overstory canopy (Alaback 1980).

In evaluating the impact of management on wildlife habitat, the quality of understory vegetation as forage must be considered, along with the amount produced. As the growing season progresses, understory vegetation becomes less nutritious and less palatable to wildlife (Klein 1965). Similarly, as understory vegetation matures following clearcutting, the rate of biomass accumulation decreases (fig. 5). As shrubs mature, annual plant production is higher above the ground and less available to deer and other ground-dwelling wildlife. Such changes must be incorporated into evaluations of the relative benefits of stand-age classes to wildlife; otherwise projections of forage biomass may be overly optimistic. If the longevity of the understory is extended by periodic thinning, for example, older shrubs with a high ratio of woody biomass to annual production could dominate understory production. A kilogram of this type of biomass would be of less value to wildlife than a kilogram of less woody understory vegetation in an old-growth stand.

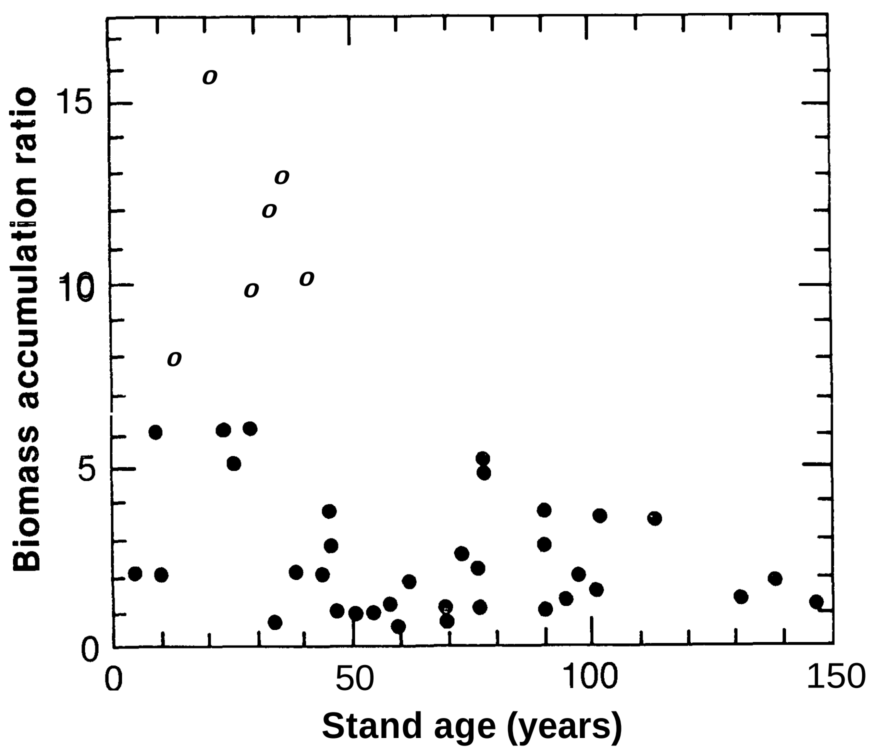

Figure 5.—Changes in understory biomass structure during secondary succession. Biomass accumulation ratio = annual production/total aboveground biomass.

Under ideal conditions (no recent windthrow, homogeneous site conditions, and uniform stocking density), the consequences of forest management on understory vegetation may be predicted on the basis of patterns described for southeast Alaska (Alaback 1982a, 1982b). The consequences of four management strategies are presented in table 7. If the primary objective is to sustain understory structural diversity and herbaceous plant growth, reserving old-growth would be the preferred alternative. Rotations of 300 years would be the next best alternative.

Repeated thinning may also sustain understory productivity, but there are insufficient data to evaluate how well this would meet the habitat requirements of different wildlife species over a forest rotation. The influence of windthrow on thinned stands, and the consequences to wildlife habitat, also are key factors to consider in evaluating this management strategy (Ruth and Harris 1979).

If an important goal is to improve the carrying capacity of second-growth forests for Sitka black-tailed deer and other wildlife that require high levels of winter forage under closed-canopy forests, then the relationship of forest canopy structure to snow interception and evaporation will have to be considered. Snowpack seriously complicates management strategies, because the open canopies that encourage understory growth also tend to have the deepest snow pack, which may minimize the availability of forage for deer in winter (Harestad 1979).

Research Needs

To assess objectively how best to manage southeast Alaska's forests for both timber production and wildlife habitat we must better understand the relationship of forest and environmental characteristics to understory vegetation. More information is needed on mature and old-growth stands so we can characterize in greater detail the relationship between changes in overstory characteristics and understory productivity over a range of soil and site conditions. We need a much clearer understanding of the relationship between stand characteristics and interception of light and snow. Continued research on basic forest structural relationships may make possible a more precise model of forest overstory-understory relationships and provide objective assessments of management strategies.

Research on the short- and long-term effects of precommercial and commercial thinning on understory vegetation should also provide insights on the response of understory plants to changes in microenvironments and make clearer the practical limitations and opportunities for influencing understory composition and productivity by silvicultural thinning. The reproductive strategies and environmental preferences of understory forage species should also be examined. Detailed information on the response of plant species to environmental changes would provide a realistic basis for modeling the effects of managemeht on understory growth and its value as wildlife habitat.

As the Forest Service manages less productive and more diverse sites for both timber and wildlife, it will be necessary to better define the environmental variation on marginal sites and the consequences of management. Departures from patterns of forest development noted on average to highly productive sites should be expected on marginal sites. An examination of stand development and understory productivity on these marginal sites immediately following clearcutting should provide insight into the way site conditions affect the course of plant succession, with resulting consequences for wildlife. Although decades of monitoring permanent plots may be necessary to a complete understanding of how soil and site factors influence forest and wildlife productivity over the course of a timber rotation, studies of early successional development should provide a first approximation of the relationship between site and development of understory.

Management of understory vegetation for wildlife also requires a better understanding of the palatability and nutritional value of common species. Studies of plant nutrition should be related to soil chemistry and ecosystem nutrient cycling, so that the nutritional value of vegetation to wildlife can be related to the response of vegetation to management. Basic information on nutrient storage and cycling in the coastal forests of southeast Alaska is urgently needed. Differences in nutrient cycling in old-growth and second-growth stands should be key topics of future research. Changes in nutrient budgets could have impacts on both forest and wildlife productivity. The climatic and geologic diversity of southeast Alaska make applications of information from fire-dominated, more xeric ecosystems tenuous at best. Questions about the role of understory vegetation in the cycling of nutrients under various soil and site conditions, and management strategies and the consequences of these strategies to wildlife in southeast Alaska, remain unanswered.

Metric Equivalents

1 kilogram/hectare (kg/ha)	= 0.8922 pounds/acre
1 kilogram (kg)	= 2.2046 pounds
1 hectare (ha)	= 2.47 acres
1 square meter (m^2)	= 10.764 square feet
1 meter (m)	= 39.37 inches
1 m^2/hectare	= 4.356 square feet/acre

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Appendix

Common and Scientific Names of Plants[1]

Common name	Scientific name
Alaska blueberry	*Vaccinium alaskaense*
Alaska willow	*Salix alaxensis*
Bearberry	*Arctostaphylos alpinum*
Black cottonwood	*Populus trichocarpa*
Bunchberry	*Cornus canadensis*
Coralroot	*Corallorhiza maculata*
Devils club	*Oplopanax horridum*
Fernleaf goldthread	*Coptis asplenifolia*
Fireweed	*Epilobium angustifolium*
Five-leaf bramble	*Rubus pedatus*
Foamflower	*Tiarella trifoliata*
Horsetail	*Equisetum arvense* -
Dryas species	*Dryas*
Ladyfern	*Athyrium filix-femina*
Mountain hemlock	*Tsuga mertensiana*
Oakfern	*Gymnocarpiurn dryopteris*
Oval-leaf huckleberry	*Vaccinium ovalifolium*
Pacific silver fir	*Abies amabilis*
Red alder	*Alnus rubra*
Red huckleberry	*Vaccinium parvifolium*
Rusty menziesia	*Menziesia ferruginea*
Salmonberry	*Rubus spectabilis*
Single delight	*Moneses uniflora*
Sitka alder	*Alnus sinuata*
Sitka spruce	*Picea sitchensis*
Sitka willow	*Salix sitchensis*
Spreading wood fern	*Dryopteris austriaca*
Subalpine fir	*Abies lasiocarpa*
Trailing black currant	*Ribes laxiflorum*
Western hemlock	*Tsuga heterophylla*
Western red cedar	*Thuja plicata*

[1]Nomenclature follows Hultén 1968.

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Preliminary information on general landscape patterns in southeast Alaska suggests that two major, compositionally distinct vegetation zones can be defined for the closed-forest type: western hemlock-Sitka spruce/Alaska huckleberry/ bunchberry on the uplands, and Sitka spruce/devils club-salmonberry on alluvial flats and terraces.

Recent clearcuts (0 to 30 years old) produce the most shrubby vegetation of any age class in the forest succession. Even-aged forests (30 to 150 years old) produce the least understory vegetation. Uneven aged, old-growth forests sustain the most structurally diverse understory vegetation. Forests with open, patchy canopies tend to produce the most understory vegetation. More data is needed before forest management techniques can be successfully used to improve the quality of habitat for wildlife over that presently found in unmanaged old-growth forests.

Keywords: Succession (secondary), biomass, understory layer, logging effects, logging (-wildlife, old-growth stands, wildlife management, Alaska (southeast), western hemlock, Sitka spruce.

The Forest Service of the U.S. Department of Agriculture is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives — as directed by Congress — to provide increasingly greater service to a growing Nation.

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