

AN ABSTRACT OF THE THESIS OF

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SITKA SPRUCE-WESTERN HEMLOCK FORESTS OF SOUTHEAST ALASKA
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Jerry F. Franklin

Several understory communities display successional stages during the first two hundred years following logging or fire disturbance in the coastal Picea-Tsuga forests of southeast Alaska. Residual shrubs and tree seedlings increase their growth exponentially after overstory removal. Understory biomass peaks at about $5000 \text{ kg ha}^{-1} \text{ yr}^{-1}$ fifteen to twenty-five years after logging. Vascular plant understories are virtually eliminated ($0-70 \text{ kg ha}^{-1} \text{ yr}^{-1}$) after forest canopies close at stand ages of twenty-five to thirty-five years. Bryophytes and ferns dominate understory biomass during the following century. A vascular understory of deciduous shrubs and herbs is reestablished after 140 to 160 years. Subsequent to this successional stage vascular understory biomass continues to increase, while bryophyte biomass and tree productivity decline. Departures from this developmental sequence are related to unusual conditions of stand establishment, soil, microclimate, or disturbance.

During the earliest phases of ecosystem development following forest canopy closure, the decline in understory development is associated with increases in tree basal area and higher percent tree canopy cover. In the old-growth forests increases in mean stand diameter, age, and biomass are correlated with increases in understory biomass. The pattern of understory development over the chronosequence is hypothesized as responding primarily to changes in the light environment wrought by developments in forest canopy structure.

The development and duration of the depauperate understory stage that follows canopy closure in southeast Alaska was hypothesized as being related to the canopy characteristics of shade tolerant, high-leaf-area Tsuga forests. Maintenance of these forests in the aggradation stages of development (0-100 years) by forest management activities would minimize vascular understory vegetation development. Even including the pulse of vegetation growth during the first 30 years, understory vegetation productivity on normal soils would be less over a 100-year forest tree rotation than the annual productivity in old-growth forests. Food for herbivores and nutrient cycling processes associated with understory vegetation would be concomitantly minimized under this forest management policy.

BIOMASS AND PRODUCTION OF UNDERSTORY VEGETATION IN SERAL
SITKA SPRUCE-WESTERN HEMLOCK FORESTS OF SOUTHEAST ALASKA

by

Paul B. Alaback

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INTRODUCTION

Since the times of Theophrastus (300 B.C.) many descriptions have been made of changes in vegetation composition following disturbance. Vegetation changes during the earliest stages of ecosystem recovery following perturbation are generally the most dynamic and well documented. These initial stages can influence the patterns of vegetation development over several decades (Egler, 1954, Horn, 1974, Cattelino et. al. , 1979). In the forest ecosystems of the Pacific Northwest north to southeastern Alaska many sites escape destruction by fire, wind and other agents so that plant succession may continue over centuries (Hemstrom, 1979, Waring and Franklin, 1979). These later stages of succession have rarely been studied by ecologists, yet offer the greatest opportunities to test hypotheses on successional development and to better understand the transition to the "climax" or the dynamic equilibrium of the old-growth system(Whittaker, 1953, Odum, 1969, Bormann and Likens, 1979).

Most studies have documented vegetation changes by estimating ground coverage by various plant species or by reconstructing forest composition through stem analysis (Henry and Swan, 1974, Oliver and Stevens, 1977). More precision and detail is gained in evaluating changes in individual species contributions to ecosystems functioning by measuring plant biomass or net primary production (Whittaker, 1975). Such measurements of plant biomass and production were originally a tedious and time consuming task, suited only for a few intensive study sites. Dimension analysis techniques have made more efficient yet sufficiently accurate estimates of plant production possible (Whittaker, 1966, 1968, Brown, 1976,

Grier and Logan, 1977, Ohmann et. al.1977) Even so, recent biomass studies have concentrated on selected intensive study sites, only a few using these techniques to document successional changes (Long and Turner, 1975, Irwin and Peek, 1979).

Southeast Alaska is particularly well suited for studies of long term forest successional development. In contrast to many other forest types little variation in understory composition is usually associated with natural or manmade disturbances in the region. Detailed examinations of changes in plant biomass or production over a wide range of sites and time spans are possible as well as more straightforward in this floristically simple system.

The objectives of this study were threefold. Rapid yet sufficiently precise techniques to assess understory production and biomass suited to the climate and logistical constraints of fieldwork in southeast Alaska needed to be developed. Of particular importance was to develop a set of species and location specific biomass prediction equations for the vegetation in the region. Secondly, changes in understory vegetation over three centuries of succession and a range in site conditions within the region needed to be documented. With this chronosequence both the pattern and the variation in vegetative development could be studied in detail over longer periods of time than have been reported for most other forest regions. Thirdly, the relationships between environmental factors and understory growth needed to be studied so that those factors associated with understory change over the chronosequence could be identified. By studying these long term successional patterns it was hoped that relationships between vegetation on the wide range of age classes present in the region would be clarified.

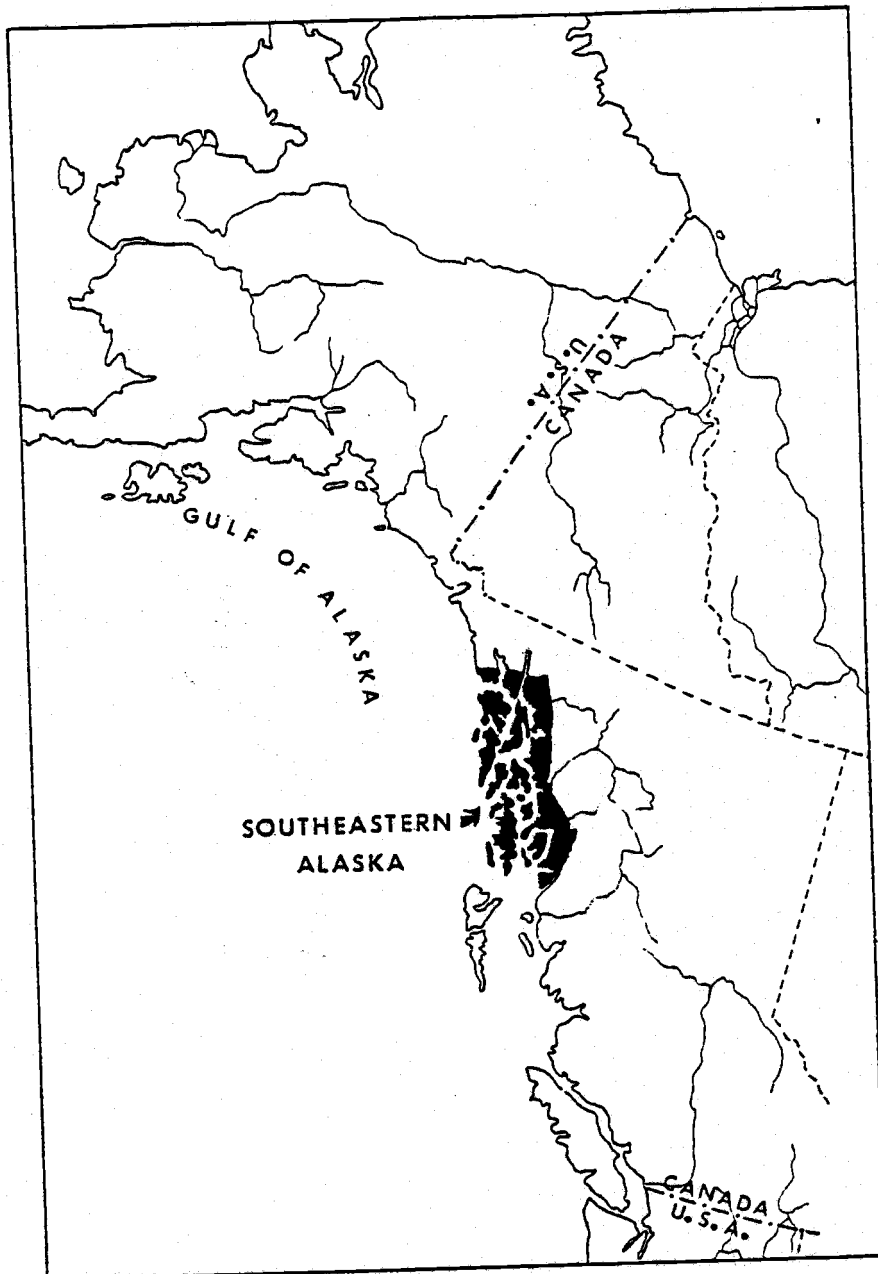


Figure 1. Study area location.

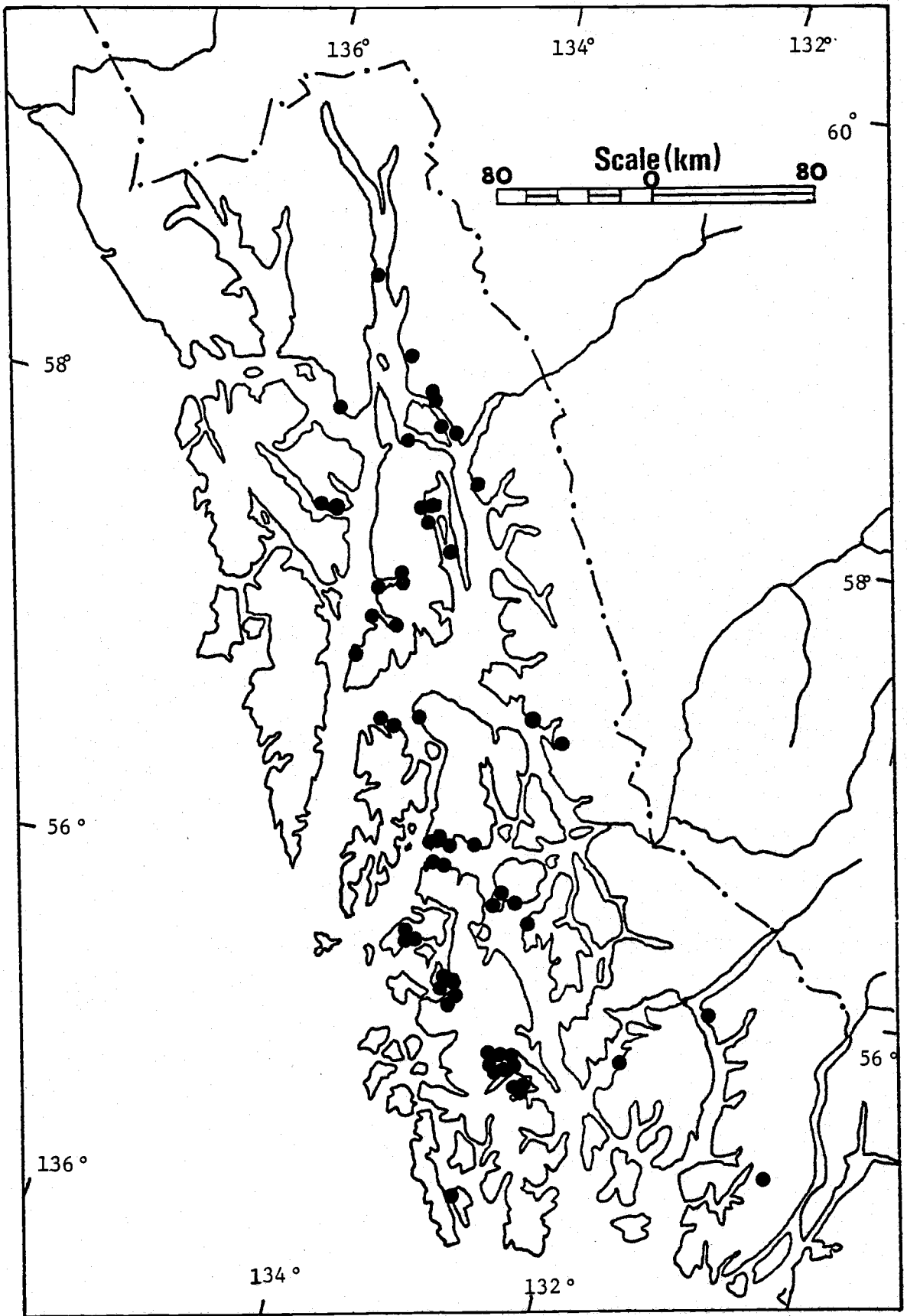


Figure 2. Study site locations.

Description of Study Area

Geography and Climate

Southeast Alaska is a remote region of steep glaciated mountain ranges, fjords, muskegs, and fog-enshrouded cool temperate coniferous forests. For the purposes of this study the region is defined as that area from Haines (59°N, 136°W) southeast to Dixon Entrance (54°30' N, 130°W), (fig 1). Averaging about 190 km in width the region extends 700 km in the northwesterly direction (fig 2).

Over this large region the climatic patterns follow a cline towards cooler temperatures and lower tree productivity with increasing latitude (Andersen, 1955, Farr and Harris, 1979). Climates in the mainland portions of the region tend to be more severe, especially when influenced by air masses over the glaciers and icefields of the British Columbia Coast Range. By contrast, the climate on the outer islands tends to be more maritime with rainy winters and cool summers (Andersen, 1955, Klein, 1965, NOAA, 1978). In general this region can be distinguished from those further south by its heavy annual precipitation (200-600 cm) and cooler growing-season temperatures. The summer drought, which so characterizes the dynamics of the Pacific Northwest and southern British Columbia coniferous forests, does not clearly effect this region (U.S. Forest Service, 1974, Stephens et. al. 1969, Waring and Franklin, 1979)

Mean monthly temperatures range from 13°C in July to 1°C in January. On the average, 1200 degree days (above 5°C) occur in the region (Farr and Harris, 1979). The highly dissected mountainous terrain of this region affect wide variations in climatic conditions (Andersen, 1955). The heaviest

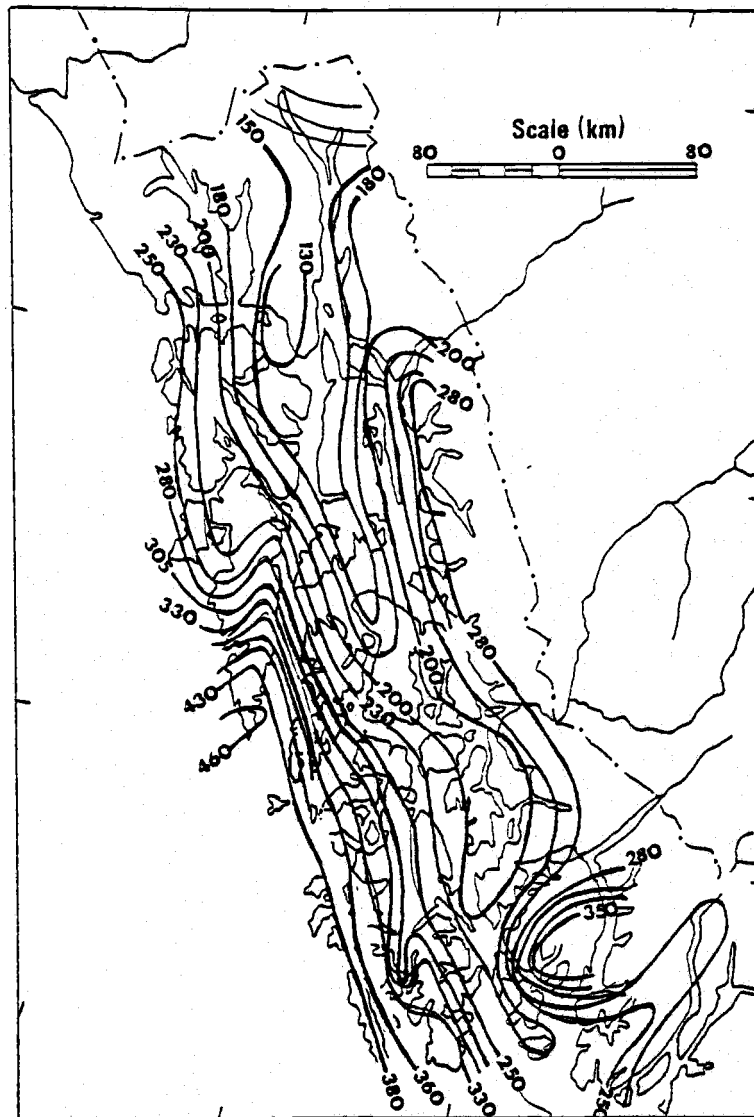


Figure 3a. Isohyetal map for Southeast Alaska.
After Anderson(1955). Annual rainfall
in cm shown.

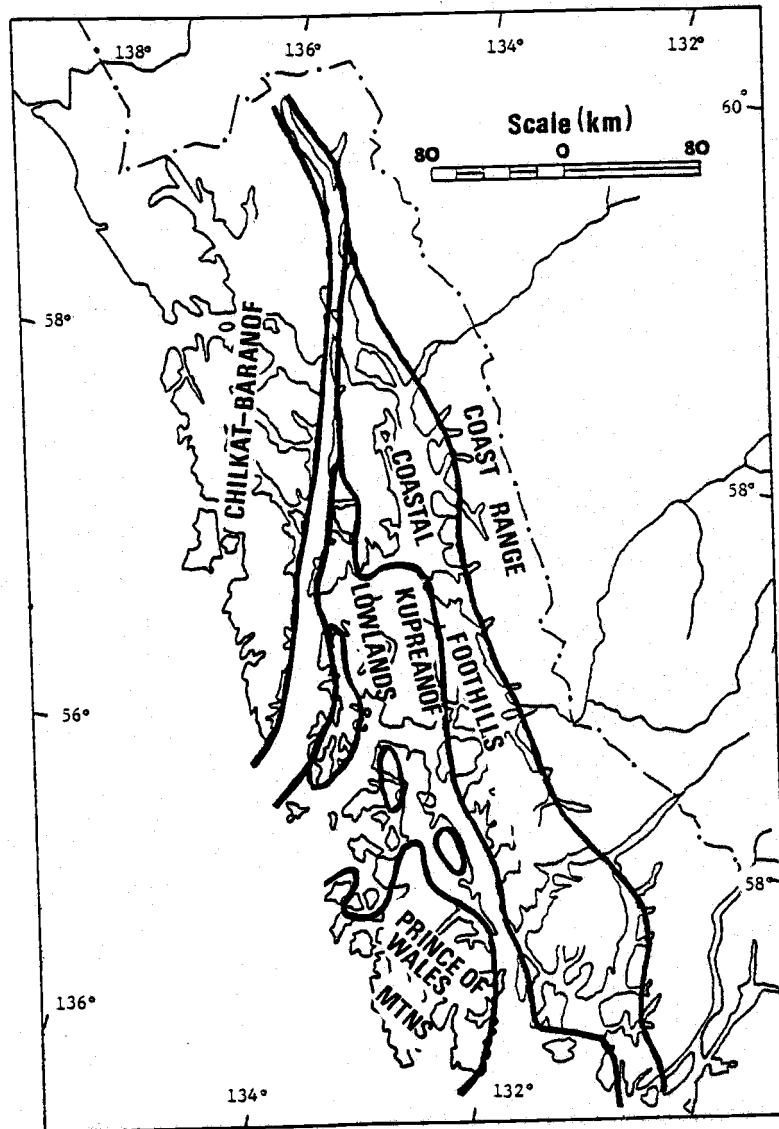


Figure 3b. Physiographic provinces of Southeastern Alaska. After Wahrhaftig(1965).

precipitation generally falls on the outer coastline, steadily declining to the east until reaching the Coast Range foothills where regional orographic effects are again associated with increased rainfall (fig 3a). The larger islands tend to reradiate enough heat to make their summer temperatures higher than in surrounding areas (Patric and Black, 1968). Topography, wind patterns and other factors can also dramatically influence local rainfall and temperatures within the region (Stephens et. al. 1969).

Geology and Physiography

Five major physiographic provinces have been defined for southeast Alaska (Wahrhaftig, 1965), fig 3b. The Coast Range forms the east-northeast part of the region with ice-locked boundary peaks which average 2100 to 2800 meters in elevation. Large rock outcrops, steep-walled glaciated valleys and unstable thin rocky soils characterize this area. Forest growth tends to be restricted by thin soils, mass movement erosion, and the harsh climates associated with glaciers and ice fields.

The coastal foothills province has more subdued topography and lower elevations. A metamorphic contact zone dominates this region (Brew et. al, 1966, Miller, 1958). The Kupreanof lowlands and the Prince of Wales Mountains provinces have the most moderate climate, lowest elevations, and maximum development of forest vegetation. Ridges generally range from 600 to 1100 meters in elevation. Drainage density is low, and the pattern is angular, suggesting a youthful stage of development with maximum control by bedrock structure (Swanston, 1974). The Chilkat-Baranof Mountain province resembles the Coast Range in its heavy rainfall and rugged heavily glaciated topography. Elevations are higher than in the Kupreanof and Prince of Wales

Mountains provinces, but lower than in the Coast Range province. Sampling in the study emphasized the central portions of the Prince of Wales, Kupreanof lowlands, and the Coastal foothills provinces, where the most moderate climates prevail,

Regional control of these physiographic features in southeast Alaska is exerted by the northwest orientation of faults, bedrock strike and lineaments. Intrusive rocks are largely of Cretaceous origin. Uplift forming the Coast Range occurred during the Tertiary (Miller, 1958). The overall geological pattern can be summarized as a northwest trending eugeosyncline with Paleozoic rocks dominating the central lowland provinces. More erosion resistant batholithic Mesozoic rocks dominate the mainland and outer coastal flanks of the mountain system (Brew et. al, 1966, Buddington and Chapin, 1929). Massive intrusion, metamorphosing, volcanism, and periodic sedimentation epochs give the region a complex overall geology. It has even been proposed that much of the land was derived from other continents during continental drift (Kerr, 1980).

Extensive glacial activity throughout the region is generally thought to have accentuated physiographic features developed prior to the Pleistocene (Lawrence, 1958). Present glacial features were largely formed during the Wisconsin advance about 10,000 years ago (Heusser, 1960). The northern portions of the area are still actively rebounding (2-4 cm per year) from the weight of the Pleistocene ice sheets (Hicks and Shofnos, 1965).

Little detailed geological information is available for the sites sampled in this study. The earlier geological descriptions of southeast Alaska were based primarily on shoreline mapping. More recent studies

have used aerial photos with some spot checks. Only in a few areas have detailed maps from on-the-ground surveys been developed(USGS,1977).

Soils

Soils in southeast Alaska are generally young (200 to 10000 years), shallow, and poorly developed (Crocker and Major, 1955, Collins,1974). Compact glacial till is extensive up to about 500 meters in major river valleys, exerting a great influence on drainage conditions and forest development in the region (Swanston, 1969). Till deposits tend to be thickest on south and west facing slopes. Most of the soils in the study area are derived from this ablation till (Collins,1974). Because of this till overburden and the heavy annual rainfall bedrock usually plays a lesser role in soil chemistry than in more southerly regions (Heilman and Gass,1974). The soil mineral fractions are generally low in nutrients due to a lack of bedrock and glacial till weathering (Swanston,1974).

Some of the best developed soil structures occur on fine silt and clay sediments of marine terraces which are extensive, up to 150 meters in elevation. Soils derived from marble and limestone with extensive subsurface drainage tend to have the lowest proportion of poorly drained areas and give rise to some of the most productive and best developed forests (Gass et. al. 1967, Jacques, 1973). By contrast, soils of hard intrusive rocks have a higher percentage of poorly drained (organic soils) areas and less productive forest vegetation(Gass et. al. 1967, Collins, 1974).

Cool growing seasons and abundant year-round moisture combine to give

high accumulations of carbon and iron oxides but little clay in these soils subsurface horizons (Stephens, 1969). Slow decay and mineralization rates for nutrients critical to tree growth are also thought to result from these climatic conditions (Taylor, 1935). Organic mats commonly range from 15 to 30 centimeters deep and are considered the primary source of nutrients for forest vegetation (Taylor, 1935, Stephens, 1968). Soils in southeast Alaska strongly attract and hold water, staying moist throughout the year (Gass et. al. 1967, Patric and Stephens, 1968). Most of the soils are classified as spodosols, having thin A2 and B21 horizons, extremely to very strongly acid sola, weak structure, and thixotropic properties (Heilman and Gass, 1974).

The soils-ecosystem classification system of Stephens et. al. (1969) is used in this study. Five major forested types are defined based on drainage characteristics, parent material, and depth. The first type (F1) represents the modal soil for well-drained low-elevation sites that have the highest tree productivity classes. The second type (F2) is distinguished by having less than 25 cm of mineral soil. The third type (F3) includes coarse, poorly developed soils and was not sampled for this study. The fourth and fifth types (F4,F5) have somewhat poor and poor drainage conditions respectively (Stephens et. al. 1969).

In this study primary emphasis was placed on well drained upland sites, where the most productive forests develop. The F2 and F4 soil types were sampled only where suitable F1 sites were not available for a given age class. Six of the seven subtypes of the F1 soil type (Stephens et. al. 1969) were sampled. These subtypes were defined primarily by parent material (ash, till, fine textured deposits, uplifted beaches,

alluvial terraces).

Vegetation

A. Previous work in the region

No comprehensive studies have been done on the structure or composition of forest vegetation in southeast Alaska. Early studies were descriptive, and directed primarily at the growth and abundance of the two principle forest trees, Picea sitchensis (Bong.)Carr. and Tsuga heterophylla (Raf. Sang.), (Taylor,1929,1932b, 1933, Heintzleman, 1949). Hulten (1968) compiled the flora for this and other regions in Alaska, developing maps of species distributions for the state. Worley (1972) studied the distribution of bryophytes in the region. Palmer (1942) and Meehan (1974) provided species lists for wildlife habitat zones in southeast Alaska. More quantitative descriptions of study sites within seral and mature Tsuga-Picea forest vegetation in the region are given by Klein (1965), Kessler (1979), Neiland (1971), and, in Glacier Bay, by Worley (1977). Studies of Tsuga-Picea forests in British Columbia have centered on Vancouver Island in the southern end of the province where climate, species composition and other environmental features differ sufficiently so that meaningful comparisons with southeast Alaska are difficult (Krajina, 1969, Cordes,1972).

Studies on vegetation successional dynamics in southeast Alaska have centered on revegetation following glaciation (Cooper, 1923a, 1923b, 1939, Lawrence, 1958, Reiners et. al. 1971). By contrast, secondary successional processes have received little attention in

this region. Harris (1974) provides the best general description of the early stages of plant succession following logging. Taylor (1929,1932a,1932b) has also provided a general discussion of early forest growth and composition following cutting. Forest growth and accumulated volume has been studied for the first 150 years following cutting in the region(Taylor, 1934, Taylor and Godman, 1950). No published studies are available summarizing understory vegetation dynamics during this time period.

B. Description

Approximately 60 percent of the land area in southeast Alaska is forested, the remaining area is alpine, muskeg (bog) or riparian (USFS, 1978). Well-developed closed-canopy forests occur from sea level up to about 600 meters in elevation. Tsuga mertensiana (Bond.) Carr. dominates forests and park-like meadows near timberline as well as on organic soils down to sea level (Harris and Farr, 1974, Stephens et. al. 1969). Tsuga-Picea forests usually occur at lower elevations or on better drained soils as a mosaic with muskegs and other wetlands (Neiland, 1971). This type comprises the majority of closed canopy forest in the region and is the subject of this study. For purposes of this study this type encompasses the Picea sitchensis, Picea sitchensis-Tsuga heterophylla, Tsuga heterophylla-Picea sitchensis, and Tsuga heterophylla-Thuja plicata communities as defined by Viereck and Dyrness (1980) at formation level IV.

Seventy-five percent of these forests are "old growth"(greater than

150 years old) while most of the remainder are of windthrow or logging origin(USFS,1978). Fire has not been an important element in the ecology of these forests (Noste,1969,Harris and Farr, 1974). Most of the disturbance in these primeval forests is thought to be caused by the infrequent high velocity winds during the fall or winter which blow down large patches of forest (Ruth and Harris, 1979).

Typical old growth stands have a dense multilayered canopy with a range of tree ages and diameters. Vaccinium alaskaense Howell., V. parvifolium Sm., and Menziesia ferruginea Sm. dominate the shrub layer. The ground layer is generally covered by carpets of feathermoss (Rhytidiadelphus loreus (Linb.)Warnst.,Hylocomium splendens(Hedw.) B.S.G.) with clumps of herbs (Cornus canadensis L.,Rubus pedatus Sm.) and ferns (Dryopteris austriaca (Jacq.)Woymar, Gymnocarpium dryopteris(L.) Newm), (table 3). The understory generally increases in density with elevation, on rocky unstable soil, or where other conditions break up the overstory canopy, Oplopanax horridum(T. and G.)Miq. is most common along rivers and on thin rocky soils where there is continual water seepage.

METHODS

Nondestructive Data

Study sites were selected to represent a range of forest ages from three years to about four hundred years using unpublished data from W.A. Farr and R.F. Taylor or aerial photos. Within each age class sites were selected that represented a range in soil, climatic, and geographic conditions so that the effects of these factors on vegetation development could be studied. For the younger stands permanent plots stratified by age and tree site index were used. Stands less than 70 years old were

TABLE 1. Study site locations, descriptions, and stand origins. Site numbers correspond to those used in subsequent tables and figures.

SITE	NAME	LEGAL DESCRIPTION	AGE ^{1/}	SITE INDEX ^{2/}	ORIGIN ^{3/}	REFERENCE ^{4/}	
1	Hood Bay I	T52SR68ENW1/4Sec	60	60	37	L	1
2	Hood Bay II	T52SR69ENEL/4Sec	27	34	39	L	1
4	Whitewater Bay	T53SR68ENEL/4Sec	27	51	37	L	1
5	Karta River	T73SR84ESEL/4Sec	2	72	33	F	1
6	Karta Lake	T73SR84ENW1/4Sec	3	72	33	F	1
7	Harris Control	T74SR84ESW1/4Sec	7	20	38	L	1
8	Harris Lt thin	T74SR84ESW1/4Sec	7	21	39	L	1
9	Clark Bay I	T73SR84ESW1/4Sec	25	3	-	L	2
10	Harris Hv thin	T74SR84ESW1/4Sec	7	21	40	L	1
11	Thomas Bay	T57SR80ESEL/4Sec	4	22	31	L	1
12	Douglas Bay	T62SR78ESW1/4Sec	21	15	36	L	-
13	Agate Beach	T62SR77ENW1/4Sec	22	45	31	L	1
14	West Zarembo	T65SR81ENEL/4Sec	2	42	42	L	1
15	Eagle River	T38SR64ENW1/4Sec	26	94	27	W	1
17	Shaheen I	T71SR79ESEL/4Sec	1	400	-	-	-
18	Shaheen II	T71SR79ESEL/4Sec	1	400	-	-	-
19	Mission Cove	T81SR84ESW1/4Sec	1	59	41	L	1
20	Sullivan Is	T34SR60ESW1/4Sec	1	187	30	F	-
21	Old Franks I	T74SR85ENEL/4Sec	27	72	40	F	1
22	Old Franks IIa	T74SR85ENEL/4Sec	22	72	23	F	1
23	Old Franks III	T74SR85ENW1/4Sec	22	73	20	F	1
24	Tuxecan I	T70SR79ESW1/4Sec	15	31	30	L	1
25	Clark Bay II	T73SR85ENEL/4Sec	35	8	-	L	2
26	Old Franks IIb	T74SR85ENW1/4Sec	22	72	37	F	1
27	Tuxecan II	T70SR79ESW1/4Sec	15	31	38	L	1
28	Bartlett Hosp	T41SR67ESEL/4Sec	9	108	37	L	4
29	Alder Creek I	T64SR76ESEL/4Sec	3	45	32	L	1
30	Alder Creek II	T64SR76ENEL/4Sec	10	45	38	L	1
31	Saks Cove	T68SR92ENEL/4Sec	26	58	36	L	1
32	Virgin Bay	T71SR89ENEL/4Sec	13	53	40	L	1
33	Edna Bay I	T68SR76ENW1/4Sec	23	45	40	L	1
35	Edna Bay III	T68SR76ESEL/4Sec	15	48	37	L	1
36	Edna Bay IV	T68SR76ENW1/4Sec	15	37	29	L	1
37	Clark Bay III	T73SR84ESW1/4Sec	25	192	35	W	2
38	Clark Bay IV	T73SR84ESW1/4Sec	25	192	35	W	2
39	Chilkat Pen.	T42SR62ENEL/4Sec	16	140	31	W	3
40	Red River	T78SR99ENW1/4Sec	5	188	-	W	5
41	Douglas Island	T41SR67ENEL/4Sec	1	64	30	M	1
42	Lemmon creek	T40SR66ENEL/4Sec	34	250	-	-	-
43	Point Barrie 1	T62SR76ENW1/4Sec	6	69	38	L	1
44	Point Barrie 2	T62SR75ENEL/4Sec	1	10	37	L	-
45	Saginaw I	T57SR71ESEL/4Sec	17	49	36	L	1
46	Saginaw III	T57SR71ENEL/4Sec	22	96	33	W	1
47	Point White	T56SR72ENW1/4Sec	17	53	33	L	1
48	Shrubby Island	T65SR80ENW1/4Sec	23	27	35	L	1

TABLE 1. Continued

SITE	NAME	LEGAL DESCRIPTION	AGE	SITE INDEX	ORIGIN	REFERENCE
49	South Zarembo	T65SR82ENE1/4Sec 7	37	37	L	1
50	Point Vandeput	T56SR78ENE1/4Sec 10	20	37	L	1
51	Kindergarten B	T65SR82ENE1/4Sec 27	100	30	F	4
52	Maybeso Valley	T73SR84ENE1/4Sec 32	21	40	L	2
53	Shaheen creek	T74SR79ESE1/4Sec 35	550	-	-	-
54	Tenakee	-	90	33	F	-
55	Mitchell Bay	T50SR68ESW1/4Sec 12	154	37	F	3
56	Killisnoo Is.	T51SR68ENW1/4Sec 7	94	46	L	4
57	Kanulku Bay	T50SR68ESW1/4Sec 25	142	32	F	3
58	Cannery Point	-	138	22	F	3
60	Windfall Harb	T46SR69ESW1/4Sec 32	90	30	W	4
61	Windfall Is.	T46SR69ENW1/4Sec 16	95	38	L	-
62	Pack Creek	T46SR69ESE1/4Sec 6	300	-	-	-
64	Dorn Island	T47SR70ESW1/4Sec 22	150	27	W	3
65	Limestone Inl	T44SR70ESW1/4Sec 23	250	-	-	-
66	Young Bay	T43SR66ESE1/4Sec 4	100	40	F	3
67	Salisbury Pt	T42SR69ESW1/4Sec 20	150	30	L	4

1/ mean age of co-dominant trees. For the old growth sites actual time since disturbance may be much greater than indicated by these data.

2/ tree height in meters at 100 years, using tables developed by Farr(unpubl).

3/ L = logging, F = fire, W = windthrow, M = mining disturbance

4/ 1 = Farr,unpubl. Stand Density Study. Data on file,Forestry Sciences Lab, Juneau.
 2 = Van Horn,unpubl. Ph.D dissertation, Univ.New Mex., Albuquerque, N.M.
 3 = Farr,unpubl. 1968. Soil Site Index Study. Data on file,Forestry Sciences Laboratory, Juneau.
 4 = Taylor,R.F. Unpublished.Site index study. Data on file Forestry Sciences Laboratory, Juneau.
 5 = Juday,G.P.,P.B. Alaback,and A.S.Harris.Unpubl. Geographic distribution of Pacific Silver Fir in Alaska. Institute of Northern Forestry,Fairbanks.

TABLE 2. Understory biomass and environmental features of sites sampled for study. All biomass values are given in kg ha^{-1} .

					UNDERSTORY				OVERSTORY				2/		3/		4/		5/	
SITE	AGE	SLOPE	ASPECT	ELEV	BIOMASS	PROD	HERB	FERN	BA	PICEA	THUJA	CANOPY	PROD	DBH	SOIL	PARENTM				
9	3	30	SE	45	1240	608	4	236	-	-	-	0	-	-	-	Flc	V			
25	8	10	SE	38	3069	522	110	76	-	-	-	0	-	-	-	F4c	T			
44	10	0	0	30	9507	4263	52	549	2	56	0	18	-	4.9	-	Fln	V			
12	15	0	0	5	5015	598	8	37	2	61	0	39	-	7.3	-	Fln	V			
50	20	0	0	2	58546	3589	159	67	6	7	0	64	-	3.5	-	Flb	B			
52	21	10	5	91	32973	5210	206	59	12	25	4	84	-	6.6	-	Flc	T			
7	21	0	0	67	547	205	3	6	22	21	0	87	-	3.9	-	Flc	T			
8	22	0	0	67	3516	442	10	2	9	14	0	91	-	8.1	-	Flc	T			
10	22	0	0	67	5889	2719	12	41	4	71	0	40	-	10.2	-	Flc	T			
11	22	0	0	8	8072	808	7	45	11	39	0	68	-	0.4	-	Fln	T			
48	27	0	0	91	12462	2026	11	40	14	67	0	92	1170	4.2	-	Fln	M			
24	31	40	S	30	5515	406	0.2	1	36	12	0	94	2440	4.4	-	Fln	S			
27	31	10	S	90	348	127	0	0	66	66	0	98	5670	8.1	-	Fln	S			
2	34	47	W	31	3	2	2	0.1	46	57	0	89	3347	23.3	-	Fln	L			
49	37	0	0	23	2768	798	7	6	53	14	0	99	4170	5.8	-	Flb	B			
45	40	0	0	46	243	21	0.5	0.2	76	15	0	95	5964	29.6	-	Fln	L			
14	42	0	0	7	45	22	0.2	0.4	75	83	0	97	6817	16.2	-	Flb	B			
13	45	0	0	7	1116	251	0.5	2	34	23	0	92	2113	7.3	-	Flb	B			
33	44	0	0	30	3123	65	0.1	0.1	46	76	0	95	3818	26.2	-	Fln	L			
29	45	0	0	30	181	35	0.2	2	48	6	0	97	3331	8.3	-	Fln	L			
30	45	0	0	30	3	3	0.1	2	61	14	0	91	4876	15.5	-	Fln	L			
35	48	10	N	152	510	29	0.2	1	48	26	0	96	4288	13.8	-	Fln	L			
4	51	20	SW	30	0.1	0.1	0.1	0	105	97	0	97	7900	14.0	-	Fln	V			
47	52	0	0	30	0.5	0.5	0	0.2	53	36	0	99	3610	12.6	-	Fln	M			
32	53	30	SW	122	0.2	0.1	0	0	65	20	0	97	5258	17.7	-	Fln	S			
31	58	0	0	30	204	130	27	89	63	27	0	90	4376	26.6	-	Fln	V			
19	59	0	0	15	16	32	0.8	26	86	44	0	96	6934	31.0	-	Flf	L			
1	60	0	0	30	0.1	0.1	0.1	0	93	12	0	84	5464	21.8	-	Fln	L			
41	64	10	S	30	1462	406	124	122	40	52	0	90	2323	22.9	-	F4r	MT			
43	69	20	S	33	147	129	12	59	83	70	0	97	5993	24.0	-	Fln	V			
21	72	0	0	30	1	0.3	0	0	56	78	0	94	4171	34.2	-	Fln	S			
22	72	0	0	30	24	4	0	0	36	5	66	95	1441	16.7	-	Fln	S			
23	72	20	S	30	13	2	0	0	75	28	49	97	2965	7.9	-	Fln	S			
26	72	10	S	61	0.2	0.1	0	0	79	52	0	99	5464	20.2	-	Fln	S			

TABLE 2. Continued.

SITE	AGE	SLOPE	ASPECT	ELEV	UNDERSTORY					OVERSTORY					SOIL	
					BIOMASS	PROD	HERB	FERN	BA	% PICEA	% THUJA	% CANOPY	PROD	DBH	SOIL	PARENTM
36	72	10	S	91	0	0	0	0	58	66	0	99	3730	8.9	F1n	L
5	71	20	E	30	2	0.8	0.6	0.1	63	43	7	96	3965	18.3	F1c	T
6	71	0	0	61	14	14	13	0.1	61	43	7	95	3847	17.4	F1c	T
60	90	50	NE	91	2423	560	162	153	80	54	0	97	4170	33.8	F2n	V
54	90	20	S	5	243	94	28	5	50	0	0	95	2910	17.8	F2n	V
56	90	0	0	5	87	74	16	55	79	81	0	95	6020	30.4	F1b	B
15	94	10	S	274	617	104	4	6	72	9	0	90	3112	22.1	F2n	V
61	95	0	0	5	94	58	5	17	107	63	0	99	7060	36.7	F1b	B
46	96	0	0	91	231	92	17	8	71	11	0	93	3994	29.8	F1f	L
51	100	10	S	15	129	70	1	1	70	36	33	95	3530	17.6	F2n	M
66	100	0	0	8	17217	683	118	139	82	37	0	96	5490	41.0	F1t	A
28	108	10	S	30	779	191	29	85	101	4	0	99	5993	29.9	F2n	V
57	142	10	S	30	186	100	62	14	92	56	0	98	3930	36.4	F1n	M
58	138	0	0	0	102	71	0.3	0	57	26	0	95	1650	15.7	F2r	V
64	150	0	0	5	917	211	87	45	82	46	0	97	3000	34.5	F4c	T
67	150	0	0	6	2349	488	121	84	79	64	0	94	3260	28.6	F1b	V
39	150	20	SE	31	8	7	1	0	105	42	0	98	4347	27.3	F4c	T
55	154	0	0	25	1417	374	176	7	78	17	0	96	3960	36.8	F1n	M
20	187	30	SW	107	1897	403	59	113	112	56	0	98	34.5	F1n	V	
40	188	10	NE	107	2501	186	46	8	53	26	2	91	19.4	F1n	V	
37	192	10	E	45	1031	78	0	0.1	63	29	0	93	8.6	F1c	T	
38	192	10	E	45	733	126	7	75	69	35	18	90	29.6	F1c	T	
65	250	60	N	61	1443	630	90	316	80	-	-	94	39.2	F4c	V	
42	250	20	E	46	5991	852	87	100	53	0	0	92	35.2	F1n	M	
62	300	10	N	28	5230	851	156	166	73	10	0	93	26.9	F4c	T	
17	400	0	0	46	539	92	1	19	71	20	0	92	28.0	F1c	T	
18	400	0	0	46	607	80	4	0	60	0	0	95	24.8	F1c	T	
53	550	0	0	5	709	413	116	261	87	43	0	86	30.2	F1t	A	

1/ tree basal area, m² ha⁻¹2/ kg ha⁻¹ based on basal area stocking, site index, and stand age using mean increment tables from Taylor(1934). Converted to dry weight by assuming wood specific gravity of .425 (Farr, 1973).

3/ mean tree diameter at breast height. Estimated from trees greater than 2.5 cm in diameter

4/ nomenclature follows Stephens et. al. 1969.

5/ S = sandstone or mudstone, V = igneous rock, M = metamorphic, T = till, L = limestone or marble, A = alluvium, MT = mining tailings, B = beach sands

easy to locate over a broad range of edaphic-environmental conditions. In southeast Alaska widespread logging did not occur more than 70 years ago and the cool wet climate largely eliminated fire as an important element in stand disturbance (Noste, 1969, Harris and Farr, 1974). Forests greater than seventy years old with establishment histories comparable to those of the younger age classes and lacking evidence of subsequent disturbance were difficult to locate over a range of environmental conditions. When a suitable stand of logging or fire origin was not available for an age class, stands of windthrow origin were occasionally sampled, (table 1).

Forests of windthrow origin are defined here as those that have lost most of the overstory canopy in a single major windstorm event. Root rotting fungi may be a major cause of stand deterioration in some cases, or may be subsidiary to basic physical stress caused by a combination of high winds, saturated soils, shallow roots and other factors (Ruth and Harris, 1979). Windthrown stands are widespread in southeast Alaska and often develop at different rates than forests of fire or logging origins. Windthrown stands also tend to be more variable than burned or clearcut stands so that adequate sampling is more difficult. To eliminate this extra source of variation, stands of fire or logging origin were preferred for sampling over those of windthrow origin.

Using these criteria, 62 intensive study sites were selected which ranged in elevation from 0 to 274 meters and were nearly uniform in slope and aspect (table 2). The selected forests were even-aged in structure, and homogeneous throughout the macroplot except in the oldest stands where an uneven-aged structure predominated. These stands represent similar environments and histories so that differences in vegetation

structure and composition should be associated primarily with differences in their age (Horn, 1974).

On each of sixty-two intensive study sites over fifty environmental and forest structural variables were measured. A soil pit was dug at sites where a complete soils description was not already available (Farr, 1968). Soil structure, depth, drainage characteristics and color were noted at each soil pit. At study sites used for the stand density project¹, tree diameter tallies as well as height and age data were obtained from W. A. Farr (unpubl.). Forest structural data were collected for the other plots. All trees within the macroplot (.12 to .5 ha) greater than 2.5 cm in diameter were measured at breast height to the nearest 0.5 cm. Standing dead trees were tallied by diameter and decay class (Fogel et. al. 1974, Maser et. al. 1979). Heights, ages, and growth increments were measured on representative co-dominant trees in each stand. These data were then used to estimate tree growth, volume, basal area, site index and tree foliar biomass (Gholz, 1979, Chambers and Folz, 1979, Taylor, 1934).

To document understory structure and biomass, forty to sixty 1-m^2 plots in clusters of four were established in a systematic grid at each site. The basal diameters and lengths of all shrubs, ferns, and selected herbs (those species whose biomass can be estimated from plant length) were measured in each 1-m^2 plot. A $.1\text{ m}^2$ rectangular microplot frame (Daubenmire, 1959) was placed in the center of each 1-m^2 plot to delineate

¹Farr, W.A. 1974. The effects of stand density upon growth and yield of hemlock-spruce stands in coastal Alaska. Study plan on file at Forestry Science Laboratory, Juneau , Ak.

TABLE 3. Summary of plant species encountered in study plots. Data compiled from mean estimates of annual production, and percent ground cover for each species in sixty-two study sites.

SPECIES	CLASS ^{1/}	% COVER	% PRODUCTION	RANK ^{2/}	% CONSTANCY ^{3/}
<u>Abies amabilis</u>	T	0.01	0.01	57	1.5
<u>Actaea rubra</u>	H	0.01	0.00	57	1.5
<u>Adiantum pedatum</u>	F	0.09	0.00	48	9.1
<u>Alnus rubra</u>	T	0.07	0.00	57	4.6
<u>Athyrium felix-femina</u>	F	1.16	0.25	19	37.9
<u>Blechnum spicant</u>	F	0.64	0.10	29	25.8
<u>Circaea alpina</u>	H	0.05	0.01	53	4.6
<u>Clintonia uniflora</u>	H	0.01	0.02	57	3.0
<u>Cladonia coniocraea</u>	L	0.50	0.00	33	40.9
<u>Dryopteris austriaca</u>	F	3.58	0.78	6	84.9
<u>Dicranum fuscescens</u>	M	1.77	0.82	10	93.9
<u>Epilobium hornemannii</u>	H	0.01	0.00	57	1.5
<u>Eurhynchium oreganum</u>	M	0.92	0.25	23	40.9
<u>Equisetum arvense</u> ^{4/}	F	0.01	0.00	57	1.5
<u>Foliose lichens</u>	L	0.82	0.00	26	77.3
<u>Galium triflorum</u>	H	0.01	0.00	57	3.0
<u>Gaultheria shallon</u>	S	0.15	0.00	43	9.1
<u>Goodyera oblongifolia</u>	H	0.06	0.00	51	6.1
<u>Gymnocarpium dryopteris</u>	F	3.02	0.18	8	71.2
<u>Hookeria lucens</u>	M	0.24	0.00	40	25.8
<u>Hylocomium splendens</u>	M	11.39	7.74	2	97.0
<u>Isoetecium stoloniferum</u>	M	0.61	0.04	31	62.1
<u>Jungermanniales spp</u>	LV	3.31	0.54	7	86.4
<u>Leucolepis menziesii</u>	M	0.01	0.00	57	4.6
<u>Luzula parviflora</u>	H	0.06	0.00	52	6.1
<u>Lycopodium annotinum</u>	F	0.10	0.00	47	10.6
<u>Lysichiton americanum</u>	H	0.03	0.00	55	3.0
<u>Linnaeus borealis</u>	H	0.01	0.00	57	1.5
<u>Maianthemum dilatatum</u> ^{6/}	H	0.70	0.01	28	45.5
<u>Marchantia polymorpha</u>	LV	0.56	0.27	32	30.3
<u>Menziesia ferruginea</u>	S	0.01	0.75	21	54.6
<u>Moneses uniflora</u> ^{7/}	H	0.64	0.00	30	60.6
<u>Other mosses</u>	M	1.57	0.47	15	69.7
<u>Oplopanax horridum</u>	S	0.87	0.04	25	28.8
<u>Osmorhiza chilensis</u>	H	0.01	0.00	57	1.5
<u>Picea sitchensis</u>	T	0.93	3.26	22	47.0
<u>Plagiothecium undulatum</u>	M	3.69	0.58	5	97.0
<u>Pogonatum macounii</u>	M	0.72	0.12	27	68.2
<u>Polypodium glycyhiza</u>	F	0.01	0.00	57	3.0
<u>Polystichum braunii</u>	F	0.01	0.00	57	3.0
<u>Polystichum munitum</u> ^{8/}	F	0.07	0.00	50	7.6
<u>Polytrichum spp</u>	M	0.48	0.09	34	43.9
<u>Porella navicularis</u>	LV	1.76	0.01	13	86.4

TABLE 3. Continued

SPECIES	CLASS	% COVER	% PRODUCTION	RANK	% CONSTANCY
<u>Pteridium aquilinum</u>	F	0.03	0.00	56	3.0
<u>Rhizomnium glabrescens</u>	M	7.04	2.78	4	92.4
<u>Ribes bracteosum</u>	S	0.01	0.00	57	1.5
<u>Ribes laxiflorum</u>	S	0.28	0.05	47	6.0
<u>Rubus parviflorum</u>	S	0.01	0.00	57	1.5
<u>Rubus spectabilis</u>	S	2.61	19.10	10	39.4
<u>Rubus pedatus</u>	H	2.03	0.05	11	59.1
<u>Rhytidiadelphus loreus</u>	M	25.09	11.24	1	95.5
<u>Sambucus canadensis</u> ^{9/}	S	0.12	0.00	45	10.6
<u>Sphagnum spp</u>	M	1.64	1.21	14	60.6
<u>Streptopus amplexifolius</u>	H	0.37	0.03	36	30.3
<u>Streptopus roseus</u>	H	0.32	0.01	37	30.3
<u>Streptopus streptopoides</u>	H	0.48	0.24	22	47.0
<u>Tiarella trifoliata</u>	H	0.20	0.03	18	69.7
<u>Tiarella unifoliata</u>	H	0.01	0.00	57	1.5
<u>Timmia austriaca</u>	M	0.22	0.02	41	22.7
<u>Thelypteris phaeopteris</u>	F	0.11	0.08	46	6.1
<u>Thuja plicata</u>	T	0.20	0.46	42	10.6
<u>Tsuga heterophylla</u>	T	2.88	18.00	9	89.4
<u>Vaccinium alaskaense</u>	S	8.44	4.97	3	87.9
<u>Vaccinium ovalifolium</u>	S	0.01	0.00	57	1.5
<u>Vaccinium parvifolium</u>	S	1.22	1.92	20	90.9
<u>Viola glabella</u>	H	0.14	0.00	44	12.1

1/ T = tree seedling, F = vascular cryptogam, H = herbaceous and low shrub,
L = lichen, M = moss, LV = liverwort, S = shrub

2/ 1 = highest relative ground cover, 57 = lowest cover

3/ the percent of study sites for which the species was recorded

4/ primarily Lobaria oregana, Peltigera canina. Also Sphaerophorus bulbosus,
and Hypnogymania enteromorpha

5/ includes Conocephalum conicum

6/ primarily Plagiothecium elegans, Ptilium crista-castrensis, and Hypnum spp.

7/ primarily Bromus sitchensis, and Poa spp

8/ P. juniperinum and P. commune

9/ primarily S. squarrosus, and S. girgensohnii

TABLE 4. Southeast Alaska biomass prediction equations. Least squares estimates were used to calculate regression parameters to predict biomass (g) from plant size classes. Log base ten transformations of both independent and dependent variables were used where a significant improvement in the coefficient of determination and a decrease in the mean squared error resulted. The two models used were:

$$1) \log_{10} \hat{Y}_i = \hat{B}_0 + \hat{B}_1 \log_{10} X_i + e_i \quad 2) \hat{Y}_i = \hat{B}_0 + \hat{B}_1 X_i + e_i$$

The model used is indicated in column three for each equation. Note: B_0 values are corrected for the mean squared error as recommended by Baskerville(1972).

SPECIES	\hat{B}_0	\hat{B}_1	$X_i^{1/}$	UNITS	$Y_i^{2/}$	n	r^2	$Sx.y$	Range X_i
A. Arborescent shrubs									
<u>Menziesia ferruginea</u>	-1.7277	2.4244	logDOG	mm	prod	24	.83	.123	1 - 24
<u>Menziesia ferruginea</u>	-1.7919	3.1899	logDOG	mm	wood	24	.93	.089	1 - 24
<u>Menziesia ferruginea</u>	-1.3997	1.9287	logDOG	mm	fol	15	.79	.083	1 - 24
<u>Menziesia ferruginea</u>	-3.2910	3.0260	logDOG	mm	twig	10	.74	.348	1 - 24
<u>Ribes laxiflorum</u>	-0.0842	0.0556	logDOG	mm	twig	6	.87	.002	2 - 7
<u>Ribes laxiflorum</u>	-1.8576	3.3567	logDOG	mm	wood	6	.80	.158	2 - 7
<u>Ribes laxiflorum</u>	-3.2735	1.2329	logDOG	mm	fol	6	.81	.158	2 - 7
<u>Rubus spectabilis</u>	-1.6151	2.8406	logDOG	mm	prod	60	.72	.109	1 - 25
<u>Rubus spectabilis</u>	-1.1090	2.5467	logDOG	mm	wood	35	.76	.058	2 - 25
<u>Rubus spectabilis</u>	-0.8803	1.8840	logDOG	mm	fol	21	.77	.072	2 - 25
<u>Rubus spectabilis</u>	-1.1895	2.0899	logDOG	mm	twig	21	.86	.049	2 - 25
<u>Vaccinium alaskaense</u>	-1.4544	1.9657	logDOG	mm	prod	191	.75	.127	1 - 26
<u>Vaccinium alaskaense</u>	-1.2556	2.7765	logDOG	mm	wood	68	.92	.089	1 - 26
<u>Vaccinium alaskaense</u>	-1.126	1.7790	logDog	mm	fol	16	.79	.164	1 - 26
<u>Vaccinium alaskaense</u>	-1.3131	1.5324	logDOG	mm	twig	19	.74	.167	1 - 26
<u>Vaccinium parvifolium</u>	-1.3950	2.1207	logDOG	mm	prod	27	.83	.105	1 - 21
<u>Vaccinium parvifolium</u>	-1.1110	3.0842	logDOG	mm	wood	19	.97	.063	1 - 21
<u>Vaccinium parvifolium</u>	-1.2032	2.0208	logDOG	mm	fol	20	.75	.310	1 - 21
<u>Vaccinium parvifolium</u>	-1.3490	1.7640	logDOG	mm	twig	14	.85	.144	1 - 21
<u>Oplopanex horridum</u>	-2.9353	3.6530	logDOG	mm	wood	21	.84	.134	5 - 30
<u>Oplopanex horridum</u>	-2.2401	2.8904	logDOG	mm	fol	16	.89	.049	5 - 30
<u>Oplopanex horridum</u>	-2.1460	2.3650	logDOG	mm	twig	18	.84	.060	5 - 30

B. Low shrubs, ferns, and herbaceous vascular plants

<u>Cornus canadensis</u>	-0.0695	0.0536	cover	%	biom	20	.95	.032	3 - 60
<u>Coptis asplenifolia</u>	0.0778	0.0342	cover	%	biom	19	.87	.021	2 - 40
<u>Maianthemum dilatatum</u>	-0.1337	0.0408	cover	%	biom	15	.93	.083	1 - 97
<u>Monese uniflora</u>	0.1677	0.0395	cover	%	biom	8	.89	.015	1 - 25
<u>Rubus pedatus</u>	0.2103	0.0164	cover	%	biom	19	.84	.020	1 - 60
<u>Streptopus streptopoides</u>	-0.2233	0.0197	length	cm	biom	8	.71	.007	1 - 54

TABLE 4. Continued.

SPECIES	\hat{B}_0	\hat{B}_1	X_1	UNITS	Y_1	n	r^2	$S^2_{x,y}$	Range of X
B. Low shrubs, ferns, and herbaceous plants continued									
<u>Tiarella trifoliata</u>	-0.3009	0.0803	cover	%	biom	22	.95	.145	1 - 75
<u>Streptopus amplexifolius</u>	-4.1929	2.3971	loglength	cm	biom	26	.99	.014	4 - 91
<u>Streptopus roseus</u>	-3.5380	1.9410	loglength	cm	biom	28	.89	.000	7 - 24
<u>Gaultheria shallon</u> ^{3/}	1.5457	0.7026	cover	%	fol	32	.83	.064	5 - 85
<u>Gaultheria shallon</u>	2.4566	1.1425	cover	%	wood	12	.95	.218	2 - 60
<u>Athyrium felix-femina</u>	-4.3280	2.3740	loglength	cm	biom	32	.98	.000	18 - 147
<u>Dryopteris austriaca</u>	-3.8260	2.2050	loglength	cm	biom	229	.98	.000	4 - 95
<u>Gymnocarpium dryopteris</u>	-4.0190	2.2105	loglength	cm	biom	55	.97	.010	5 - 50
<u>Blechnum spicant</u>	-3.2460	1.8480	loglength	cm	biom	78	.78	.010	14 - 56
<u>Asplenium viride</u>	-4.0516	2.2520	loglength	cm	biom	30	.98	.000	13 - 42
<u>Polystichum munitum</u>	-3.7482	2.2591	loglength	cm	biom	32	.95	.017	8 - 106
<u>Lysichiton americanum</u>	-3.0171	2.2815	length	cm	biom	4	.97	.110	28 - 57
<u>Thelypteris phaeopteris</u>	-3.9040	2.2815	loglength	cm	biom	13	.97	.000	13 - 27
<u>Clintonia uniflora</u>	-4.0932	2.4713	loglength	cm	biom	59	.96	.008	6 - 18
<u>Tsuga heterophylla</u>	-1.0326	2.8080	logDOG	mm	biom	205	.99	.025	1 - 29
<u>Tsuga heterophylla</u>	-1.2975	2.2490	logDOG	mm	fol	110	.97	.046	1 - 29
<u>Tsuga heterophylla</u>	-1.3263	2.7891	logDOG	mm	wood	110	.98	.053	1 - 29
C. Bryophytes and lichens									
<u>Eurhynchium oregonum</u>	1.2819	0.1233	cover	%	biom	8	.86	.028	2 - 90
<u>Hylocomium splendens</u>	-0.8069	1.0968	logcover	%	biom	30	.91	.010	1 - 90
<u>Jungermannia lanceolata</u>	-3.8930	2.3000	logcover	%	biom	28	.89	.030	22 - 88
<u>Lobaria oregana</u>	-1.2062	1.7255	logradius	cm	biom	40	.90	.039	1 - 16
<u>Pogonatum macounii</u>	-0.3612	0.1775	cover	%	biom	12	.94	.987	1 - 90
<u>Plagiothecium undulatum</u>	-0.0658	0.0880	cover	%	biom	17	.81	.950	1 - 15
<u>Rhizomnium glabrescens</u>	0.7071	0.0952	cover	%	biom	13	.81	1.373	1 - 80
<u>Rhytidiadelphus loreus</u>	-0.8178	1.0209	logcover	%	biom	29	.87	.044	1 - 90

1/ cover = ground cover estimated from microplots
 DOG = diameter of shoot at ground surface

2/ biom = total above ground biomass, fol = foliar biomass, twig = annual twig biomass
 wood = total above ground biomass - foliar biomass - annual twig biomass,
 prod = annual twig and foliar biomass (does not include increment of woody stem)

3/ from Gholz et al (1979)

the area for making cover class estimates of all plant species or species groups encountered (table 3). These data were used to estimate understory standing crop biomass and production using equations developed from destructive analysis (table 4). At the center of each 4-m² plot cluster, tree canopy cover and its variance was estimated from four spherical densiometer readings (Strickler, 1959). To further characterize understory-overstory structural relationships, the distance and diameter of the nearest tree greater than 2.5 cm in diameter in each of four quadrants was also measured.

Overall plot aspect, slope, shape (convex, concave, or flat side slope or transverse slope), and physiographic position (mid-slope, ridge-top, marine terrace, alluvial flat) were recorded. Elevation, latitude and longitude were taken from 15' USGS topographic maps. An aneroid altimeter was used where more critical elevation estimates were needed.

Destructive Data

Over 1400 samples of understory vegetation separated into foliar, woody, and annual growth segments by species were collected during the summers of 1977 to 1979. Specimen size classes were measured in the field then oven dried at 70°C for 24 hours in labelled paper bags, using the recommendations of Forrest (1968). Simple linear regression analysis was then used to develop relationships between cover, basal diameter, or length and component biomass. Multiple regression analysis indicated that less than 5% of the variation in biomass could be accounted for by knowing the collection site. Equations developed on



Figure 4 . Stand age 20 years, Maybeso Valley, site 52. Peak understory production for the chronosequence. Shrubs dominate understory biomass.

a series of study sites were therefore considered sufficiently homogeneous to justify pooling of data to give generalized predictor equations applicable to all study sites in the region. Samples were collected during the middle part of the summer (July-August) at which time most species were assumed to be close to peak biomass. Evidence supporting this assumption came from a covariance analysis of plant biomass regressed against Julian calendar date adjusted to a common growing season for all sites after taking account for that variation associated with plant size (diameter, percent cover, or length). In all cases less than five percent of the variation in biomass was explained by knowing sampling date. Remeasurement of two sites throughout the sampling season also failed to show clear phenological effects on biomass production estimates. These equations were used to estimate understory biomass and production for the three years of nondestructive data. Shrub production estimates were derived from annual twig and foliage biomass data only. Therefore these data underestimate total above-ground production, which would include woody stem increment.

RESULTS

General Successional Trends

Shrubby and herbaceous vegetation as well as tree seedlings were found to quickly respond to the more favorable growth conditions created by forest overstory removal (fig 4). During the first twenty

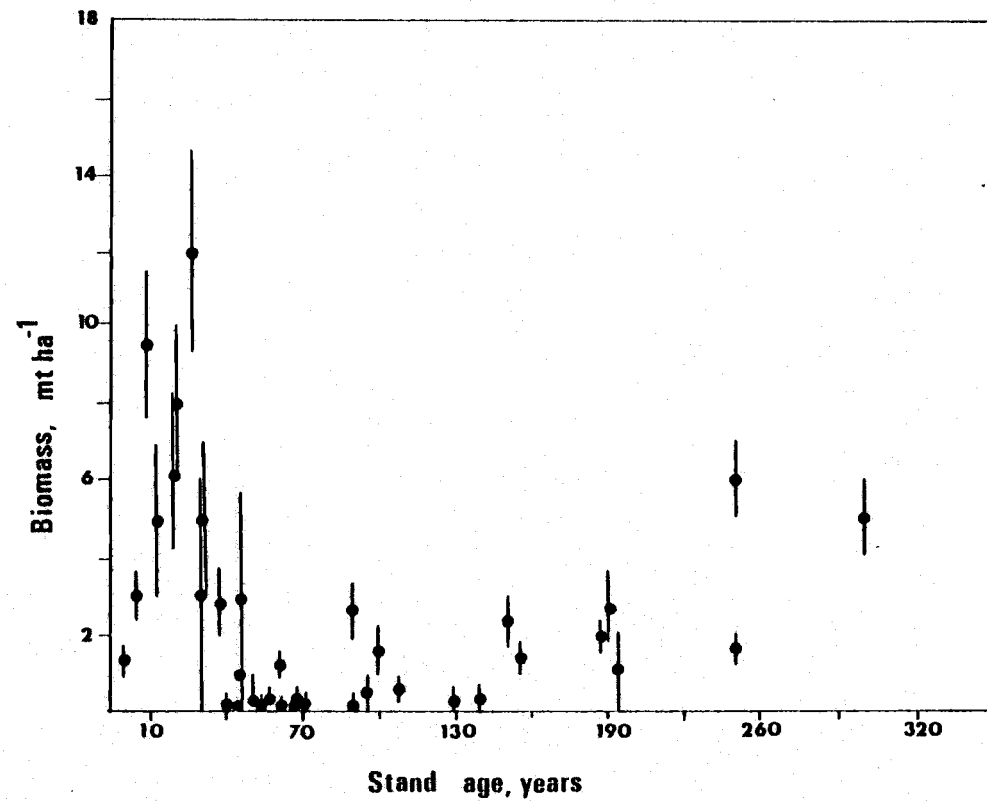


Figure 5. Understory aboveground biomass accumulation patterns.
 Bars represent 95 % confidence limits. $n = 40 - 60$ for each point.
 Not all plots in the 20 to 90 year age range are shown
 due to their similar biomass values (see table 2).

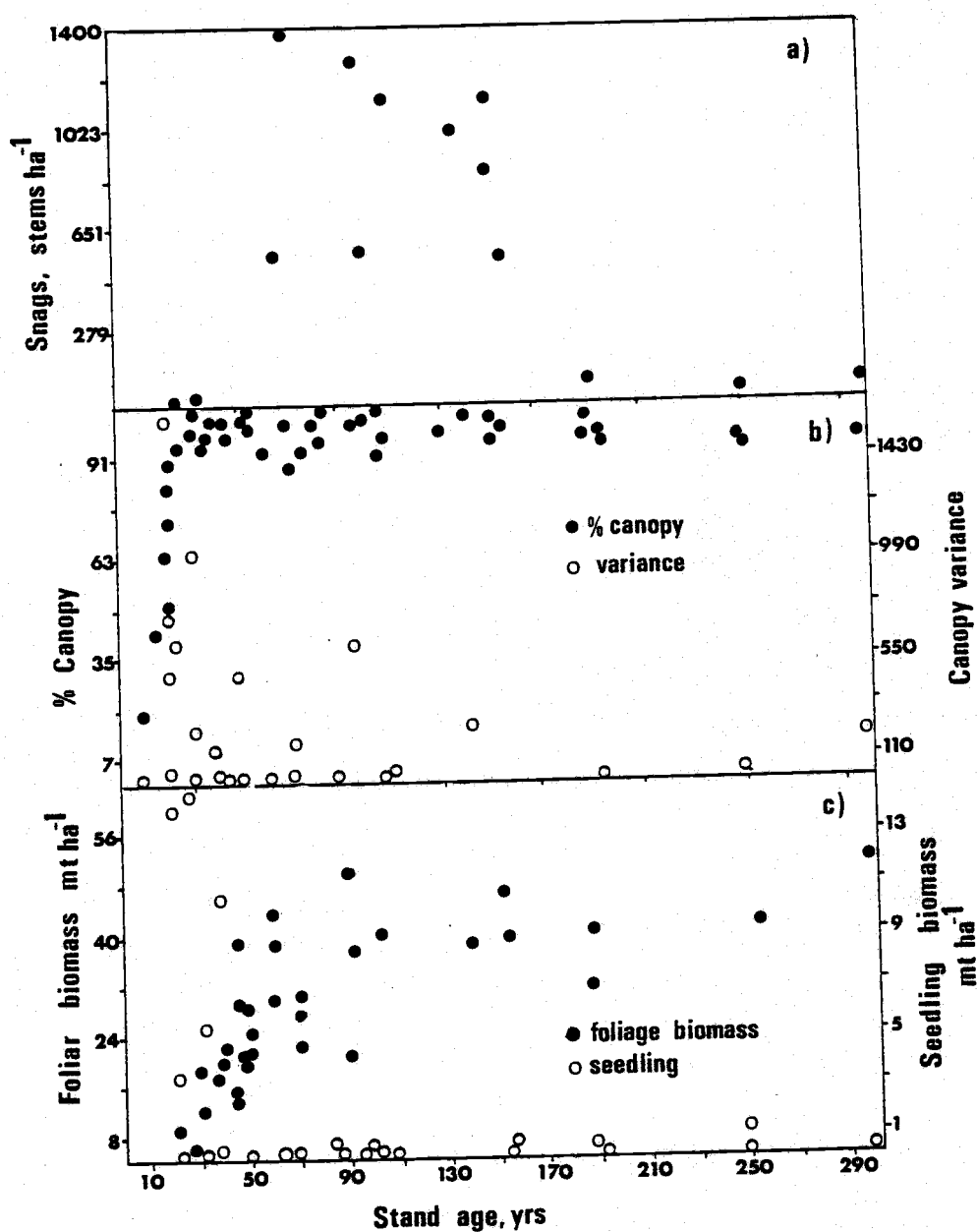


Figure 6. Forest structural changes during succession.
 a) standing dead trees greater than 2.5 cm in diameter
 b) average %canopy cover, and variance in mean
 c) tree foliage biomass and aboveground seedling biomass.

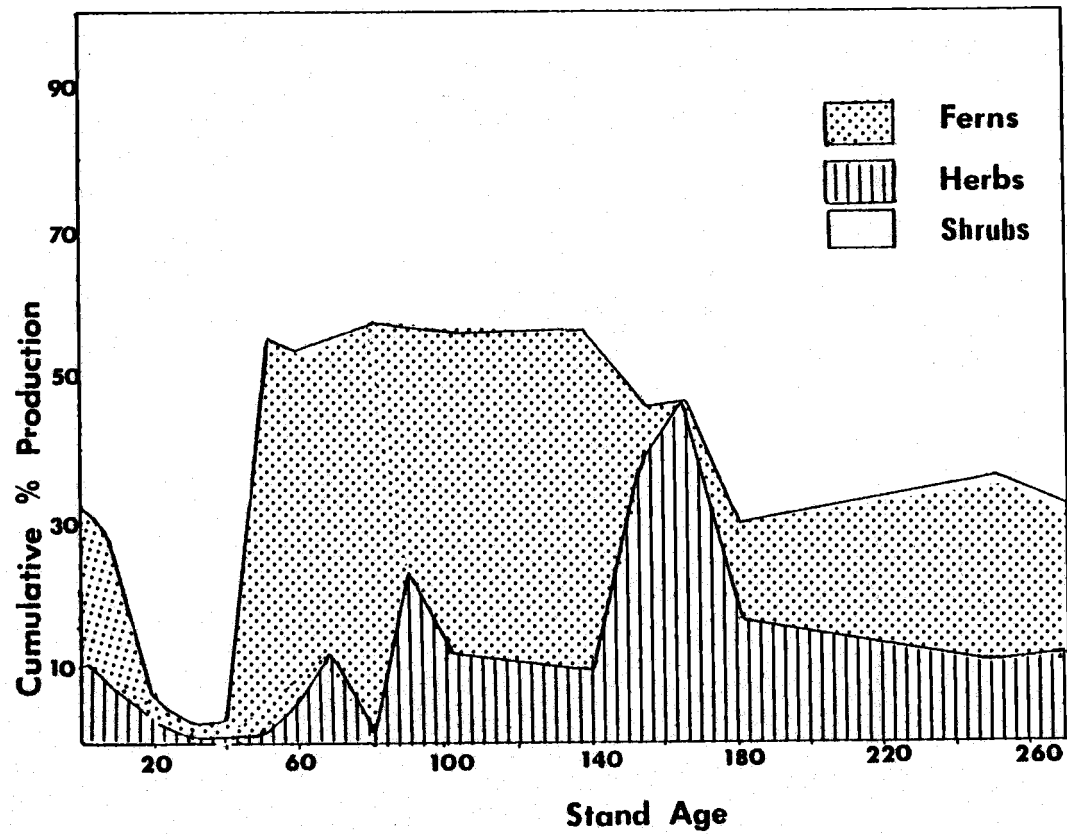


Figure 7. Understory structural changes during succession. Based on mean values of annual production by ten year age class.

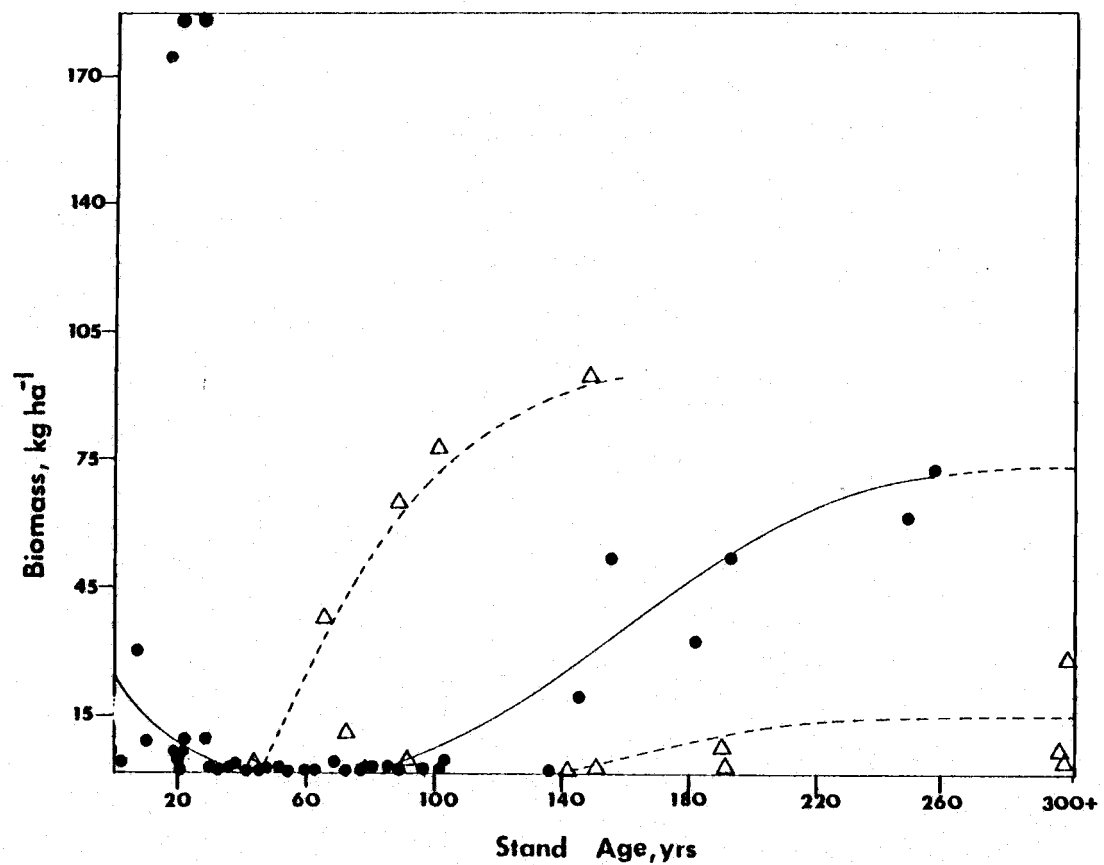


Figure 8. Herbaceous plant successional patterns. Values represent biomass estimates of Cornus, Coptis, and Rubus pedatus. Triangles represent windthrown stands.

years of succession following logging understory production increased exponentially with time (fig 5). Decreased competition with trees, increased light, improved temperatures, and nutrient availability probably all play a role in stimulating this growth (Taylor, 1935, Likens et. al. 1978). No distinct "reorganization phase" (sensu Bormann and Likens, 1979) or decline in understory production following disturbance was apparent during the first five years. The youngest stand, which was three years old, already attained levels of understory production comparable to old growth forests (table 2). By twenty years production increased to as much as $5210 \text{ kg ha}^{-1} \text{ yr}^{-1}$. Most of this growth represents a response of the woody shrub species. Vaccinium alaskaense sprouts heavily after disturbance. Vaccinium in combination with colonizing Rubus spectabilis and Ribes laxiflorum represented an average of over 90% of the understory production in these young forests. Tree seedlings (less than 2.5 cm in basal diameter) also showed this pattern of successional development (fig 6c). The other understory strata show varying responses to overstory removal (table 2). Dryopteris and Blechnum generally develop in dense clumps when tree regeneration is sparse. Dryopteris dramatically increases biomass in these young stands, frond lengths often exceeding 10-12 dm (compared to 1-3 dm in mature forest). These ferns tend to decline as Vaccinium and Rubus form an increasingly dense canopy layer with tree saplings 20-25 years after cutting. Low shrubs and herbaceous phanerogams may also respond to better growing conditions following cutting, but in most stands these plants showed a decline shortly following forest cutting (fig 7,8). Herbaceous vegetation can be negatively

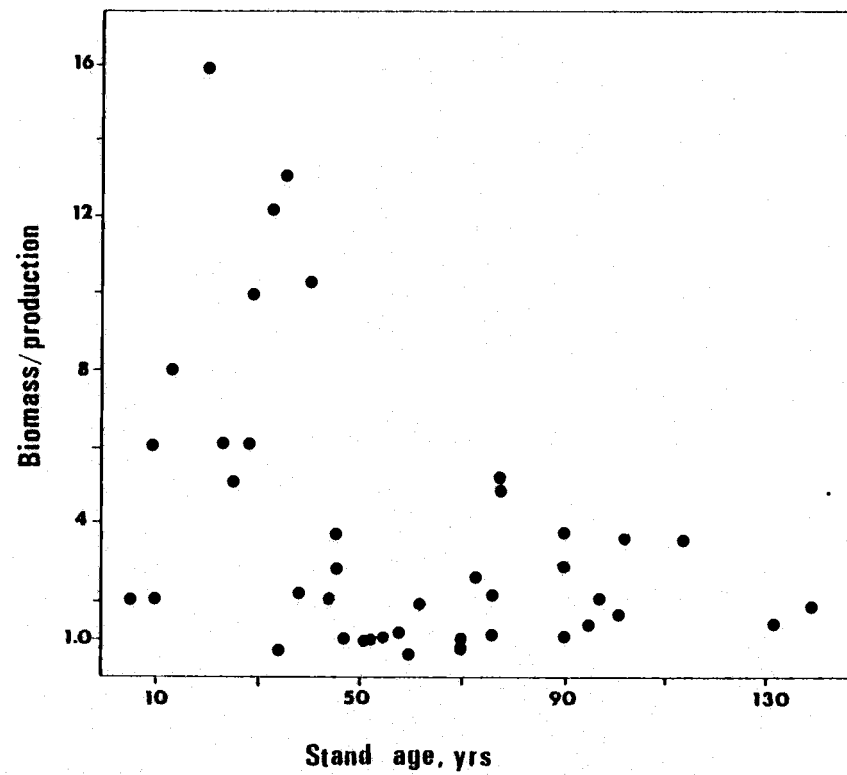


Figure 9. Biomass accumulation ratio changes over the chronosequence. High ratios indicate dominance by large woody shrubs.



Figure 10 . Stand age 27 years, Shrubby Island. Rubus and Vaccinium are at or past peak biomass for Chronosequence.

influenced by the growth of woody shrubs during this stage. At twenty-year-old plots in the Harris River Valley, for instance, Rubus spectabilis formed a dense canopy cover with only scattered Hylocomium and Rhytidiadelphus mosses or leaf litter beneath (site 10, table 2).

Sprouting shrubs during the first five to ten years after logging had a relatively high percentage of herbaceous succulent tissues of greatest importance to ungulates and other herbivores (Klein, 1965, Schoen and Wallmo, 1979). The lignified or dead woody components of understory vegetation steadily increased during this phase of succession so that by the time shrubs were shaded out by the tree canopy, succulent tissues (young twigs and deciduous leaves or the annual production) were an insignificant component of the understory (fig 9). The peak in understory biomass production and accumulation occurred at about 15-20 years after logging. Standing crop biomass declined more slowly than annual production after twenty years owing to the high percentage of woody material (table 2).

The twenty- to thirty-year age class encompassed the most dynamic stages of understory biomass development. The development of a dense forest overstory canopy, "canopy closure", generally occurred during the latter part of this age class (fig 10). Slight differences in environmental or forest structural parameters generally resulted in large differences in understory growth during this stage. At Tuxekan Island, for example, two sites were measured that were part of the same clearcutting operation thirty-one years previous. Both had similar soil structure and parent material, but differed in tree growing site potential (site index) by eight meters. At site 24, near sea level

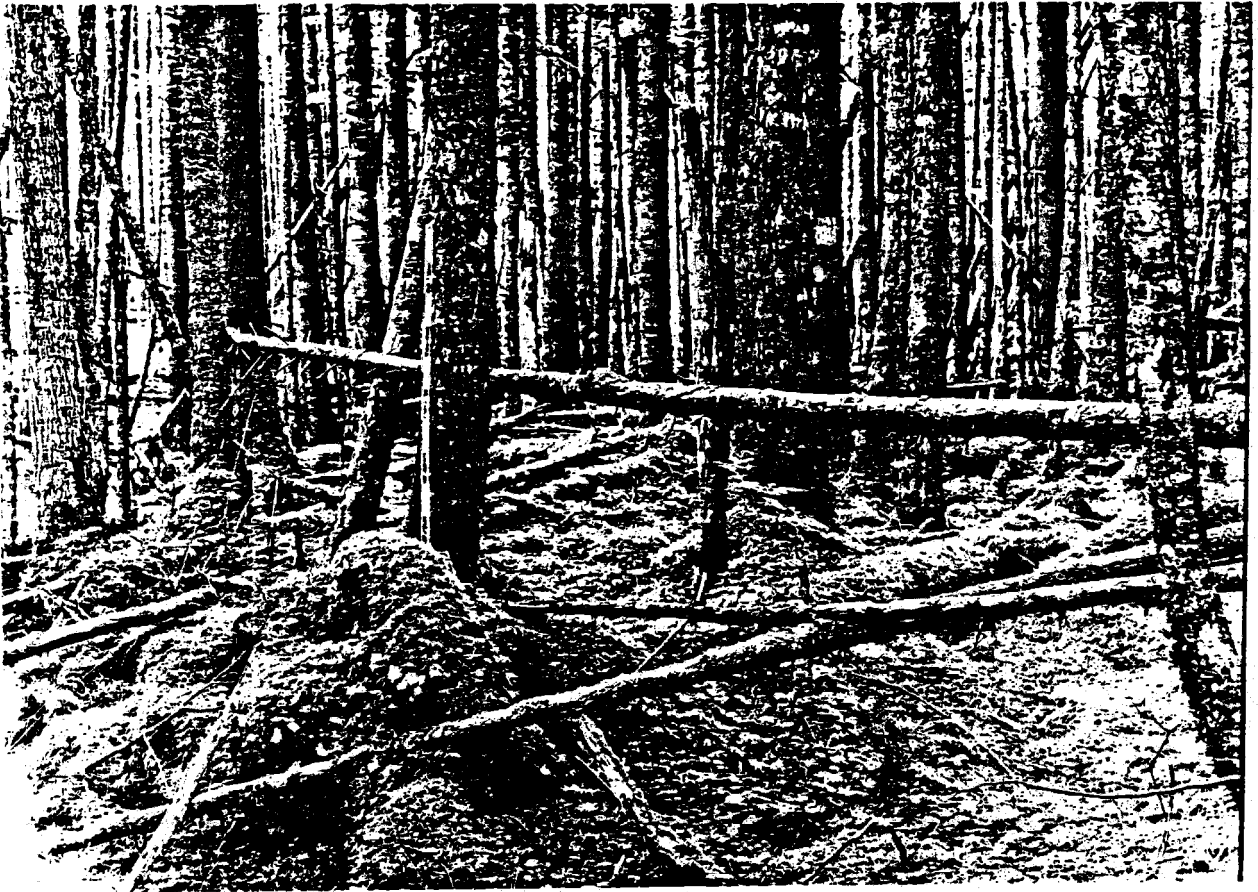


Figure 11. Stand age 100 years, Kindergarten Bay, Etolin Island. The depauperate understory stage. Understory dominated by Rhytidiadelphus and Hylocomium.

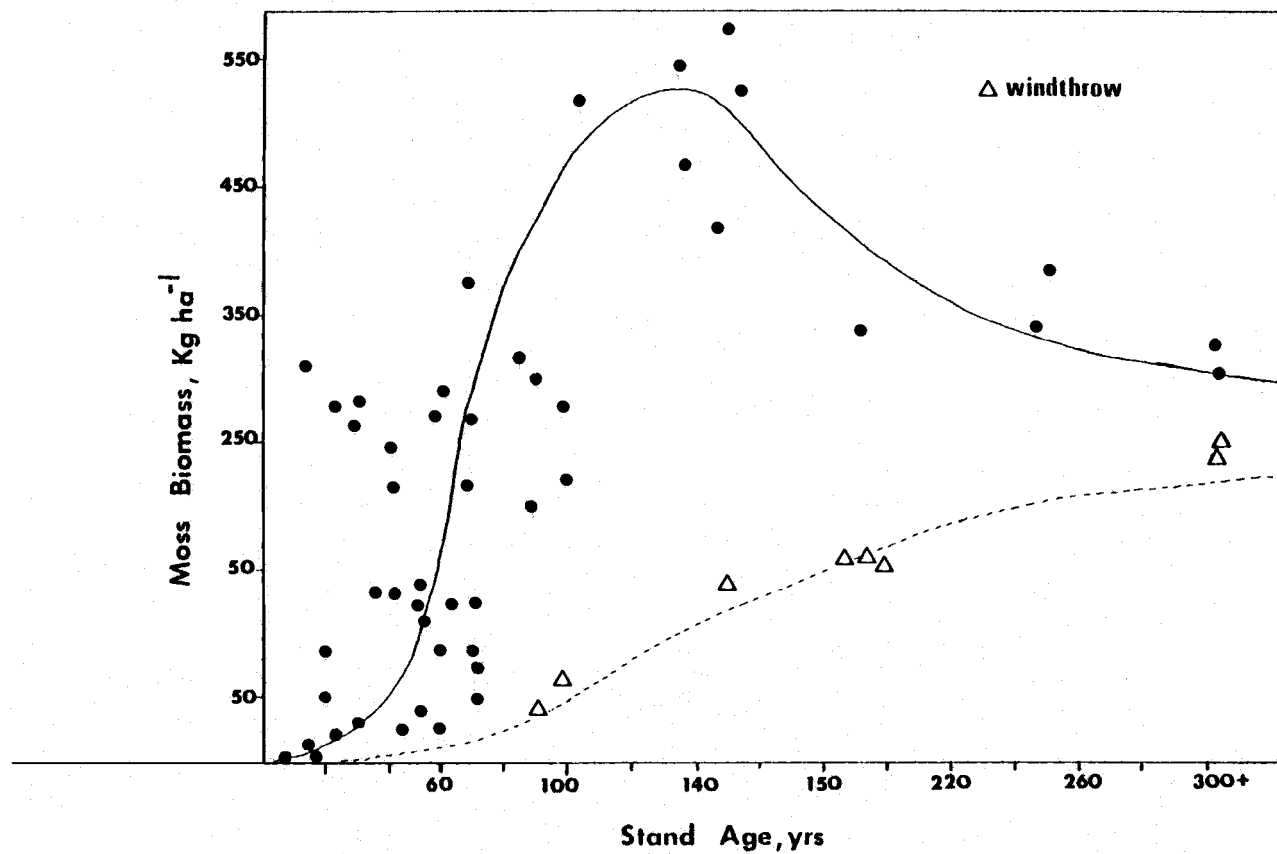


Figure 12. Bryophyte successional patterns. Sites with a significant portion of the overstory canopy disturbed by windthrow are indicated.

a slower developing Tsuga dominated forest was present. A well developed, but highly clumped woody understory persisted with a biomass of over 5500 kg ha^{-1} . At site 27, sixty meters higher in elevation, a fast growing spruce dominated forest developed with only six percent the understory biomass of site 24 (table 2). Tree basal area was twice that of the lower stand, and canopy closure more complete.

Tree site index was not found to clearly relate to patterns in understory successional development over the full chronosequence. Within these younger age classes, however, site index was consistently associated with earlier canopy closure so that less understory dry matter production would be expected over the early successional stages on normally developed high sites.

In southeast Alaska understory production normally stays below $70 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for about one century after canopy closure. A decline in both understory standing crop biomass and annual production generally occurs during this time span. This decline is primarily related to the elimination of Rubus spectabilis and Vaccinium alaskaense under closing gaps in the canopy. After forest canopy closure mosses, particularly Rhytidiadelphus and Hylocomium, form extensive carpets (fig 11). By fifty to seventy years these feather mosses form layers over all but the most recent logs as well as the forest floor, greatly exceeding the biomass of understory vascular plants (fig 12). Beside root mounds and logs or tree stumps small decumbant evergreen Vaccinium parvifolium, Moneses uniflora and leafy liverworts (Jungermanniales) also persist beyond canopy closure. During this stage in succession small clumps of rhizomatous ferns, such as Gymnocarpium dryopteris and Dryopteris austriaca, occur on both decaying wood and duff layers

on the forest floor.

At fifty to sixty years Dryopteris, Gymnocarpium and, in some sites, Blechnum ferns begin to dominate understory production. The dominance of ferns over herbs forms a distinct phase in the successional development of the vegetation in this region (fig 7). Fifty to seventy years after canopy closure ferns are an insignificant forest vegetation component, rarely recognizable as a distinct stratum in the forest. In older stands fern production generally increases with time.

The decline in fern dominance at around 150 years generally corresponds to a steady increase in the herbaceous phanerogam stratum, and a sharp increase in shrub production (fig 7). Tree growth steadily declines after the first century, losses to mortality and fungal attack becoming more significant (Taylor, 1934, Laurent, 1974). Moss standing crop biomass also shows a strong pattern during this time period (fig 12). A significant increase in accumulated bryophyte biomass occurs during the first 150 years following logging or fire ($\alpha = .001$, $r = .66$). Peak biomass occurs at 140 to 160 years on a variety of sites in both the Petersburg and Juneau geographic regions. The decline in moss biomass corresponds to an increase in shrub and herb components over the last stages of successional development.

The moss biomass of a particular site in the 20 to 100 year age class depends on a number of interacting factors, mostly relating to the disturbance creating the forest (as it effects competing vegetation) and the microclimatic conditions of the wood and needle substrates on the forest floor. Studies of production by Hýlocomium and related feather mosses show a strong dependence on high atmospheric humidity



Figure 13. Stand age 192 years, Clark Bay, site 38. The old growth stage. Vascular understory stratum has re-established, especially Vaccinium spp. and Tsuga.

and frequent precipitation or fog drip (Busby et. al., 1979, Callagan et. al., 1978, Tamm, 1953). A negative relationship between solar insolation and Hylacomium growth is supported by laboratory data (Hoddinott and Bain, 1979). The decline of bryophyte biomass in the older age classes in southeast Alaska thus appear to be a result of competition with understory plants combined with an increase in moisture stress associated with increased tree canopy openings during the 150 to 200 year age-class.

The final stages of understory development represent a transition to the dynamic equilibrium of an old growth forest, in which a hemlock-dominated forest of climax structure develops (Whittaker, 1953 and fig 13). In these forests dominant trees generally exceed 250 years of age. A greater range of tree size classes are generally present in these forests. A greater variety of forest floor substrates and microenvironments in which the understory plants may grow generally occur under these forest canopies. The decaying wood components of the ecosystem generally increase over time so that they become a more conspicuous element in the forest than in rapidly aggrading even-aged systems. The enlarged bases of the oldest trees (200 cm or more in diameter) tend to favor growth of some herbs and low shrubs on Rhytidiadelphus mats. The more heterogeneous canopy structure of these older forests appears to allow for the development of greater epiphyte biomass and diversity as has been documented in the Pacific Northwest (Pike et. al. 1975, 1977). Lobaria spp. , Hypnogymania enteromorpha, Sphaerophorus, Usnea spp and Peltigera canina are particularly common as fragments blown from the canopy or as actively

growing thalli on the forest floor.

Tree seedling biomass (Tsuga heterophylla, Thuja plicata) paralleled understory vegetation patterns by increasing between even-aged second growth and older uneven-aged forests. Most of these seedlings were concentrated on well decayed logs and stumps (decay class 4 or 5 of Fogel, 1974). Understory plants showed highly variable spatial patterns under old-growth forests. In some, Vaccinium developed a nearly continuous stratum. In other stands shrubs were confined to edges of logs, root mounds, or stumps, forming distinct clumps. The uneven-aged old growth forest thus differed both structurally and functionally from younger even-aged forests, and was generally the most heterogeneous of any class.

Relation of Understory Dynamics to Forest Structure

Although the majority of sites sampled fit the pattern of successional development described above, some clear exceptions were also noted. In order to better understand the factors leading to the observed anomalies, each of the understory strata were studied in relation to measured biotic (forest structure) and abiotic (environmental) factors.

For this study understory plant growth is considered a function of five main classes of factors: tree competition, historical factors, grazing, soils, and microclimate. The relationships of each of these classes of factors with understory growth are summarized in the following

sections,

Forest structure is generally thought to influence understory vegetation by altering microclimate. In a wet maritime climate at low elevations, moisture and temperature would not normally be expected to limit understory growth. The most dramatic change in the microclimates of these stands observed over the chronosequence was the change in light reaching the forest floor.

Much effort was expended to try to measure light under the forest canopy so that it could be related to understory growth. Both photocell and chemical light meters were employed to measure light levels under a series of forest canopies. Mechanical and low light resolution problems plagued the photocell, preventing collection of meaningful data. Using the method of Friend (1961) ozalid paper was used to index twenty-four hour insolation. The variability of clouds and precipitation during the summer was found to preclude meaningful comparisons between many sites unless measurements were taken simultaneously over several days. Indirect indices of canopy light interception were therefore sought.

The low proportion of sunny days in southeast Alaska (10-20 per field season) was thought to minimize the influence of sunflecks to understory vegetation. Diffuse radiation has been shown to relate well with understory plant growth (Blackman and Rutter, 1948). An estimate of both the mean and variance in below-canopy light conditions was thus needed to take account of the complex relationship of the irregular canopy surface to direct and diffuse radiation interception. Side lighting was suspected as being of particular importance since patches of productive vegetation were observed to develop frequently

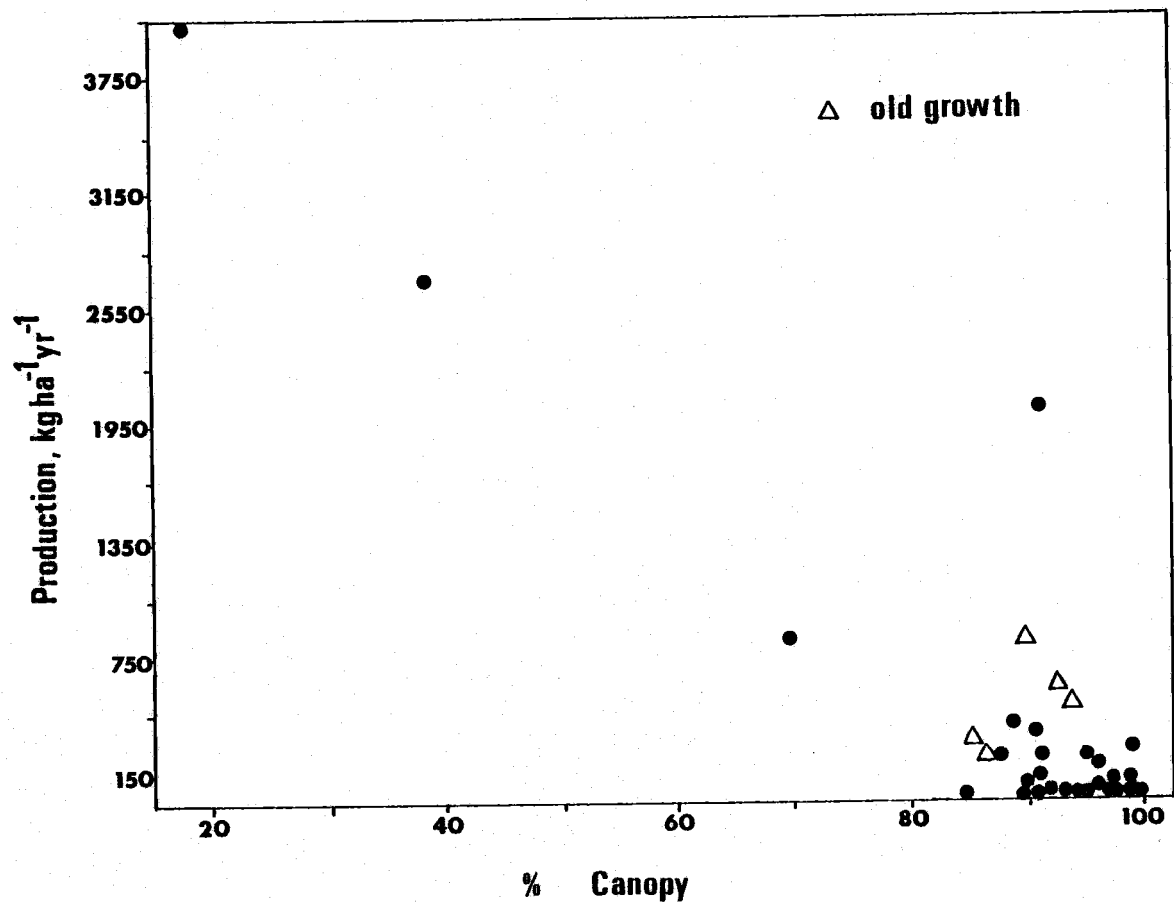


Figure 14 , Relation of canopy coverage to understory growth. Young growth stands on anomalous soils not shown. Stands greater than 150 years old are indicated.

in areas more open to one side as well as directly under canopy gaps. By using the spherical densiometer a quick but rough estimate of percent canopy cover over the entire hemisphere is possible (Strickler, 1959). These estimates of mean, variance, and minimum gap in canopy cover were used as indices of light interception for this study.

Percent tree canopy cover was found to have a negative relationship with understory development during the first 100 years ($r = .7$, $\alpha = .01$). The majority of sites had canopy cover exceeding 90%. Considerable variation in understory vegetation occurred under these dense canopies (fig 14). The variation in radiant energy with respect to canopy cover made resolutions of dense canopy differences difficult, limiting the usefulness of this approach to studying canopy understory relationships.

Tree foliar biomass was thought to be an alternative index of canopy density, and thus proportional to light penetration through the canopy. A weaker relationship was suggested between foliar biomass and understory production for this data set ($r = .58$). The development of foliar biomass over time also suggests that the understory pattern is independent of that influence. Tree volume and foliar biomass followed the same basic pattern of development over time as has been suggested for temperate forest ecosystem biomass in general (Odum, 1969, Bormann and Likens, 1979, Kira and Shidei, 1967). All forest tree components rapidly accumulated biomass during the first stages of succession (the "aggradation phase") then continued to accumulate biomass at successively lower rates to the old-growth stages (fig 6c). The bimodal peaks in understory production in the 15-20 year and 200-300 year age classes are not predictable from these variables, suggesting that

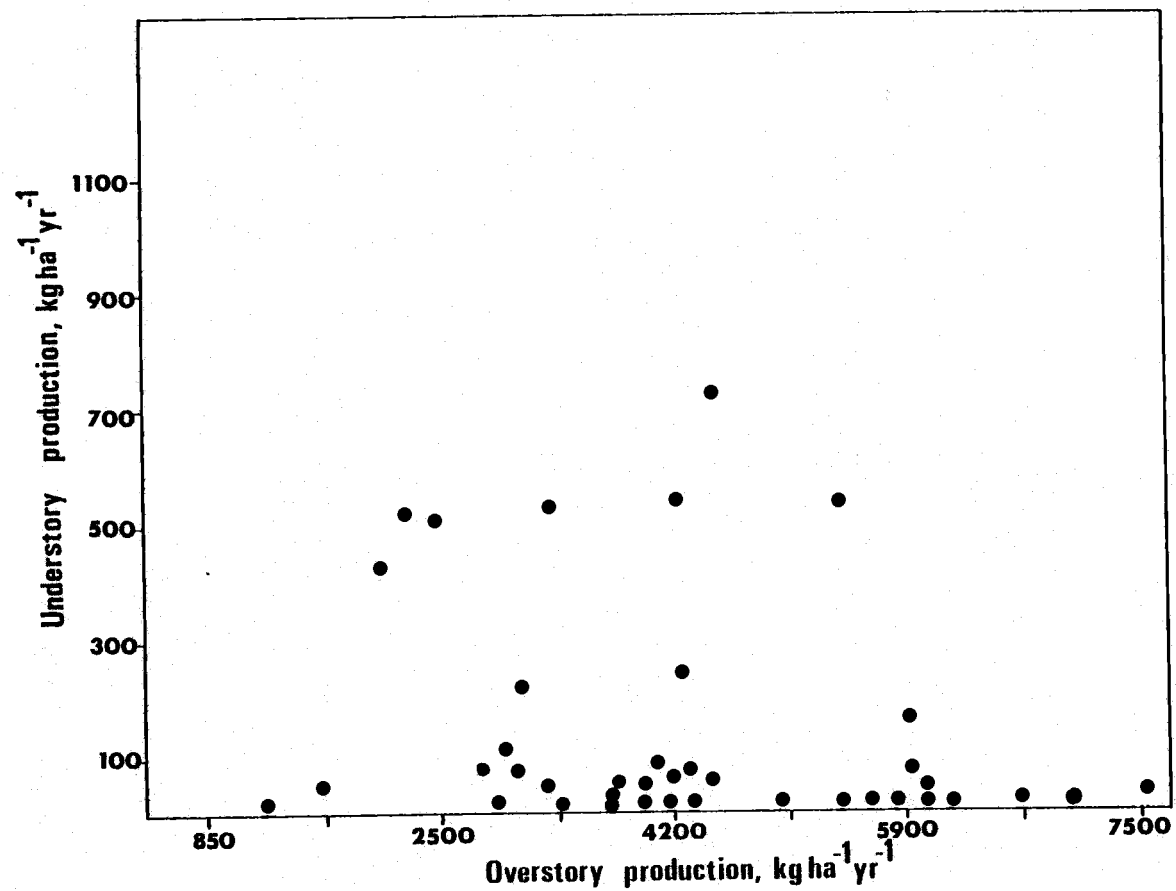


Figure 15 . Relation of overstory growth to understory. Tree production data taken from Taylor(1934). Stands greater than 150 years old not included.

the understory is operating independently of these factors. Previously reported correlations of understory growth and overstory foliar biomass or leaf area are perhaps also only applicable to rapidly aggrading systems in which these variables are better correlated to the operational factors (Major, 1950) that are governing understory growth.

B, Competition for belowground resources

A second category of forest tree influence on understory growth includes direct competition for nutrients and other resources below ground. The rate of nutrient uptake and resource use by trees should be proportional to their growth rate. If the understory is being influenced by tree competition unrelated to canopy structure, tree growth as indexed by wood production should be negatively related to understory production. Little negative correlation was found between wood production (Taylor, 1934) and understory production for plots aged 30 to 150 years (fig 15). At Youngs Bay (site 66) a well developed understory producing $683 \text{ kg ha}^{-1} \text{ yr}^{-1}$ persisted despite high wood production ($5490 \text{ kg ha}^{-1} \text{ yr}^{-1}$). The lowest levels of tree production occurred on low site stands 72 and 138 years old with little understory production (3, 5 and $71 \text{ kg ha}^{-1} \text{ yr}^{-1}$, respectively).

Taylor (1934) estimated peak wood production for low elevation Picea-Tsuga forests in southeast Alaska at around 70 years, a gradual decline in production continuing to the old-growth stages. Significant variation in wood production was encountered in each age class relating to tree growing site and density (basal area) differences across the

chronosequence. The decline in tree vigor and production in the 100-150 year age class may be related to the increased understory development during this time period, but this is not supported by wood production (diameter increment) data. When more detailed forest production data become available including foliar and branchwood production, respiration, mortality, and especially below ground carbon assimilation, these relationships can be more thoroughly evaluated.

Historical Factors Influencing Succession

A. Stand Establishment

Historical factors are variables that could effect relationships between forest structure and understory vegetation. The more important factors are the type of disturbance eliminating the previous forest, in addition to rates and patterns of tree regeneration (Dyrness, 1973, Likens and Bormann, 1979, Odum, 1960). In other studies of succession these kinds of variables have had a profound influence on species composition and structure, often determining the long term pattern of successional development. In southeast Alaska the mild wet summers, a relatively depauperate flora and a high percentage of residual plants persisting after the destruction of the old-growth forest minimizes the impacts of these factors on successional processes. Some annual "ruderal" species (sensu Grime, 1979) do colonize recent clearcuts or fires in the region but were not a significant component of understory biomass (5%) in any of the study sites.

No clear differences were noted between cable logging systems (A-frame, hi-lead, skyline) on understory development patterns.

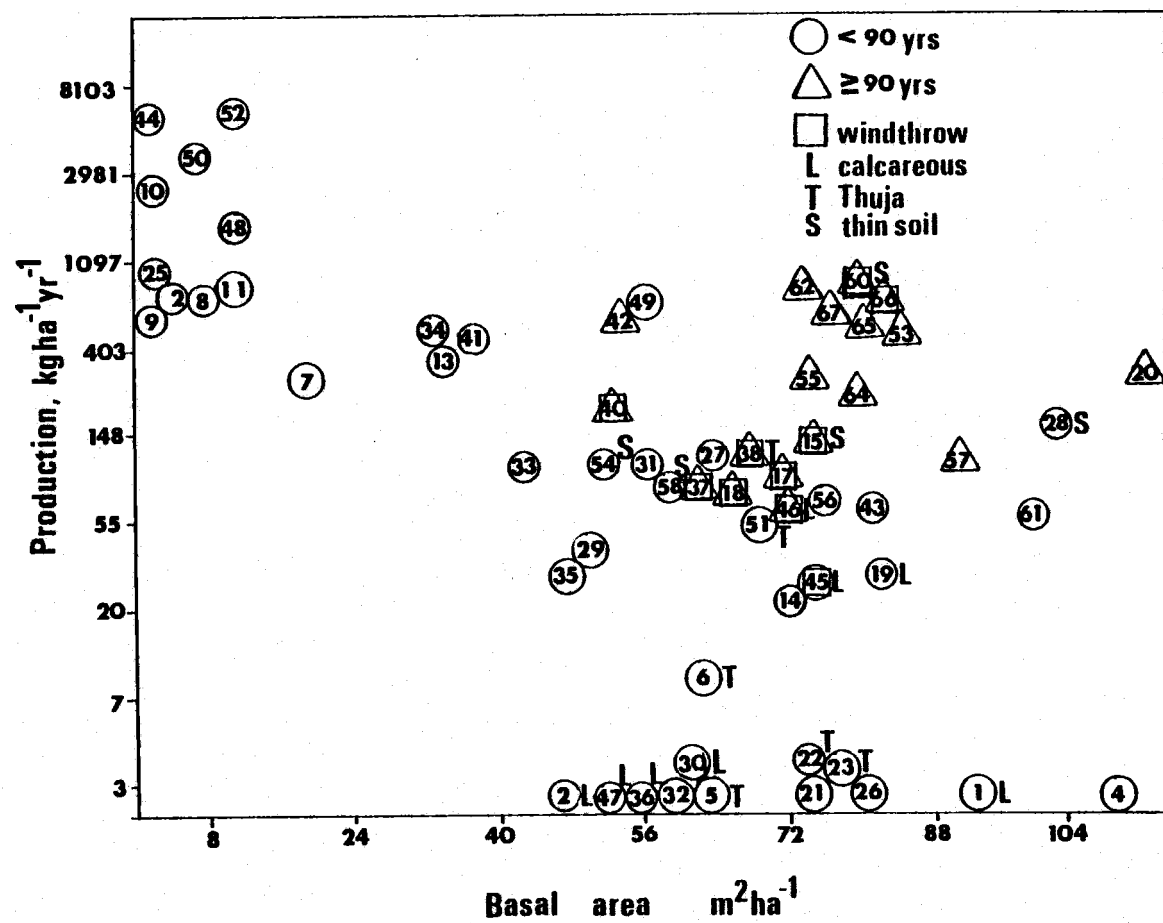


Figure 16. An ordination of study areas by understory production and tree basal area.

Tractor logging tends to be more destructive, however, and where done on fragile beach soils may substantially alter the nutritional and physical structure of the soils thereby retarding successional development (Gass et. al. 1967, Froelich, 1978). Clearcuts with the greatest degree of topsoil disturbance or mass movement erosion tended to favor colonization by shade intolerant species like Rubus spectabilis.

Clearcuts in which topsoil disturbance was minimal tended to favor reestablishment of those species present in the original forest, such as Vaccinium alaskaense and V. parvifolium. These species changeover patterns are consistent with early successional patterns observed in coniferous forests elsewhere (Kellman, 1969, Dyrness, 1973).

At Douglas Island (site 41) a productive and diverse understory developed a full century before most other sites developed this structure. Stand establishment history clearly distinguishes this stand from all others, and helps explain this anomalous understory structure with respect to stand age. During the early 1900's when most of the trees were established, Douglas Island was a center of mining activity. Sulphur fumes and mining tailing from the gold mine eliminated the original forest, and retarded tree reestablishment (Muir, 1915, Schoepfoster et. al. , 1974). At 64 years understory production was over four times that measured for other sites in its age class and well distributed between ferns, herbs, and shrubs (table 2). The tree canopy was more open and the tree basal area was only 69% of that expected for a stand of that age and site (Taylor, 1934). The increase in understory production can be explained by reduced tree basal area without any consideration of the edaphic anomalies unique to the site (fig 16).

The only type of disturbance history that was associated with a change in the long-term pattern of understory successional development was windthrow. Most young-growth sites of windthrow origin had thin soils and significant slopes (see environmental variable section) resulting in orders of magnitude greater understory production than at other sites of the same age. By contrast windthrown sites greater than 140 years old had less than normal understory development. At Clark Bay (sites, 37,38) 52-year-old Tsuga saplings formed a distinct stratum beneath the 190-year-old dominants under which few herbs or shrubs developed. During the winter of 1979 a major storm blew down much of the stand, which may give rise to yet another canopy layer. Other stands greater than 100-years-old that were thought to be subject to periodic windthrow did not have so obviously altered a forest structure, other than by their diameter distribution patterns and diverse canopy structure. All of these older stands thought subject to windthrow were distinguished from others in their age class by having understory production similar to young-growth stands of the same basal area (fig 16).

As the canopy is disturbed by windthrow during the aggradation phase of succession understory production is generally stimulated, probably by increased light. If windthrow disturbance occurs periodically, leaving enough canopy dominants to maintain stand integrity during the transition or old-growth phase, secondary Tsuga or Thuja canopy layers generally develop making a denser than normal canopy. This denser canopy is associated with decreased understory growth. Thus windthrow can either enhance or degrade the understory growing environment depending on the intensity of disturbance, periodicity, and stand age.

B. Tree regeneration effects on understory production

The other major group of historical factors that can be related to successional dynamics deals with the pattern of tree regeneration following stand disturbance. Southeast Alaska coniferous forests differ from most others in the western U.S. in having abundant natural tree regeneration within two to three years of disturbance. The persistence of residual Tsuga seedlings and saplings can be particularly effective in allowing a rapid reestablishment of trees following logging or windthrow (Jaech et. al. 1979). Increased tree seedling densities are associated with large decreases in understory production. Excluding the one site in the Maybeso Valley, 81% of the variation ($\alpha = .005$) in understory production on stands measured prior to canopy closure could be explained by knowing the tree density. The understory production estimates from nearby areas of the same slope, aspect, elevation, and soil type were much lower than those measured in the Maybeso Valley. Harris(1974) indicates that the Maybeso was heavily disturbed during logging operations. An increase in mass movement erosion activity was also documented near the Maybeso study plots in contrast to that observed in the Harris River area (Swanston, 1970). The uniqueness of the Maybeso site may relate to this disturbance history.

To further study the relationship of tree density and understory development prior to canopy closure three .09 ha plots were established in the Harris River area, 5 km to the south of the Maybeso. Trees on two of the plots were thinned at different intensities, four years prior to plot measurement. The most heavily thinned plot (4.9 x 4.9 m

spacing) attained near normal understory production for its age class within those four years ($2720 \text{ kg ha}^{-1} \text{ yr}^{-1}$) but became almost exclusively dominated by Rubus. Herb and fern production of the thinned stand were proportionately less than production in the unthinned stand, and were far below levels measured at the Maybeso.

Only in the extreme case of tree establishment being significantly delayed could patterns of tree establishment have along term effect on understory successional dynamics. Even in contrasting environments at Harris River and Maybeso Valley, for example, canopy closure should still occur within ten years at both sites producing similar understory structure for the next century (fig 5, Taylor and Godman, 1950).

Herbivore effects on understory structure

Effects of herbivory in secondary succession are frequently ignored by plant ecologists yet may dramatically alter vegetation structure. Odocoileus hemionus sitkensis (Sitka black-tailed deer) is the most abundant ungulate in the low elevation forests and the one most likely to cause a distinct grazing effect on vegetation. Klein (1965) and Merriam (1965) have suggested deer browsing dramatically decreased Vaccinium and Cornus frequency on Coronation Island, where an unusually dense herd existed. On their more continental study site at Woronkofski Island deer browsing seemed to have little effect on the vegetation. Although a variety of information has been collected on Odocoileus population trends and indices few precise population estimations have been made in the region, much less on the specific sites measured for this study. Rough population trend information is available for the major islands

and distinct patterns of deer use of forest vegetation have been suggested for the region (Bloom, 1978, Olson, 1979, Wallmo and Schoen, 1980).

Browsed (damaged) Vaccinium and Cornus shoots were observed primarily in old-growth (200 - 250 years) forests on Admiralty and central Prince of Wales Islands. The only possible browsing evidence in the younger forests were occasional missing twigs of the evergreen from of Vaccinium parvifolium or , in canopy gaps, V. alaskaense. Even in these instances the effects of browsing were minimal on species composition and biomass. Browsed Vaccinium spp were short in stature and more highly branched in comparison with unbrowsed shrubs. Those stands with evidence of browsing had understory production equal to or exceeding others in the same age class.

Odocoileus has been reported to be at low population levels in the regions sampled during the time this study was conducted (Johnson and Wood, 1979, Olson, 1979). With higher ungulate population densities understory vegetation structure might be substantially altered, especially on the smaller islands. Sites measured for this study were considered representative of understory successional dynamics in the absence of effects caused by ungulate grazing. A separate study would be needed to adequately assess how species successional dynamics might be altered by more intense animal interactions.

Environmental variables in relation to successional dynamics

A. Soil effects

Forest canopy structure and historical factors explain the majority of variation in understory biomass over the chronosequence. Extremes in soil

characteristics were also found, however, to be associated with changes in the structure of understory vegetation. By using covariance analysis (Draper and Smith, 1966) ten to twenty percent of the variation in forest understory production was accounted for by knowing soil type, after having allowed for that variation associated with tree basal area and canopy cover (table 5). Thin rocky (F2n), somewhat poorly drained (F4c), alluvial terrace (F1t), and uplifted beach (F1b) soils were particularly associated with biomass values divergent from understory on modal soil types (F1n).

The effect of soil characteristics on vegetation development is most pronounced during the earliest stages of succession, prior to tree canopy closure. These stages were the most dynamic for the understory. Near Hollis two logged areas (sites 9,25) were studied that had far less biomass and production (20% of the average) than would be expected at other stands of similar ages. Both occurred on somewhat poorly drained soils, which generally give rise to a mixed Tsuga-Thuja forest. Nearby forests on better drained sites had average to above average understory production for their age (sites 10,52).

By contrast, sites located on uplifted beach soils (F1b, Saltchuck series) tended to have above normal understory production. These sites are most susceptible to disturbance during logging operations, and tend to have lower basal area densities of trees during the first ten years following logging than those on better developed soils. Two sites of the same age, slope, aspect, and elevation were measured in the Petersburg region with contrasting soil types. Site 11 had a well developed (F1n) soil and only 25% the understory production measured at site 50 where a shallow (F1b) developed. Other sites on uplifted beach soils measured after canopy closure also had abnormally high understory production for their

age (site 49,14).

Soil differences were also found to be associated with anomalies in understory structure during the later stages of succession. The most dramatic differences in understory growth and composition were found on thin, rocky soils (F2n, Tolstoi). Most stands sampled on these shallow soils had significantly above average understory production. At Windfall Harbor (site 60) eightfold the average understory production for its age class was measured. Taylor (unpubl) measured plots in another part of the stand in 1929 (stand age 40) at which time the understory was negligible. Thus this stand did go through a depauperate understory stage, but sufficient light and other resources were available on the wet rocky soil by age 90 to allow for the development of a productive and diverse understory. Many areas within the large windthrown stand had a nearly continuous Oplopanax stratum and perennial water seepages, including some with negligible slope. Oplopanax normally grows alongside streams and in moist microsites. The widespread occurrence of this shrub throughout the stand was unique and suggestive of dramatically different growing conditions than those found in other sites. Poor drainage and high rock content in the thin soil at Windfall Harbor were, as in sites 41,15,54,58, and 28 the most dramatic environmental features of the stand.

The lone exception to the pattern of increased understory development with shallow soils occurred at Cannery Point where a F2r (McGilvery series) soil type was found. This type is distinguished from the others (F2n) by having less than 5cm of mineral soil between bedrock and a thin organic mat. A continuous layer of Hylocomium dominated the understory as it does on many rock bluffs in the region. This soil appears to represent the extreme in poorly developed forest soils, so that although tree density

(and presumably competition) was minimal for the site and age (89% of normal, Taylor, 1934) the understory was still poorly represented. The second-growth stands measured on the other F2 soil types generally had an above average shrub production, but were low in herbaceous production as in other stands of that age with deeper soils (table 2).

Parent material and genesis distinguished the other anomalous soils. Soils that developed on calcareous materials (limestone, marble) had below-average understory production for their age class. Calcareous sites with good internal drainage, gentle slopes, and deep soils tended to have the highest tree growth potential in the region (Gass, 1967, Stephens et. al. 1969). These sites thus tend to develop a denser basal area stocking of trees, often resulting in a denser canopy leading to less favorable understory growing conditions. The only obvious exception to this rule was at site 19 where an above-average shrub layer developed in a forest only 58 years old. The highest tree site index of the study was measured at this site. This stand apparently developed with below normal tree density, since many dominant trees had heavily branched open growth forms. Recent windthrow also opened up large gaps in the canopy, allowing for further understory growth.

Forests growing on river alluvium also had abnormal understory structures. Along Shaheen Creek park-like stands of Tsuga and Picea developed on deep, well-drained loamy alluvium. Ferns and other herbaceous plants formed a nearly continuous understory but a paucity of shrubs resulted in low total understory production. By contrast, at Youngs Bay a gray impermeable layer developed beneath the alluvium, leading to poorer drainage. Trees were widely spaced on old root mounds and logs with a nearly continuous Vaccinium layer inbetween trees. Understory production

at Youngs Bay was five fold that expected for a stand of that age (table 4).

The soil characters best related to understory development in the covariance analysis are qualitative variables (i.e. soil type). Soil depth, texture, color, and structure are not clearly related to understory growth even though they are used to define soil types. The lack of an identified understory response to these individual factors may relate to the non-linear character of the response surfaces, as well as to important interactions between these variables in relation to understory growth. By using a soils classification specifically developed to stratify tree growing potentials, important soil characteristics were summarized as units so that they integrated the environmental characteristics associated with soils in relation to understory growth.

B. Microclimatic effects

Percent slope, aspect, and latitude data were used to index microclimatic differences between sites within age classes. The relationship between understory growth and these variables were studied so that more information would be gained on how environmental factors may influence understory growth over the chronosequence. Among the physiographic types sampled in the full data set mid-slope, ridge, alluvial terrace and beach were the most significantly different from the other sites after taking account of the understory variability associated with tree canopy cover. Most of the younger forests (<100 years) sampled had gentle slopes and occurred at similar elevations. Those ten sites sampled with significant slopes and aspects (20-47%) in this age class did not have signif-

TABLE 5. Covariance analysis of understory with respect to overstory and environmental variables.

DATA SET	^{1/} n	COVARIATE	SLOPE	r ²	OTHER INDEPENDENT VARIABLES ^{2/}	r ²	SIGNIFICANCE
A. Forest Structure							
F	55	age	-	.023	%canopy ^{***} , foliar biomass, canopy variance ^{**}	.56	.010
F	55	age	-	.023	basal area ^{***} , volume, density [*]	.40	.050
YG	30	age	-	.360	%canopy ^{***} , foliar biomass, canopy variance	.67	.000
M	20	age	+	.69	basal area, density index, volume	.73	.000
M	20	age	+	.69	dbh [*] , variance in dbh, volume	.79	.000
M2	25	dbh	+	.22	%canopy [*] , variance in canopy, aspect ^{***}	.60	.005
B. Environmental variables							
YG	30	age	-	.36	aspect, slope, latitude	.37	.050
M	20	age	+	.69	aspect, latitude [*] , slope	.81	.000
YG	30	%canopy	-	.58	physiography	.70	.000
M2	25	dbh	+	.22	soil type	.53	.050
M2	25	dbh	+	.22	parent material [*] , physiography [*]	.66	.050
YG2	37	basal area	-	.60	volume, soil type	.71	.000

1/ F = full data set - sites 41,25, YG = young growth(90 yrs) - sites 41,12,9, 25, M = mature and old growth - sites 60,66, M2 = all mature stands - site 15, YG2 = all stands (90 years).

2/ * = sig at = .05
 ** = sig at = .01
 *** = sig at = .005

icantly different understory production values except where thin rocky soils were also present (sites 60,54).

By contrast, the older age-class data suggests that slope, aspect and physiographic type can be related to changes in understory growth and structure (table 5). In these age-classes a broader range of slopes and aspects were sampled since flat well-drained undisturbed sites were more difficult to locate. Slope was significantly correlated with increased understory production ($\alpha=.05$). North aspects tended to have more understory growth than south aspects, ($\alpha=.01$) despite lower potential insolation levels.

Such data are difficult to interpret since these variables do not directly relate to plant growth, but are assumed correlated with other factors that are operationally important to plants. These variables tend to be significantly associated with each other. A correlation of increased understory growth with side slopes, beaches and ridgetops is interpreted by this writer, for instance, to reinforce the importance of thin soils (on ridgetops) soil parent material and genesis (on alluvial terraces and uplifted beaches), and slope (between terraces and ridges, mid-slopes are the steepest). A pronounced tendency of increased understory growth on north facing slopes is suggested as further evidence that the primary environmental influence on understory vegetation in mature forest (after canopy closure) is the change in microclimate wrought by the forest canopy. Andersen (1955) and Godman (1950) have suggested that south-and east-facing slopes are best for tree growth in southeast Alaska. Clearly the understory is not favorably responding to diminished potential insolation, increased moisture and lowered temperatures on

north facing slopes. The major beneficial effect of north facing slopes for the understory must, therefore, be in the diminished tree density and vigor associated with excessively wet soils.

Environmental effects on understory growth from this study conform with those described by Siccama (1970) for the northern hardwood region, Zobel et. al. (1976) for the west-central Cascades of Oregon, and by Daubenmire (1978) for the North American continent. Those factors leading to less favorable growing conditions for trees tend to be associated with increased understory production and diversity.

DISCUSSION

Comparisons with successional patterns in other forest types

It is difficult to make direct comparisons of understory biomass successional patterns observed in southeast Alaska with other temperate forest regions. Few studies have been conducted on understory biomass dynamics, and none to this writers knowledge on a range of sites within age-classes extending over more than eighty years. A lack of standardization and in some cases a lack of documentation of methods or definitions employed add further complexity to making comparisons between studies. Studies in hardwood forests are particularly difficult to compare with Picea-Tsuga forests since the multilayered canopy including shrubby trees and woody shrubs makes definitions of understory or overstory vegetation difficult. The complexity of changes in canopy modifications of incident radiation throughout the season also makes comparisons difficult with these diverse forests (Anderson, 1964).

By comparing the biomass estimates from this study with adequately

documented estimates from other coniferous forest types more insights may be gained as to how generalized the long term biomass successional patterns observed in southeast Alaska may be for coniferous forest systems. Since few studies have emphasized the range of age classes of this study comparisons will be made within each of the principle stages of understory development following disturbance.

Published understory biomass values for coniferous forests prior to canopy closure range from 39,130 kgha^{-1} in nearby British Columbia (Webber, 1977) to 2,000 kgha^{-1} in England (Ovington, 1962). The majority of the plots measured in southeast Alaska are high in comparison with coniferous forests in Europe (Pseudotsuga menziesii and Pinus sylvestris, Ovington, 1962) but within the range of reported values for western North America (4,500-39,000 kgha^{-1}). The understory standing crop biomass of southeast Alaska sites on normal soils can reach 32,000 kgha^{-1} in contrast to reported values for ecosystems dominated by Pseudotsuga which average 7,500 kgha^{-1} (Long and Turner, 1975; Irwin and Peek, 1979). The rapidity of tree establishment, or growth of residual understory trees in southeast Alaska suggests further that these forests have higher tree biomass, hence total above-ground ecosystem biomass than the more southerly forests at this age. All published studies consulted that dealt with successional dynamics indicated that the 15 to 25 year age-class represented the peak in understory production.

Forest canopy closure generally occurs between 25 and 35 years following stand initiation. This stage represents the most dynamic portion of understory successional development for most systems. Published values for understory biomass in this age-class range from 0.0 kgha^{-1} in coastal

Oregon (Grier, 1976) to 32000 kg ha^{-1} in a 32 year old Pseudotsuga stand in Washington (Heilman, 1961). Stands in southeast Alaska were low to average in comparison to published values. Stands without complete tree canopy closure had as much as $12,500 \text{ kg ha}^{-1}$ understory, the remainder being $0-5 \text{ kg ha}^{-1}$,

After canopy closure forests are commonly referred to as "mature", rapidly aggrading systems. High wood production is generally maintained until about 100-150 years following forest establishment (Kira and Shidei, 1967, Odum, 1969). The majority of published understory biomass studies have dealt with this age class, ranging in values from 100 kg ha^{-1} in a 41-year-old slow developing Picea glauca forest in Minnesota (Alban et. al. , 1978) to $68,000 \text{ kg ha}^{-1}$ in a Pinus nigra forest in England (Ovington, 1962). The forests of southeast Alaska appear to be distinguished from most other forest types by their lack of understory development during the majority of these intermediate stages of succession. Biomass values for this age class ranged from 0.0 to 3128 kg ha^{-1} , two-thirds being well below 100 kg ha^{-1} ($n=22$ stands). From the data presented in this study, this depauperate understory stage would be expected to persist to around a stand age of 150 years.

Few studies have been conducted on "old-growth" forests. In the Pacific Northwest understory biomass has been estimated on 450-year-old Coniferous Biome intensive study sites. Understory standing crop biomass was estimated between 5,600 and 10,260, most being between 6,000 and 7,000 kg ha^{-1} (Russel , 1974, Grier and Logan, 1977). In "climax" Picea stands in the Great Smokey Mountains, Whittaker (1966) reports biomass values 100 to 21,000 or an average of $7,300 \text{ kg ha}^{-1}$. Two-to three-hundred-year-old southeast Alaska stands averaged 5,000 to $6,000 \text{ kg ha}^{-1}$.

Many studies in other regions suggest that sites are subject to fire, windthrow, or widespread insect attack during stand development but are nonetheless representative of average stand conditions in the regions. Forest of fire origin in the western U.S. generally establish tree seedlings slowly since small understory trees only infrequently persist from the original forest. Dry summers in these areas can make for an austere seedling environment, further slowing regeneration. Seral intolerant trees generally dominate forests under post-fire conditions, but generally do not form as dense a canopy as forests dominated by the more shade tolerant species (Horn, 1971, Drury and Nisbet, 1973). In the Oregon Cascades, for instance, mature second-growth forests with pure single canopy layered Pseudotsuga may have a lush herbaceous understory. Adjacent stands will frequently have a multilayered Pseudotsuga-Tsuga or even Thuja strata with only a trace of understory development. By contrast in southeast Alaska, Tsuga, one of the most shade tolerant western trees (Minore, 1979) generally dominates the forest allowing for a denser high leaf-area canopy. On an individual tree basis Tsuga also has a higher average foliage weight than Pseudotsuga and other seral species (Gholz, 1979). The wet cool growing seasons in southeast Alaska should be conducive to the observed rapid establishment of a dense tree canopy following windthrow or logging. The few studies that have reported tree canopy coverage and understory biomass data confirm that the less rainy climates to the south tend to have less dense canopy coverage than even the most open (but undisturbed) forests in southeast Alaska, during these phases of succession (Young et. al., 1967, Dodd et. al., 1972, Telfer, 1972, Maclean and Wein, 1977, Hawk et. al., 1979).

The most dramatic difference between southeast Alaska biomass estimates and those in other forest types appears to be in the dynamics of intermediate successional stages. The maintenance of a depauperate understory after a century or more in southeast Alaska seems particularly noteworthy in contrast to other studies of forest succession. Little information is available on the increase in understory biomass with stand age after canopy closure in other coniferous forest systems. Long and Turner (1975) found a steady decrease in understory biomass between 20 and 70 years in a western Washington watershed. Maclean and Wein (1977) suggest that increased understory development may begin as early as 50-60 years following cutting in New Brunswick. In the central Oregon Cascades full vegetative development has been noted in pure Pseudotsuga forests 80 to 90 years following cutting. Russel (1974) theorizes that understory reestablishes in as little as 20 to 40 years following canopy closure in that region. Clearly more work needs to be directed towards documenting these patterns of late successional understory dynamics in other systems so that the differences between southeast Alaska and these other systems and their variates can be more thoroughly evaluated.

Contributions towards a model of understory biomass dynamics

In the past decade much effort has been expended towards mathematically describing successional changes in ecosystems through system models (Botkin et. al., 1972, Shugart et. al., 1973, Innis, 1977). A major goal of this work is to study what factors can be related to changes in species composition over time. Few models have included understory biomass dynamics over long time spans. Those that have included understory biomass have

not given information on relationships between understory growth and overstory canopy structure. In order to best characterize understory dynamics over a range in age and forest structure, relationships between forest canopies and understory growth must be examined in greater detail.

Various authors have related understory biomass to tree basal area, canopy cover, or tree density. Some studies have suggested that correlations of understory growth with decreased tree basal area or more open canopies could be used to evaluate the relative importance of direct tree competition and light interception, respectively. The multi-dimensional relationship of forest structure to understory development, however, creates complex inter-relationships. These make indirect measures of forest structural influences, such as tree basal area and percent canopy cover difficult to use in distinguishing causal factors effecting understory growth. The data from this study suggests that tree basal area is a better predictor of understory biomass than canopy cover for the younger sites. The lack of correlation of tree growth with understory growth, however, suggests that competition for below ground resources was not an important factor influencing understory growth. The poorer correlation of percent canopy cover with understory growth was probably influenced by the lack of variation in canopy cover classes over much of the chronosequence(fig 14). The study sites were better stratified by tree basal area since a more even distribution of basal areas occurred across the chronosequence (fig 16).

Understory growth-environmental interactions can be illustrated by ordinating study sites by tree basal area and the log of understory production. Several sites had below-average understories for their basal areas (fig 16). Most were observed to have developed on calcareous soils

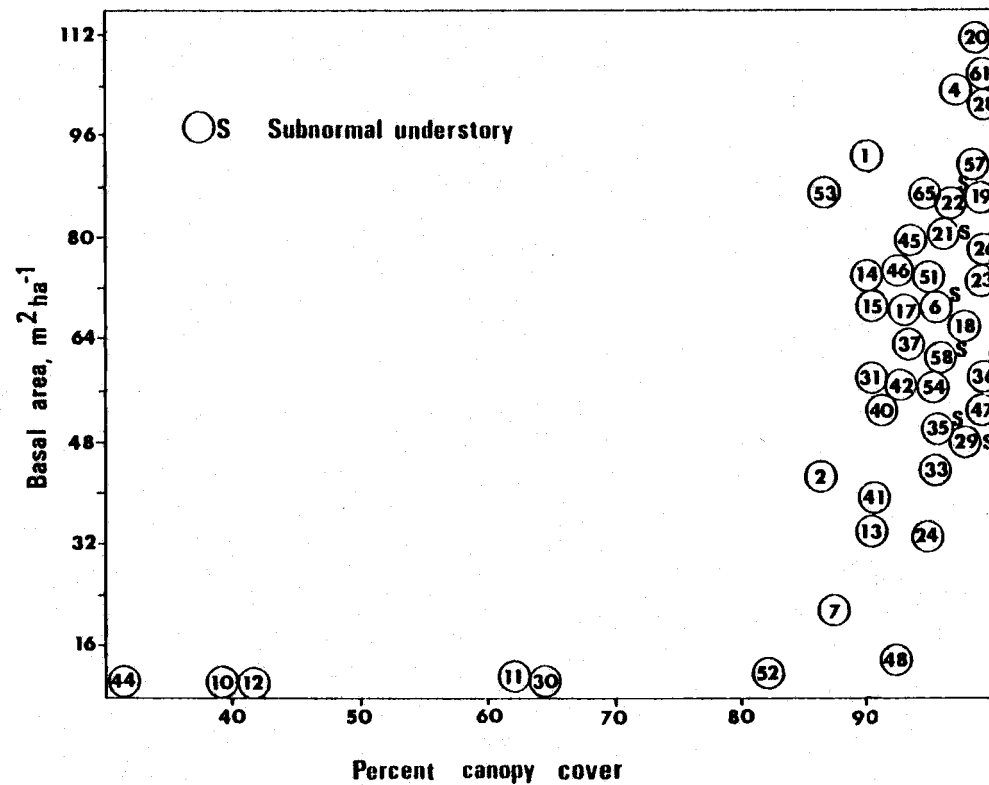


Figure 17. Relation of basal area to canopy coverage. Numbers in circles correspond to site numbers in tables 1 and 4. Sites with below average understory biomass are indicated.

or on sites containing significant portions of Thuja in the canopy. By plotting basal area against canopy cover many of these anomalous sites can be shown to have denser than normal canopies for their basal area classes (fig 17). The young-growth stands with greater than normal understory production developed on thin soils, anomalous soil parent materials, or were of windthrow origin. The only young-growth stands influenced by windthrow that did not have above normal understories for their basal areas developed on calcareous soils. These relationships are consistent with the hypothesis of forest vigor and density as the primary controlling factors in understory growth, since calcareous soils and thin rocky soils generally represent the extremes in forest growth site quality in this region. Tree basal area is hypothesized here as being important to understory growth during the aggradation phases of succession by its relationship to light interception by the overstory canopy.

The uniqueness of the older sites understory growing environments was suggested by their almost total lack of stratification by tree basal area class (fig 16). In contrast to the younger stands, indices of increasing tree biomass such as mean diameter and volume showed positive correlations with understory growth (table 5). Thus in rapidly aggrading ecosystems highly productive dense forests are associated with minimal understory growth. These sites should reach peak production earliest and proceed the most rapidly to a more open mature canopy structure (Taylor, 1934). In older stands these forest structural parameters might be best interpreted as representing the "physiological age" of the forest as it relates to the opening up or diversification of canopy structure with age.

Over short segments of successional development seventy to eighty percent of the variation in understory biomass could be related to forest structural parameters using a multiple regression analysis (table 5). To best represent understory changes over longer time periods, however, more information will be needed on the relationships of these parameters to those factors that are operationally important to understory growth over the chronosequence. Foremost among those to be investigated should be canopy interception, diffusion, and other modifications of incident solar radiation.

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