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# FOREST COMMUNITY STRUCTURAL CHANGES DURING SECONDARY SUCCESSION IN SOUTHEAST ALASKA

by

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ABSTRACT--Sitka spruce-western hemlock forests originating from windthrow, logging, or fire display characteristic developmental patterns over time in southeast Alaska. The early stages are the most dynamic, and the most productive for the understory. Understory biomass and production peaks 15-25 years after stand establishment at 1700 $kg \cdot ha^{-1} \cdot yr^{-1}$. Vaccinium and Rubus shrubs dominate this phase. After forest canopy closure bryophytes increase cover and biomass for at least one century. At age 150-200 Vaccinium reestablishes developing a conspicuous layer. Beyond 200 years the highest structural diversity is attained. These older forests also have the most useable forage for ungulates. Departures from this developmental sequence were related to stand establishment history disturbance patterns, edaphic and microclimatic conditions. In the overstory, Picea is most abundant during the early stages of succession. It declines in importance during the first century following disturbance, but often sustains individual tree growth throughout the chronosequence. Tsuga dominates the forest canopy throughout the succession on windthrown and other less productive sites. Data from this study suggests that the management of Picea sitchensis-Tsuga heterophylla forests in 0-100 yr old age classes will lead to a reduction of the most structurally diverse stage of forest development, and that with the highest potential for sustained wildlife forage productivity.

KEYWORDS--Secondary succession, Southeast Alaska, understory biomass, Picea sitchensis, Tsuga heterophylla, production, old-growth forests.

## INTRODUCTION

Few botanical studies have been conducted in the Alexander Archipelago of southeast Alaska. This region has an extensive array of coniferous forests relatively free of disturbance by human activities, or by large wildfires. As a consequence these forests offer a rare opportunity to study the dynamics of forest vegetation over relatively long periods of time. Six decades ago William Skinner Cooper and colleagues recognized this opportunity in their classic studies of revegetation processes following glacial retreat in Glacier Bay (Cooper 1923a, 1923b, 1939; Lawrence 1958). Little research has been published on secondary successional processes in southeast Alaska, despite the growing economic importance of understanding these processes for resource management activities.

This study documents changes in forest composition and biomass of cryptogams, herbs, shrubs, and trees during the first three centuries of successional development following perturbation in southeast Alaska. In addition relationships of several environmental factors to patterns in successional development are presented.

### Study Area

#### Climate--

Southeast Alaska is defined here as that region extending 700 km from Haines (59°N, 136°W) southeast to Dixon entrance 54°30'N, 130°W, Fig. 1). The region has a generally cool moist maritime climate. Annual precipitation at sea level averages 200 to 400 cm (Anderson 1955). The summer drought which so characterizes the ecology of Pacific Northwest forests does not significantly influence this region. Monthly rainfall generally peaks in October or November.

Mean monthly temperatures range from 13°C in July to 1°C in January at or near sea level where most weather stations are located. On the average 1200 degree-days above 5°C occur in the region (Farr and Harris 1979). The combination of cool year around temperatures and abundant moisture generally leads to low water stress for most plant species. Rapid colonization of glacially scoured substrates by cryptogams and vascular plants is another consequence of the mild climatic conditions.

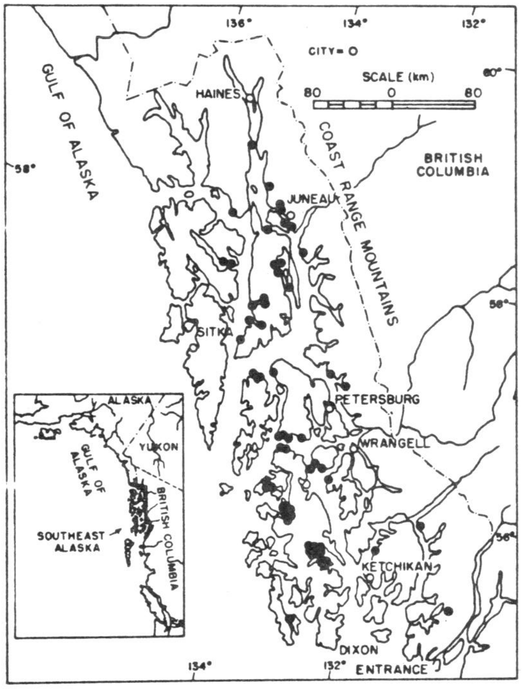

FIGURE 1. Geographic distribution of study sites.

### Geology and soils--

The Alexander Archipelago has a diverse and poorly understood geological history. The batholith of the British Columbia Coast Range dominates the eastern boundary of the study area. The region is characterized by large rock outcrops, steep-walled glacial valleys and unstable thin rocky soils. In the central region between the Coast Range and the Chilcat-Baranof Mountain chain to the west the topography is more subdued and is lower in elevation. A metamorphic contact zone dominates the eastern portion of this region. Sedimentary rocks including limestones, sandstones, and graywacke are common as are extrusive and intrusive igneous rocks (Buddington and Chapin 1929).

As a consequence of wet climate and diverse geologic history the soils of southeast Alaska exert an important influence on vegetation growth and composition, making soil types useful for the classification of the major ecosystem types[1]. Most of the soils in southeast Alaska are young, shallow, and poorly developed (Collins 1974). Compact glacial till is extensive and is an important factor in the development of bogs. Some of the best developed forest types occur on silt and clay sediments in extensive marine terraces to 150 m in elevation. Soils derived from limestone and marble tend to have the lowest proportion of poorly drained areas, giving rise to some of the most productive forest ecosystems. In contrast soils of less erosive igneous rocks have a higher percentage of poorly drained (non-forest) and less productive forest vegetation (Collins 1974).

### Vegetation--

Approximately 60% of the land in southeast Alaska is forested. The remaining area is alpine, muskeg (bog) and riparian (U.S. Forest Service 1978). In contrast to most coniferous forest ecosystems in western North America fire has not played an important role in the ecology of these forests (Noste 1969, Harris and Farr 1974). Most of the forest perturbations are thought to be caused by infrequent high-velocity winds blowing down large patches of trees during the fall and winter (Ruth and Harris 1979).

## Methods

In order to document the change in forest community structure following ecosystem perturbation, plots were selected over a wide range of forest ages and environmental conditions. Plots were selected having homogeneous vegetation as well as easy accessability. The selected plots had nearly uniform slope and aspect, and were less than 274 m in elevation. Within each age class a range in soils and geographic locations was sampled. For most of the younger stands permanent plots stratified by age and tree site index were used[2]. Forests greater than 70 yr old without evidence of subsequent disturbance were difficult to locate over as wide a range of environmental conditions as was possible for the younger age classes. When a suitable stand of logging or fire origin was not available for an age class, forests of windthrow origin were sampled.

At each plot understory vegetation was sampled in a systematic grid of 60 one meter square subplots. Within each 1-m square subplot the basal diameters of all shrub shoots, and the lengths of all fern fronds were measured. The lengths of *Lysichitum americanum* and *Clintonia uniflora* leaves as well as *Streptopus* spp. shoot lengths were recorded. Percent ground cover was estimated for all plant species encountered within a 0.2 x 0.5 m frame placed in the center of each microplot (Daubenmire 1959). These data were used to estimate biomass and productivity for all herbs, shrubs, mosses and tree seedlings (< 2.5 cm DBH) encountered on these subplots using regression equations developed for southeast Alaska (Alaback 1980). Diversity of herbs, shrubs, mosses and tree seedlings on each plot was estimated using Simpson's (1949) index. Average biomass, production and percent cover for each species on each plot were used to calculate these indices.

At each plot forest tree structural variables were measured over the entire macroplot. Macroplot size varied from 0.08 to 0.5 ha. Larger plots were used for older forests with lower tree densities so that an

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[1] Stevens, F. R., C. R. Gass, R. F. Billings, and D. E. Paulson. 1969. Soils and associated ecosystems of the Tongass. USDA For. Serv. Alaska Region, Juneau. Unpubl.

[2] Farr, W. A. 1974. The effects of stand density upon growth and yield of hemlock-spruce stands in coastal Alaska. Unpublished study plan. Pacific Northwest Forest and Range Experiment Station, Forest Sciences Laboratory, Juneau, Alaska.

adequate sample of trees were taken, and sufficient data taken for variables influenced by spatial factors such as tree basal area. The diameter at breast height for all trees greater than 2.5 cm was measured for most plots. The only exceptions were on nine young-aged plots in which subsamples of tree diameters were taken due to the inefficiency of measuring all of the highly dense small diameter trees. The distance from the understory vegetation microplots to the four nearest trees 2.5 cm or more in diameter and their diameter was recorded during the 1978 and 1979 field seasons. Data on tree height, diameter, and age for those sites used in previous studies were obtained from the U.S. Forest Service[2]. Relationships between tree height and diameter for each site were used to estimate tree heights for all trees in the stand. These data were used to estimate tree volume, basal area, density, tree spacing, site index, and biomass (Taylor 1934, Chambers and Foltz 1979, Gholz et al. 1979).

In order to document the environmental conditions for each site, data on topography, soils, and forest canopy were gathered. Overall plot slope, aspect, shape (convex, concave, flat-sided) and physiographic position (mid-slope, ridge-top, marine terrace, alluvial flat) were estimated in the field. Elevation, latitude, and longitude were taken from 15 minute U.S. Geological Survey topographic maps. Soil morphology was described for those sites where a complete soils description was not already available. Soil horizon, names, depths, drainage characteristics, color, texture, and consistency were recorded. Forest canopy coverage was estimated from 60 spherical densiometer readings using the recommendations of Strickler (1959).

## RESULTS

### General Community Structure

Eighty-two species of understory plants were encountered in the 62 sites sampled in this study including 38 species of herbaceous plants, 28 species of bryophytes, 11 species of shrubs, and 5 tree species (Table 1). Over 70% of the vegetation cover is composed of the 10 most abundant species, each of which occurs on 70% or more of the sites. The ten most abundant species average 7.1 percent cover. The other species each average 0.4 percent cover. The bryophytes are the most widespread occurring on most of the sites. The herbaceous vascular plants are less abundant and are more restricted by stand age class or disturbance history than are the bryophytes.

An average of 12 species were encountered in each plot. Species richness varied from 2 to 28 species. The greatest species richness and least species dominance for vascular plants occur in forests less than 25 yr old (Lambda = 0.501, 0.0 = most diverse, 1.0 = least diverse) (Simpson 1949). Stands between 40 and 90 yr tend to have the least diverse understory (Lambda = 0.976). Dominance by bryophytes is the most pronounced on these sites. The most diverse sites in terms of equitable distribution of dominance between strata occur in the older forest types (> 200 yr).

Sites with forests less than 30 yr old were dominated by woody shrub species (Table 2). On the moist mesic sites and those with the least soil disturbance Vaccinium alaskaense, V. parvifolium, and Menziesia ferruginea dominated. In wet microsites ferns like Athyrium felix-femina or Dryopteris austriaca and Ribes laxiflorum are an important component of understory biomass. Among the bryophytes Sphagnum squarrosus, S. girgensohnii, Leucolepsis menziesii, and Conocephalum conicum are restricted to wet microsites within the forest. Most of these occur in colonies less than 1 m in diameter. Other bryophytes such as Rhizomnium glabrescens and Porella navicularis are restricted to rotting standing dead trees or logs with well decayed (or absent) bark. Ferns and ericaceous perennials including Moneses uniflora also grow on or under these decaying wood surfaces in closed canopy forest.

Under canopy gaps on well drained soils woody shrubs often dominate understory production. Vaccinium alaskaense has the highest constancy in these microsites, while other shrubs such as Rubus spectabilis and Sambucus canadensis have greater fidelity, occurring only in canopy openings after canopy closure. Cornus canadensis and other small non-woody shrubs also increase their productivity under canopy gaps. In contrast to shrubs, herbs, especially the ferns, are often equally abundant both in closed canopy forest and under canopy gaps (Table 3).

Sixty-two sites were sampled for this study ranging in age from 3 to 600 yr. Sites less than 100 yr were generally of logging origin. Among the older sites 13 were of fire origin, 7 of windthrow origin, and 7 stands were of unknown origin. Those forests less than 150 yr were stratified by site index as well as by age and geographic location (Fig. 1). The older sites were stratified by soil types and by age of the oldest trees.

Four main stages of understory successional development are evident over the chronosequence (Fig. 2). These stages are defined in terms of changes in the structure and productivity of the understory vegetation. The first stage is the most dynamic, and includes the pulse of vegetation growth during stand establishment. The second includes the peak in tree productivity with a depauperate understory dominated by bryophytes. The third stage of understory development is characterized by an increase in understory vascular plant production and ecosystem biomass. The last and most poorly understood stage represents the uneven-aged "old-growth" forest in which the herbaceous stratum generally has its greatest relative understory productivity.

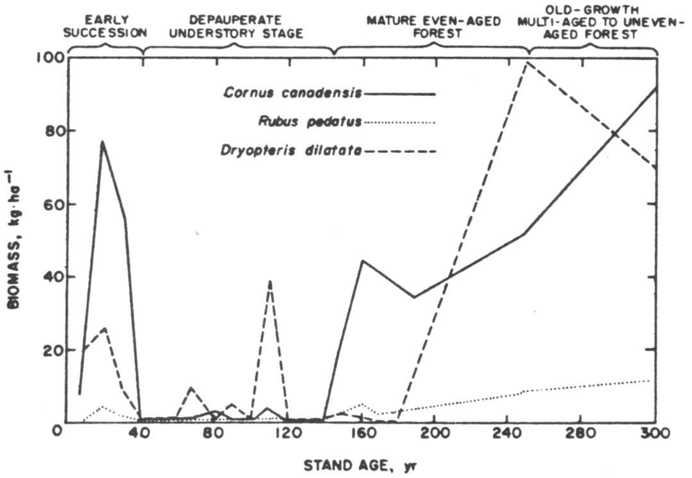

FIGURE 2. Herbaceous plant dynamics during succession.

TABLE 1.

OCCURRENCE OF UNDERSTORY PLANT SPECIES ON THE 62 STUDY SITES.

| Species[a] | Class[b] | % Cover | % Production | Rank[c] | % Constancy[d] |
|---|---|---|---|---|---|
| *Abies amabilis* | T | 0.01 | 0.01 | 57 | 1.5 |
| *Actaea rubra* | H | 0.01 | 0.00 | 57 | 1.5 |
| *Adiantum pedatus* | F | 0.09 | 0.00 | 48 | 9.1 |
| *Alnus rubra* | T | 0.07 | 0.00 | 57 | 4.6 |
| *Asplenium viride* | F | 0.01 | 0.01 | 57 | 4.6 |
| *Athyrium felix-femina* | F | 1.16 | 0.25 | 19 | 37.9 |
| *Blechnum spicant* | F | 0.64 | 0.10 | 29 | 25.8 |
| *Circaea alpina* | H | 0.05 | 0.01 | 53 | 4.6 |
| *Cladonia coniocraea* | L | 0.50 | 0.00 | 33 | 40.9 |
| *Clintonia uniflora* | H | 0.01 | 0.02 | 57 | 3.0 |
| *Coptis asplenifolia* | H | 0.90 | 0.01 | 24 | 37.9 |
| *Cornus canadensis* | H | 1.52 | 0.53 | 16 | 60.6 |
| *Dicranum fuscescens* | M | 1.77 | 0.82 | 10 | 93.9 |
| *Dryopteris austriaca* | F | 3.58 | 0.78 | 6 | 84.9 |
| *Epilobium hornemannii* | H | 0.01 | 0.00 | 57 | 1.5 |
| *Equisetum arvense* | F | 0.01 | 0.00 | 57 | 1.5 |
| *Eurhynchium oreganum* | M | 0.92 | 0.25 | 23 | 40.9 |
| Foliose lichens[e] | L | 0.82 | 0.00 | 26 | 77.3 |
| *Galium triflorum* | H | 0.01 | 0.00 | 57 | 3.0 |
| *Gaultheria shallon* | S | 0.15 | 0.00 | 43 | 9.1 |
| *Goodyera oblongifolia* | H | 0.06 | 0.00 | 51 | 6.1 |
| Graminoid spp.[f] | H | 0.01 | 0.00 | 57 | 3.0 |
| *Gymnocarpium dryopteris* | F | 3.02 | 0.18 | 8 | 71.2 |
| *Hookeria lucens* | M | 0.24 | 0.00 | 40 | 25.8 |
| *Hylocomium splendens* | M | 11.39 | 7.74 | 2 | 97.0 |
| *Isothecium stoloniferum* | M | 0.61 | 0.04 | 31 | 62.1 |
| *Jungermanniales* spp. | LV | 3.31 | 0.54 | 7 | 86.4 |
| *Jungermannia lanceolata* | LV | 1.33 | 0.03 | 17 | 63.6 |
| *Leucolepis menziesii* | M | 0.01 | 0.00 | 57 | 4.6 |
| *Linnaeus borealis* | H | 0.01 | 0.00 | 57 | 1.5 |
| *Listera* spp.[g] | H | 0.28 | 0.01 | 38 | 22.7 |
| *Luzula parviflora* | H | 0.06 | 0.00 | 52 | 6.1 |
| *Lycopodium annotinum* | F | 0.10 | 0.00 | 47 | 10.6 |
| *Lysichitum americanum* | H | 0.03 | 0.00 | 55 | 3.0 |
| *Maianthemum dilatatum* | H | 0.70 | 0.01 | 28 | 45.5 |
| *Marchantia polymorpha*[h] | LV | 0.56 | 0.27 | 32 | 30.3 |
| *Menziesia ferruginea* | S | 0.01 | 0.75 | 21 | 54.6 |
| *Moneses uniflora* | H | 0.64 | 0.00 | 30 | 60.6 |
| *Oplopanax horridum* | S | 0.87 | 0.04 | 25 | 28.8 |
| *Osmorhiza chilensis* | H | 0.01 | 0.00 | 57 | 1.5 |
| Other mosses[i] | M | 1.57 | 0.47 | 15 | 69.7 |
| *Picea sitchensis* | T | 0.93 | 3.26 | 22 | 47.0 |
| *Plagiothecium undulatum* | M | 3.69 | 0.58 | 5 | 97.0 |
| *Pogonatum macounii* | M | 0.72 | 0.12 | 27 | 68.2 |
| *Polypodium glycyrrhiza* | F | 0.01 | 0.00 | 27 | 3.0 |
| *Polystichum braunii* | F | 0.01 | 0.00 | 57 | 3.0 |
| *P. munitum* | F | 0.07 | 0.00 | 50 | 7.6 |
| *Polytrichum* spp.[j] | M | 0.48 | 0.09 | 34 | 43.9 |
| *Porella navicularis* | LV | 1.76 | 0.01 | 13 | 86.4 |
| *Pteridum aquilinum* | F | 0.03 | 0.00 | 56 | 3.0 |
| *Rhizomnium glabrescens* | M | 7.04 | 2.78 | 4 | 92.4 |
| *Rhytidiadelphus loreus* | M | 25.09 | 11.24 | 1 | 95.5 |
| *Ribes bracteosum* | S | 0.01 | 0.00 | 57 | 1.5 |
| *R. laxiflorum* | S | 0.28 | 0.05 | 47 | 6.0 |
| *Rubus parviflorum* | S | 0.01 | 0.00 | 57 | 1.5 |
| *R. pedatus* | H | 2.03 | 0.05 | 11 | 59.1 |
| *R. spectabilis* | S | 2.61 | 19.10 | 10 | 39.4 |
| *Sambucus canadensis* | S | 0.12 | 0.00 | 45 | 10.6 |
| *Sphagnum* spp.[k] | M | 1.64 | 1.21 | 14 | 60.6 |
| *Streptopus amplexifolius* | H | 0.37 | 0.03 | 36 | 30.3 |
| *S. roseus* | H | 0.32 | 0.01 | 3 | 30.3 |
| *S. streptopoides* | H | 0.48 | 0.24 | 2 | 47.0 |
| *Thelypteris phegopteris* | F | 0.11 | 0.08 | 46 | 6.1 |
| *Thuja plicata* | T | 0.20 | 0.46 | 42 | 10.6 |
| *Tiarella trifoliata* | H | 0.20 | 0.03 | 18 | 69.7 |

TABLE 1 (continued)

| Species[a] | Class[b] | % Cover | % Production | Rank[c] | % Constancy[d] |
|---|---|---|---|---|---|
| *T. unifoliata* | H | 0.01 | 0.00 | 57 | 1.5 |
| *Timmia austriaca* | M | 0.22 | 0.02 | 41 | 22.7 |
| *Tsuga heterophylla* | T | 2.88 | 18.00 | 9 | 89.4 |
| *Vaccinium alaskaense* | S | 8.44 | 4.97 | 3 | 87.9 |
| *V. ovalifolium* | S | 0.01 | 0.00 | 57 | 1.5 |
| *V. parvifolium* | S | 1.22 | 1.92 | 20 | 90.9 |
| *Viola glabella* | H | 0.14 | 0.00 | 44 | 12.1 |

[a] Nomenclature follows Hale and Culberson (1970) for lichens, Worley (1970b) for mosses, Worley (1970a) for liverworts, and Hulten (1968) for vascular plants, except where more recent nomenclatural changes have been published.

[b] T = tree seedling, F = vascular cryptogam, H = herbaceous and low shrub, L = lichen, M = moss, LV = liverwort, S = shrub.

[c] 1 = highest relative ground cover, 57 = lowest cover.

[d] The percentage of study sites for which the species was recorded.

[e] Primarily *Lobaria oregona* and *Peltigera canina*. Also *Sphaerophorus globosus* and *Hypnogymnia enteromorpha*.

[f] Primarily *Bromus sitchensis* and *Poa* spp.

[g] *Listera cordata* and *L. caurina*.

[h] Includes *Conocephalum conicum*.

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

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

[k] Primarily *S. squarrosus* and *S. girgensohnii*.

TABLE 2.

TREE SEEDLING (< 2.5 CM DBH) AND SHRUB BIOMASS SUMMARY.

|  | Successional Stage: |  |  |  |
|---|---|---|---|---|
| Species | Early Succession 0-30 yr | Depauperate Understory 31-130 yr | Mature Even-aged 131-250 yr | Old-growth 250+ yr |
| A. Shrubs | (kg ha$^{-1}$) |  |  |  |
| *Menziesia ferruginea* | 125.7 | 4.7 | 27.4 | 36.5 |
| *Oplopanex horridum* | -- | 0.1 | 5.4 | 3.3 |
| *Ribes laxiflorum* | 14.7 | 1.7 | — | 0.2 |
| *Rubus spectabilis* | 1031.0 | 11.5 | 1.9 | 48.5 |
| *Vaccinium alaskaense* | 829.3 | 16.4 | 69.2 | 378.0 |
| *Vaccinium parvifolium* | 170.7 | 19.6 | 52.8 | 24.0 |
| B. Tree Seedlings |  |  |  |  |
| *Picea sitchensis* | 1574.3 | 16.7 | 2.8 | 10.2 |
| *Thuja plicata* | 90.0 | 7.6 | — | 0.1 |
| *Tsuga heterophylla* | 6042.3 | 64.9 | 133.2 | 822.5 |

TABLE 3.

SUMMARY OF CANOPY GAP - UNDERSTORY VEGETATION RELATIONSHIPS

| Sources | % Cover Under Gaps[a] | % Cover Under Canopy | % Under Gaps |
|---|---|---|---|
| A. Shrubs | | | |
| *Rubus spectabilis* | 2.5 (0.37)[b] | 0 (0) | 100.0 |
| *Vaccinium alaskaense* | 8.5 (1.35) | 3.6 (0.49) | 70.2 |
| *V. parvifolium* | 0.4 (0.06) | 0.20 (0.06) | 64.3 |
| Total | 11.39 | 3.8** | 75.0 |
| B. Herbs | | | |
| *Coptis asplenifolia* | 1.16 (0.15) | 0.43 (0.12)** | 73.0 |
| *Cornus canadensis* | 11.30 (0.35) | 0.87 (0.28)** | 93.0 |
| *Dryoperis austriaca* | 3.71 (0.35) | 3.10 (0.78) | 54.5 |
| *Gymnocarpium dryopteris* | 2.70 (0.31) | 3.10 (0.80) | 46.6 |
| *Rubus pedatus* | 2.42 (0.23) | 1.58 (0.37) | 60.5 |
| Total | 21.29 | 9.08** | 70.1 |

[a] Subplots with less than 80% tree canopy cover in any quadrant.

[b] Percent cover is the arithmetic mean for all microplots under gaps or closed canopy. The standard error of the estimate is given in parenthesis.

*Significant difference at α = 0.05.
**Significant difference at α = 0.01.

## The Early Successional Phase

In contrast to seral stages studied in the Pacific Northwest, in southeast Alaska herbaceous annuals are a much less important component of understory production during the first 20 yr of succession (Mueller-Dombois 1965, Long and Turner 1975, Dyrness 1973). In maritime climates perennial herbs and shrubs persist through most disturbance events in the absence of fire, giving them a competitive edge over other colonizing plants (Kellman 1969, Alaback 1980). Since fires are relatively rare in southeast Alaska this may be an important factor in explaining why colonizing herbaceous annuals are so unsuccessful (Kellman 1969, Dyrness 1973). *Dryopteris austriaca*, *Athyrium felix-femina*, and *Cornus canadensis* form dense patches where tree regeneration or woody shrubs have not invaded the site. The other herbs only modestly increase their productivity during this phase (Fig. 2).

The bulk of understory growth during stand establishment is by vigorously sprouting woody shrubs and tree seedlings (Table 3). *Rubus spectabilis* dominates sites which had extensive soil disturbance during stand establishment. On most sites *Vaccinium alaskaense* dominates the shrub stratum. *Vaccinium parvifolium* and *Menziesia ferruginea* also maintain their highest productivity during this phase of development.

The magnitude and importance of shrub productivity during this early part of the chronosequence is greatly underestimated by percent ground cover data (Fig. 3). Estimates of shrub production from percent cover data incorrectly suggest that the old-growth stage is the most productive. Data from this study suggest that species which accumulate woody biomass and vertical structure generally have the most imprecise relationship between biomass and percent cover. Consequently, inferences of changes in the dominance of these species from percent cover data must be evaluated cautiously.

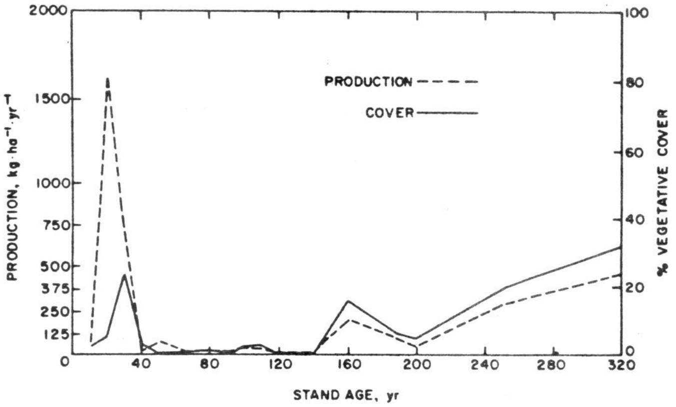

FIGURE 3. *Vaccinium alaskaense* dynamics during succession.

Taylor (1932) generalizes that on well drained sites in southeast Alaska an average of 50% of the tree seedlings colonizing clearcuts are *Picea sitchensis*. The proportion of *Picea* seedlings colonizing after disturbance is affected by a diversity of ecological factors notably available nitrogen (Taylor 1935). On sites less than 30 yr old measured for this study *Picea* composed 0 to 61% of seedling biomass. The highest proportion of *Tsuga heterophylla* and *Thuja plicata* was measured on the wettest sites, and those with the least soil disturbance associated with stand establishment. Higher proportions of *Picea* were measured in forests close to the shoreline and along large river terraces. On typical sites *Tsuga* maintains the highest biomass throughout the chronosequence. Seedling biomass peaks in the ten to twenty yr age class (Table 2).

## Depauperate Understory Phase

On stands 25 to 30 yr old the crowns of *Tsuga* and *Picea* form a nearly continuous canopy cover. A near total elimination of the shrub and herb strata accompanies tree canopy closure (Fig. 2, 3). In dense stands 20 to as much as 150 yr the forest floor is dominated by bryophytes and conifer needles. The most depauperate stands are 30 to 45 yr old. Cryptogams such as *Plagiothecium undulatum*, *P. denticulatum*, *Cladonia coniocraea* and *Rhizomnium glabrescens* which are usually associated with decaying bark and other woody debris are among the most common plants in the understory.

As rapidly growing forests mature, bryophytes increase their dominance in the understory (Fig. 4). At stand age 30 to 40 moses are primarily restricted to logs and other decaying wood. By stand age 40 to 50 *Rhytidiadelphus loreus* and *Hylocomium splendens* form thick carpets over logs and the forest floor. *Dicranum fuscescens* frequently forms clumps surrounded by the *Rhytidiadelphus* mats on decaying wood. *Rhytidiadelphus* cover is highly variable within an age class but tends to reach its highest degree of dominance at stand age 40-150 yr. Much of this variability may relate to differences in stand establishment history as it relates to forest floor and log substrate environmental conditions.

*Hylocomium* dominance increases within the 40-150 yr age class, declining thereafter (Fig. 4). It does not normally develop the large pure mats characteristic of *Rhytidiadelphus* in *Tsuga* dominated forests. *Hylocomium* can form almost pure carpets over a wide range in stand age in specialized microsites such as above exposed shoreline-facing cliffs and rock outcrops where *Picea* is generally more dominant.

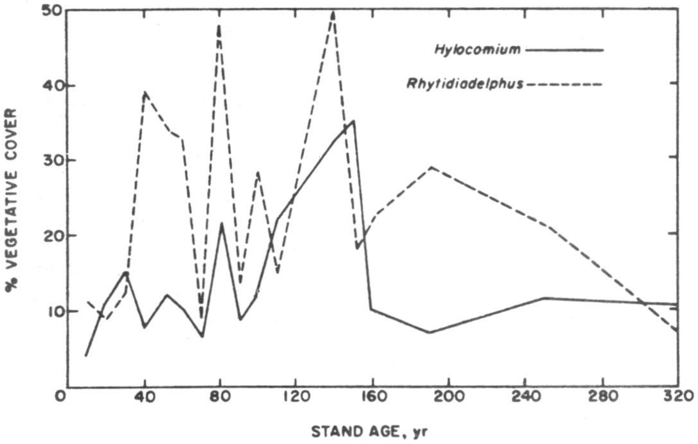

FIGURE 4. Bryophyte dominance during succession.

*Dryopteris* and *Gymnocarpium* increase their productivity during the latter decades of the depauperate understory successional phase. By stand age 60 to 70 these ferns are no longer restricted to woody substrates, often forming a distinctive stratum in the understory. On mesic sites with thin rocky soils, *Dryopteris* can attain 80 kg/ha/yr production (8-fold the average productivity for this age class). Where calcareous substrates are exposed in forests of this and older age classes *Asplenium viride* and other specialized species commonly grow.

Forest overstory productivity is highest during the depauperate understory successional stage. Taylor (1934) studied wood volume and growth increment over a range of sites in southeast Alaska, including many of the sites sampled in this study. He estimated peak bole wood production at around 70 yr. Using Taylors' curves for the sites sampled in this study wood increments range from 6 to 16 m$^3$/ha/yr (Fig. 5). The most productive site is 100 yr old. In general the most productive sites have a higher proportion of *Picea* basal area than the other sites. In the southern half of the study area, especially in the Ketchikan area, Thuja had the highest proportion of tree basal area on the least productive sites. Only at Red River and Kindergarten Bay do *Picea* and *Thuja* attain comparable abundance within the same stand.

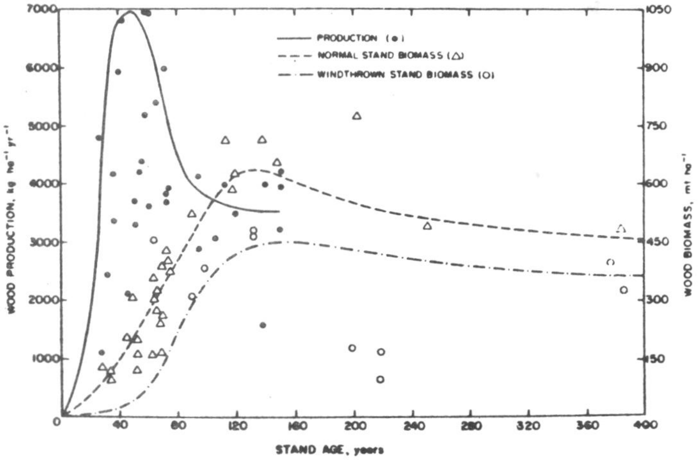

FIGURE 5. Forest biomass accumulation and productivity during secondary succession. (Hand fitted curves represent maximum biomass and productivity values for each age class.)

The depauperate understory successional phase is the most dynamic in terms of tree species compositional changes. Among western conifers *Picea* is considered intolerant to intermediately tolerant of shade (Minore 1979). Few *Picea* seedlings (less than 2.5 cm in diameter) were found in forests older than 30 yr which had completed canopy closure (Table 3). *Picea* abundance thus declines after stand establishment, but due to its great longevity (trees over 600 yr were measured in this study) it remains an important forest component throughout the chronosequence.

Since *Picea* abundance varies with site conditions it is difficult to accurately portray changes in *Picea* abundance directly from chronosequence data. By deleting those sites with anomalously high *Picea* composition (Killisnoo Island, Kanulku Bay, Chilcat Peninsula, Dorn Island, and Salisbury Point) due to localized site conditions (i.e., salt spray, or river alluvium), a general pattern of *Picea* dynamics over time is discernable (Fig. 6). Forests up to 80 yr old tend to have equivalent *Picea* and *Tsuga* foliar biomass. Data from this study suggests that *Tsuga* continues to accumulate foliar biomass and increase its proportion of stand basal area through stands aged 100 yr. By contrast, *Picea* declines in foliar biomass during this period then stabilizes after 100 yr. Taylor (1932) generalizes that *Picea* basal area declines from 50 to 25 percent of stand basal area during secondary succession.

For the plots measured in this study *Picea* relative basal area ranged from an average of 37% in 20 yr old stands to an average of 12% in stands greater than 250 yr old.

## Understory Reinitiation: Mature Even-Aged and Uneven-Aged Old Growth

Forests aged 150 to 250 yr although still primarily even-aged, tend to have a more diverse canopy structure and heterogeneous understory than in the previous successional stage. *Streptopus* spp., *Cornus canadensis* and

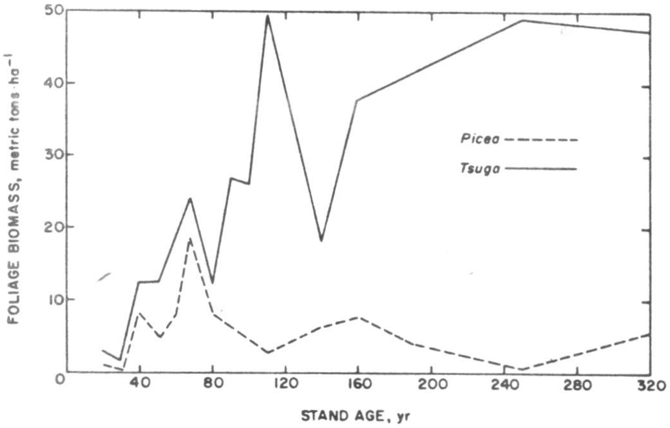

FIGURE 6. Tree foliage biomass compositional changes during succession.

Rubus pedatus sharply increasé their productivity between stand age 150 and 250 yr. Rubus pedatus attained its highest productivity during this successional phase. Gymnocarpium and Dryopteris also tend to increase in biomass but decrease in relative dominance during this period. The variation in understory production structure is greater within this age class than any other closed canopy forest type. Stands maintaining a high tree density can remain in the depauperate understory stage for over one century. Similarly forests subject to windthrow of canopy dominants tend to develop a second dense canopy layer of Tsuga and/or Thuja leading to less light reaching the forest floor and less than average understory productivity. Stands developed on steep rocky thin hummocky soils tend to develop a more open overstory canopy leading to a highly productive and luxuriant understory throughout this age class.

The most significant change in understory structure during this phase of succession is the establishment of a woody shrub stratum. Vaccinium parvifolium, which persists primarily as a trailing evergreen shoot 1-2 mm in diameter during the depauperate understory stage, often develops into an upright sprouting woody shrub by stand age 150-200. Vaccinium alaskaense, Tsuga heterophylla, and Menziesia ferruginea also increase their productivity during this phase of successional development (Table 2). For stands aged 150-250 yr shrub production averages 175 kg/ha/yr, in contrast to sites in the depauperate understory stage which average 50 kg/ha/yr. Individual shrub shoots tend to be shorter in stature and have less woody biomass in these sites than shrubs in early successional sites (Alaback 1980).

Canopy trees change little in basal area and height during this successional phase. Overall mean canopy tree heights range from 35 to 45 m for this age class. Basal area averages 55 to 75 $m^2$/ha. Picea density declines in this part of the chronosequence but the remaining trees usually maintain their status as canopy dominants or co-dominants and often exceed the ubiquitous Tsuga in diameter growth. In the forests over 250 yr old Picea is reduced to as little as 1-2 trees per hectare, but these trees are among the largest measured in the study (150-300 cm in diameter) and often represent a significant proportion of stand foliar biomass (Fig. 6).

## DISCUSSION

Cattelino et al. (1979) and Egler (1954) have shown the important role of initial conditions on the course of secondary succession. In sites measured for this study as well, conditions during stand establishment are inferred to have a profound influence on forest development. Sites originating from windthrow for example tend to accumulate biomass more slowly and are dominated by Tsuga (Fig. 5). Vaccinium alaskaense and Dryopteris austriaca maintain their productivity longer after stand establishment on these stands in contrast to those developing after logging or fire.

In those sites in which tree establishment was delayed or modified so that a high tree density was not attained by 5-10 yr high understory production was maintained longer than in normally developed stands. In the most productive sites open-grown Picea indicated this understocked condition. Vaccinium alaskaense and Rubus spectabilis can maintain moderate productivity in pockets of these stands. Poor sites with low tree density have a more open canopy and full development of a productive understory by stand age 60 to 90 yr.

Nine sites were sampled that significantly differed in understory structure from others in their age class. Most of these sites had anomalous soil morphology. Forests on thin rocky soils with seepages and locally poorly drained sites with a significant cover of Thuja tended to have a lower than average shrub production (362 kg/ha in Harris River, Clark Bay 8 yr, and Douglas Bay, in contrast to 3021 kg/ha at Thomas Bay, Point Vandeput, and Maybeso Valley). In general, the sites with the least timber productivity tended to have the most productive understory.

Most forest succession studies have centered on the pulse of vegetation growth immediately following clearcutting and the subsequent decline during tree canopy closure. Few studies have presented data on the transition from the depauperate understory stage to uneven-aged old-growth. In Washington Long (1976) showed a decline in understory after canopy closure, and an increase in understory biomass in stands 250 yr old. Only three mature forest age classes were studied (46, 250, and 550 yr). Russel (1974) theorized that woody shrubs establish in the Douglas-fir dominated forests of the west central Cascades of Oregon in as little as 20 to 40 yr following canopy closure. MacLean and Wein (1977) working in New Brunswick, suggest that increased understory development may occur as early as 50-60 yr following logging. In southeast Alaska the depauperate understory stage is maintained over a longer period of time than has been reported for forest successional processes in other regions. In order to fully evaluate the uniqueness of this pattern of development more data is needed on long term successional patterns in these other regions.

Many environmental variables were measured on sites sampled for this study for purposes of identifying the factors that are most important in influencing the course of successional development. No single factor was identified as the controlling driving variable over the process of succession. The complexities of environmental interactions at each site obscure such relationships. Canopy density and overstory foliar biomass were among the most important factors related to understory development on these plots (Alaback 1982).

As an increasing percentage of the remaining uneven-aged old-growth forests are converted to rapidly growing even-aged forests, basic information on the structural differences between old-growth forests and managed forests during their entire 100 yr cycle will be needed to objectively evaluate the ecological consequences of these changes. Data from this study suggests that younger forests over a wide range of sites and ages in southeast Alaska have a distinctive pattern of understory development. Over a 100 yr management cycle only the first 30 yr have high understory productivity. Those resources and ecosystem functions associated with the understory strata are minimized for the last 70 yr of a 100 yr management cycle. Much variation on this scheme should be expected on any given site, however, depending on present and past environmental conditions in addition to stochastic factors. Franklin et al. (1981) have shown many other structural and functional attributes of old-growth ecosystems not generally found in younger forests. The full consequence of eliminating old-growth forests will not be evident until we more completely understand the differences between the structure and functioning of these ecosystems in each ecological zone.

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