Successional pathways of a grand fir (Abies grandis) forest based on thirty-three years of evidence

Carol Leslie Cloonan
The University of Montana

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Successional Pathways
of a
Grand Fir (Abies grandis) Forest
based on
Thirty-three Years of Evidence

by

Carol Leslie Cloonan
B.S., University of Wisconsin-Green Bay, 1980
Presented in Partial Fulfillment of the Requirements
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Approved by:

Chairman, Board of Examiners

Dean, Graduate School

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Since the advent of fire suppression at Yellow Bay Forest, a grand fir community in northwestern Montana, the forest canopy has closed and reproduction has become increasingly limited to the small openings created by dead trees. Successional changes occurring within the forest were directly measured from data collected in 1951 and 1985. Data from fourteen .023 ha plots were used to determine if more than one successional pathway was evident and how differences in trends related to site conditions and species' vital attributes.

During the 33-year period, two major successional pathways occurred within the forest. One pathway, characterized by an increase in grand fir dominance, occurred in the moister, more southern plots. The pathway associated with the drier plots increased in both grand fir and Douglas-fir (Pseudotsuga menziesii) dominance. While overstory compositions of the two groups of plots became more distinct over time, their understory compositions became more similar. Grand fir dominated reproduction in most of the forest. This species established well under the small canopy openings characteristic of the current disturbance regime. Douglas-fir, dependent on larger openings to become established, did not survive to even the sapling stage in the understory.

If current conditions continue in the south end of the study area, grand fir will increase in dominance. Grand fir and Douglas-fir will continue to codominate in the northern, drier region at least as long as the overstory Douglas-firs survive. The continuance of codominance depends on a major disturbance to open the canopy sufficiently to allow Douglas-fir to reestablish.
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CHAPTER 1

INTRODUCTION

Succession is a directional cumulative change in the species which occupy a given area through time (Barbour et al. 1980). Early ecologists developed successional theories, striving to fit all plant community change into one successional pattern. The inherent complexity of ecological phenomena, however, did not lend itself to the development of an all-encompassing theory. Ecologists now accept that multiple patterns and pathways of plant succession exist, varying as much as the environmental and historical phenomena on which they depend. The analysis and comparison of individual cases of plant succession now dominate successional research and preclude the development of a universal model.

Ecologists have employed a variety of methods to avoid waiting decades to observe changes in forest composition over time. These methods rely on inference to create predictive models. The only proof of these predictions, however, is to observe how forests actually develop over time. Long-term studies of permanently marked sites provide direct evidence for the appraisal or revision of current successional models. Many more studies, covering more vegetation types, need to be undertaken to establish a definitive database of successional studies.

Analysis of forest succession may address several levels of resolution. Typically, a large portion of a forest or a homogeneous stand representing the composition of the forest is sampled. Studies where data are aggregated for a whole forest or a homogeneous stand often
overlook the forest's internal heterogeneity and thus, certain forest dynamics. In this study, I use long-term data from 14 permanently-marked plots to directly assess compositional change. Species growth rates, life history attributes and ordination techniques were used to determine what pathways are occurring and to evaluate what successional theories are applicable. Data from individual plots, as well as for the forest as a whole, are analyzed. Individual plots are grouped according to the similarity of their compositional changes and potentially their pathways of succession.

I chose a grand fir (Abies grandis) forest in northwestern Montana for the study, because of the availability of historical data and its suitability for a long-term study. The site, as part of the University of Montana Biological Station at Yellow Bay, has a high potential for remaining relatively free of disturbance. Its proximity to a center of university research also ensures continued monitoring of the site.
Clements' (1916) treatise on plant succession was one of the first all-encompassing models of vegetation change. Clements' holistic, organismic theory of succession dominated the field until the 1950s. Elements of his theories have been incorporated into many contemporary succession models (e.g., Odum 1969). This classical model, called both relay floristics (Egler 1954) and the facilitation model (Connell and Slatyer 1977), depicts succession as a stage-by-stage process with the plants' modification of the site as the driving force (Miles 1979).

The facilitation model describes succession as a directional, single-pathway, deterministic change of vegetation (Connell and Slatyer 1977). A discrete plant community characterizes each stage of succession. Each community modifies its environment until the site becomes more suitable for a community of later-succession species which then assume dominance. The dominance of a stable, self-maintaining plant community, the "climax type" marks the final stage in this sequence. A major change in environmental conditions or a catastrophic event renews this process (Miles 1979, Barbour et al. 1980).

As a deterministic model of succession, Clements' theory has been repeatedly contested and rejected (Gleason 1927, Egler 1954, Drury and Nisbet 1973, Connell and Slatyer 1979, Peet and Christensen 1980). The major objections to Clements' theory are that his discrete stages are
delineated arbitrarily, that the importance of site modification is overemphasized and that succession is in actuality a probabilistic, not a deterministic process (Miles 1979).

Gleason (1927) contested Clements' rigid concepts, viewing succession as a mobile phenomenon to be explained through general principles—not fixed laws. Gleason (1927) recognized that succession need not be predictable and that a true climax (sensu Clements 1916) does not exist because the causes of succession never cease, even if they are not observable.

In opposition to Clements' widely accepted ideas, Egler (1954) proposed that the "initial floristic composition" of a site determines later shifts in species dominance and that any species that inhabits a site as an adult can colonize the site in its early developmental stages when competition is low (Figure 1). According to Egler (1954), species assume dominance at different points in time because of their unique life history characteristics, such as growth rate and longevity.

Connell and Slatyer (1977) drew on Egler's ideas to distinguish the 'tolerance' and 'inhibition' models of plant succession. In the tolerance model, later species, i.e., those species which become dominant later in the succession sequence, establish successfully regardless of whether earlier species preceded them. Climax species assume dominance because they tolerate reduced levels of resources, e.g., light, moisture, or nutrients (Connell and Slatyer 1977).

Egler's (1954) premise that any species of a successional sequence can colonize a site in its early developmental stages also holds in the inhibition model. This model proposes that by tying up the limited resources, early colonists inhibit the invasion and growth of other
Figure 1. Two conceptual models of plant succession. The thickness of a line indicates the relative importance of a species (Barbour et al. 1980).

The Relay Floristics Model

The Initial Floristics Composition Model

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species. Probability dictates that the shorter-lived, early-arriving species will more often be replaced than the longer-lived, later-arriving species producing a sequence leading from short- to long-lived species (Connell and Slatyer 1977).

All three models, facilitation, tolerance, and inhibition, agree that those species with colonizing characteristics will dominate initial reproduction on a disturbed site. The three models vary on how species establish themselves later in the successional sequence. Early succession species either modify the environment to the benefit of later species (facilitation), do not make the environment any more or less suitable for late species (tolerance), or they make the environment unsuitable to potential colonizers (inhibition) (Connell and Slatyer 1977).

No one model accounts for all successions, or even for a whole succession sequence, as Clements' (1916) model claimed. The multitude of successional pathways is a function of the variety of mechanisms that species employ to reproduce, establish, grow, and compete (Miles 1979).

Each of the three models of succession described above operates under some circumstances, though none under all. Clements' (1916) facilitation model operates on recently disturbed sites where pioneer species improve conditions for later colonizers by lowering the pH, by increasing nitrogen levels and organic matter content and by stabilizing shifting substrates (Connell and Slatyer 1977). Egler's (1954) tolerance model seems to operate to some degree in all successional sequences (Miles 1979). Connell and Slatyer (1977) remark, however, that no convincing evidence exists which proves that early succession species do not in some way facilitate or inhibit the establishment of later species.
as the tolerance model necessitates. The inhibition model operates in many situations where early- and mid-succession species secure space or monopolize light, inhibiting the invasion or growth of species (Connell and Slatyer 1977). In their studies of the *Pinus taeda* and mixed hardwood forests of the North Carolina Piedmont, Peet and Christensen (1980) demonstrate how both facilitation and inhibition models operate at different stages of succession. During the growth phase, when mortality dominated the Piedmont, succession followed Egler's (1954) theory which states that succession is a function of the differential longevity of trees.

Recent models of plant succession incorporate the various models, e.g., the facilitation, tolerance, and inhibition models, and place great importance on the life histories and competitive relationships of component species. These recent models describe succession using a synthesis of alternative approaches which are not mutually exclusive or competing (Peet and Christensen 1980).

Recent reviews of traditional and contemporary concepts of succession (Drury and Nisbet 1973, Connell and Slatyer 1977, Noble and Slatyer 1980) advocate a population-based approach emphasizing the attributes of the component species that are vital to their successional role, i.e., their life histories and responses to competition. Noble and Slatyer (1980) developed a technique predicting succession in frequently disturbed sites by using vital attributes. The vital attributes of a species, as defined by Noble and Slatyer (1980), are its method of arrival or persistence, its ability to establish and mature, and the time taken to reach critical life stages. A fourth vital attribute, life form, may be added to increase the model's effectiveness (Noble and
Multiple pathways of succession can occur on a site undergoing various replacement sequences (Miles 1979). The multiple pathway model devised by Cattelino et al. (1979) permits the use of variable successional pathways depending on species composition, intensity of disturbance, and stand age when the site is disturbed. Their model uses vital attributes to predict the successional pathways that will occur following fires of various intensities and frequencies.

Another recent model, the cone model of secondary succession (Huschle and Hironaka 1980), includes facilitation, tolerance, and inhibition pathways. The climax plant community is represented by the tip of the cone and its associated seral communities by sectors which form the cone base (Huschle and Hironaka 1980) (Figure 2). Seral plant communities follow one of various pathways depending on community characteristics and interactions. The various pathways converge as they near climax because no new species can invade and persist at this point. Cones of climax communities overlap at the base where competitive pressure on the seral communities is low.

The cone model of plant succession simplifies the real world, as do the other succession models. The most important function of succession models is their ability, separately or together, to increase our understanding of plant succession (Peet and Christensen 1980).
Figure 2. Cone model of secondary succession. Cones represent two similar vegetation types. Overlap of cones illustrates plant communities belonging to both vegetation types (Huschle and Hironaka 1980, from Hann 1982).
Methods of Studying Succession

Ecologists study long-term changes in vegetation to gain understanding in and to derive general models of vegetation dynamics (Cottam 1984).

The time-scale necessary to measure changes in forest vegetation complicates the study of forest succession (Hibbs 1980) and the validation of succession models. To directly evaluate vegetation change, "permanent plots" must be remeasured over time. To establish permanent plots for long-term study, researchers need unselfish foresight as the knowledge gained may be beyond their own careers. The future suitability of permanent plot or "time-series" data relies on careful planning.

At present, the available permanent plot data is limited in the length of time it covers, the variety of vegetation types studied and its suitability for successional studies.

Until recently, most permanent plot analyses interpreted data for not more than 10 to 20 years (Whitney 1984). Studies by Stephenson (1965), Schmelz et al. (1975), Abrell and Jackson (1977), and Christensen (1977) analyze from eight to twenty-two years of vegetation change. The recent recognition of the value of this type of data (Franklin 1982) has motivated a search for suitable established plots and has resulted in a number of successional studies covering longer time periods. Boggess and Bailey (1964), Stephens and Waggoner (1980), Ebbers (1983), Hemon et al. (1983), Hibbs (1983), Parker and Leopold (1983), Peet (1984), Whitney (1984), and McCune and Cottam (1985) analyzed from twenty to fifty years of vegetation change.
The majority of published permanent plot studies, including all twelve listed above, focus on the eastern forests. A limited number of permanent plot transect studies analyze grassland vegetation (e.g., Humphrey and Mehrhoff 1958, Robertson 1971) and mountain vegetation (e.g., Ketchledge and Leonard 1984). Stickney (1980) and Franklin (1982) both work with permanent plots in the western United States.

Stickney (1980) has analyzed the first six to nine years of plant succession after burning on 20 sites in northwestern Montana. Plots were all subject to either wildfire or a broadcast slash burning following clearcutting. Predominantly larch (*Larix occidentalis*)/Douglas-fir (*Pseudotsuga menziesii*) forests were studied in the Northern Rocky Mountain region.

Franklin (1982) documents permanent plots established in the Pacific Northwest. The oldest plots in old growth forest, located in Thornton J. Munger Research Natural Area in the southern Washington Cascades, were established in 1947. The mensurational plots established by the USDA Forest Service during the early 1900s provide important baseline data for successional studies. Though logging and its associated roadbuilding destroyed most of these plots, a sufficient number remain valuable for successional studies. Oregon State University has established and maintained permanent plots over a broad range of forest types and environmental conditions at H.J. Andrews Experimental Forest, Mount Rainier, Olympic National Park, and many research natural areas. Many of the plots in the Pacific Northwest lack key data because mensurational, silvicultural, or timber objectives rather than ecological objectives determined data collected. Concerned with the suitability of much of these data, Franklin (1982) remarks,
"This wealth of forest plots should not obscure the need for establishment of ecologically oriented successional plots because forest growth plots typically lack key information even when they are in the right vegetation types or locales...."

The lack of suitable long-term data led to the development of several research methods to document succession. These methods include the reconstruction of past vegetation through historical and ecological records, size- and age-class analyses and the use of chronosequences.

Successional studies have compared existing vegetation with old records such as written descriptions, land survey records and photographs. Such comparisons lack objectivity and are qualitative rather than quantitative. Historical records reflect the biases of the writers and surveyors (Vale 1982). For example, in documenting witness trees along section lines, surveyors may have recorded certain trees because of species, size, longevity, commercial importance, or location (Barbour et al. 1980). Differences in vegetation noted from paired photographs also may be misinterpreted. Vegetation viewed in old photographs may reflect conditions at one time of the year or a short-term climatic change rather than typical conditions for that time period. These three types of historical records may help determine the general characteristics of the vegetation but can not quantify the changes. For example, researchers may accurately use old photographs to determine changes in plant cover and lifeform, but not changes in species composition (Vale 1982).

Ecological reconstruction of past vegetation includes inference from relicts as well as detailed analyses of stands. Relicts may be individual plants as well as vegetated areas that have been protected
from human disturbance. Relict plants help to characterize past vegetation. For example, a forest tree with broad, low branching suggests the previous existence of a savanna. The comparison of relict areas to undisturbed areas illustrates the effects of human activity. The interpretation of relics relies heavily on inference but is useful for descriptive purposes. Stand history may also be reconstructed by analyzing rotting wood fragments, fire scars and xylem rings (Henry and Swan 1974, Oliver and Stephens 1977). Such labor-intensive studies are practical only for small areas.

Size- or age-class analyses are frequently used to infer successional trends. Tree ages are determined by increment boring. Tree sizes usually expressed as diameter at breast height, are more easily obtained than ages, and therefore are used more frequently in this type of analysis. "Inferences from size class analyses have provided us with most of our knowledge on the successional status of various tree species in various environments.... Many studies show us how useful size-structure analyses can be..." (Franklin 1982).

The size or age structure of a stand reflects the dynamics of the species populations (Vale 1982). "Density data broken down by size-class may suggest past disturbances and recovery from such disturbances in a stand" (Schmelz et al. 1975). Size-class data may identify changes in the reproductive status of a species due to disturbances (Vale 1982).

Typical interpretations of size- or age-class distributions follow. In a climax community, i.e. one with "permanent possession of the habitat", one might expect each climax species to be represented in each age class (Daubenmire 1968). A forest community with progressively fewer individuals in ever larger or older classes is usually maintaining
itself (Vale 1982). If a species' age-class series is truncated at either end, the species cannot, in most cases, be considered a climax species due to the interruption in its life cycle (Daubenmire 1968). Few individuals in small or young age classes indicate that a species is not successfully reproducing while an abundance in these age classes suggests that the species is invading (Vale 1982).

Such interpretations, however, should be approached cautiously. Accurate interpretation requires knowledge of species life histories. An age-class structure without a progressively decreasing population in older classes does not always indicate that the population is not stable. An interruption in the age-class series may result from cyclical patterns which are not evident in a sample covering a limited time period. For example, the eastern hemlock (*Tsuga canadensis*) may have few young trees at a given time because it sometimes reproduces in cycles (Vale 1982). When drawing conclusions based on age- or size-class series, one must be aware that sapling densities may change over years or decades and that mortality rates, susceptibility to disease and shade tolerance of saplings vary from species to species (Barbour et al. 1980).

Size classes are often used as an approximation of age, though the relationship of the two parameters varies considerably. Daubenmire (1968) found that tree diameters can be used to estimate age reasonably well if size classes are broad enough and if different species are not assumed to have similar age-size relationships. Franklin (1982) strongly warns that assuming a close relationship between size and age, a relationship that has been frequently disproved, may result in gross misconceptions. Antos (1977) found that "seedling"-sized, shade toler-
ant grand fir trees varied from less than 40 to 120 years of age.

In spite of the ambiguous relationship between age and size, Daubenmire (1968) attests that "a graded series of sizes has approximately the same successional significance as a graded series of ages." Franklin's (1982) findings agree that "useful ecological inferences do not necessarily depend on high age-size correlations."

Many studies infer vegetation change by sampling a series of similar, nearby plots of various successional ages, i.e. chronosequences (Barbour et al. 1980). The plots must represent a wide range of known, successional ages. A series of plots may be adjacent as those established in the path of a retreating glacier or scattered through an area. In scattered plots, successional age may be determined from land use records or ecological clues, but is most often determined from tree ages (Barbour et al. 1980). The validity of this method demands that the study plots differ in age but do not differ significantly in topography, parent material, slope, aspect or macro-climate (Barbour et al. 1980, Daubenmire 1968). This heavy dependence on inference and the improbability of finding plots differing only in age tend to cloud the results of chronosequence studies with suspicions (Christensen 1977, Cottam 1984).

Permanent plot studies avoid the problems of inference and generalities that are inherent in other methods of documenting succession. The superiority of permanent plot analyses has just recently been realized. The lack of time series data has greatly limited our understanding of plant succession (McCune and Cottam 1985). Vale (1982) agrees that permanent plot studies warrant greater attention and Franklin (1982) calls the development of permanent plots, "the most
important research need in forest succession." The superiority of permanent plot data is clear. With permanent plot data, one can more accurately assess stand dynamics and successional trends (Peet 1984). Only this type of data allows structural properties, such as size distribution, to be directly linked to successional processes (Peet and Christensen 1980).

Permanent plot data allow accurate demographic study, evaluation of the impact of disturbances and development and validation of succession models. For demographic studies, changes in species composition and importance, population structure, species distributions, species diversity (Christensen 1977) and a species' role or position in the canopy (Hibbs 1983) can be computed directly. Also, each species' survival, growth and recruitment rates can be analyzed in detail (Hibbs 1983, Christensen 1977). Long-term data aid in evaluating the impact of disturbance and the recovery of vegetation after the disturbance is eliminated. Research concerning the impact of recreation, e.g. trampling from hikers, and the impact of acid deposition on the natural environment relies on the use of permanent plots and transects (Ketchledge and Leonard 1984).

Permanent plot data can be used to project short-term forest growth (Peet 1984) and to develop and evaluate successional models. "We can build all the successional models, and make all the short-term studies we want; but the real proof of our predictions is to observe the actual development of forest stands over time" (Franklin 1982).
**Species Attributes**

The adaptive characteristics of species present in a forest stand greatly influence the successional pathway followed. These vital processes or "attributes" include a species' method of regeneration and reproduction, the conditions required for its establishment and persistence and the timing of its critical life history events (Noble and Slatyer 1980).

Several current successional models are reductionist, i.e. the models' foundations emphasize species-level attributes. Species' vital attributes dictate the potential response of the population, in terms of survival, establishment and growth, to the dynamic competitive environment. The population processes, in turn, influence community-level properties, such as succession (Peet and Christensen 1980).

To accurately represent changes in plant composition, quantitative succession models must be based on plant species' vital attributes (Keane 1984). A synopsis of important attributes of tree species present in the Yellow Bay forest follows. Scientific names follow Hitchcock and Cronquist (1973). References to Antos (1977) and Antos and Habeck (1981) refer to a study of the grand fir forests of the nearby Swan Valley and peripheral areas. Most of the areas sampled by Antos were located between Swan Lake and Condon, Montana. The Yellow Bay Forest, one of the 56 natural stands sampled by Antos, is slightly older and drier than the average stand that Antos (1977) sampled.
Grand Fir (*Abies grandis*)

Grand fir, a major forest dominant, is potentially the climax species (*sensu* Pfister et al. 1977) over much of the lower Swan Valley. Grand fir maintains high cover in most Swan Valley stands (Antos 1977), in both the understory and overstory (Fowells 1965).

Disease plays an integral role in grand fir's life history. Young grand fir often develop heart rot (*Echinodontium tinctorium* Ell. and Ev.) (Fowells 1965) and by 90 years of age trees usually have serious rot. Though many adult trees often live over 200 years, exact ages are difficult to determine due to pandemic stem rot (Antos 1977).

Grand fir is more shade tolerant than most associated western Montana conifer species. Though growth at times is suppressed, the species can survive under dense shade for many years (Fowells 1965, Antos and Habeck 1981). In this suppressed state, trees may increase in diameter only 1 to 2 mm per year (Antos and Habeck 1981) and have short, stunted crowns (Fowells 1965). An understory tree, 1 to 4 m tall, may be from 40 to 120 years old. When a gap forms in the canopy, allowing direct overhead light to reach the suppressed trees, grand fir responds well (Antos 1977). Released from suppression, grand firs build their crowns rapidly, partially due to epicormic branching (Fowells 1965). Grand fir also establishes well by seed in canopy gaps. An individual which receives overhead light while young has a very good growth potential (Antos 1977) and may attain a dominant canopy position (Antos and Habeck 1981).
Larch (Larix occidentalis)

In the Swan Valley grand fir forests, larch is a major seral constituent of most stands and remains a minor constituent of many older (>250 years) stands (Antos 1977).

Larch establishes best after hot fires as germination success is higher on ash or mineral soil than on duff (Fowells 1965) or beneath dense shrub and forb cover (Antos and Habeck 1981). Under favorable conditions, young larches grow rapidly, i.e., at twice the rate of Douglas-fir and at four times the rate of Engelmann spruces of similar age. Older, healthy trees grow slowly but steadily (Antos 1977). Capable of living more than 700 years (Fowells 1965), larch usually remains healthy for 300 years (Antos 1977).

Larch seedlings tolerate partial shade (Fowells 1965), but for much of their lifespans, larches are the least shade tolerant of all conifers present in the Swan Valley grand fir forests (Antos 1977).

Douglas-fir (Pseudotsuga menziesii)

Douglas-fir is a major seral constituent of and is widely distributed in grand fir stands of the Swan Valley (Antos 1977).

Douglas-fir regenerates best in partial shade. Less shade tolerant than grand fir and more tolerant than ponderosa pine and larch (Antos 1977), Douglas-fir will grow rapidly for many years in full sunlight. Trees have a maximum life expectancy of 500 years and longer (Fowells 1965). Even though Douglas-fir initially grows more slowly than larch, many eventually will assume dominance because they tolerate some shade (Antos 1977).

Douglas-fir is usually considered a subclimax species as it is most
often found with more tolerant species. Douglas-fir, however, can withstand suppression for short time periods and still respond to release, though not for the long periods exhibited by grand fir. In the prolonged absence of fire, grand fir may assume dominance over Douglas-fir (Fowells 1965).

**Engelmann Spruce** (*Picea engelmannii*)

Though more abundant at higher elevations, Engelmann spruce only forms a minor component of grand fir stands. Young spruces, which establish on almost any type of seed bed, play a minor role in young grand fir stands and in the gaps of late seral stands (Antos 1977). Spruce matures in 300 years and is long-lived. Spruce tolerates shade better than Douglas-fir, ponderosa pine and western larch (Fowells 1965).

**Ponderosa Pine** (*Pinus ponderosa*)

Although uncommon in grand fir forests, a few old-growth ponderosa pines are sometimes found in drier areas (Antos 1977).

On drier sites, young pines outcompete other species' regeneration due to their rapidly-growing taproot which protects them against drought (Fowells 1965). To regenerate on moister sites, where it grows with more shade-tolerant conifers, ponderosa pine requires fire or some other disturbance to open up the stand (Arno and Hammerly 1977). Though ponderosa pine is more shade tolerant than larch but less tolerant than Douglas-fir, a mature tree can withstand shade for up to 40 years. Ponderosa pines may live 400 to 500 years (Fowells 1965).
**Paper Birch (Betula papyrifera)**

Though fairly ubiquitous in grand fir forests of northwestern Montana, paper birch seldom achieves great abundance. Like larch seedlings, birch seedlings require moist mineral soil (Antos 1977) or rotten logs for germination. Full light is required for all stages of the birches' life history (Fowells 1965). Initially, birch grows rapidly (Antos 1977). This short-lived species matures in 60 to 75 years and dies by the age of 140. Birch experiences heavy mortalities throughout its lifespan (Fowells 1965).

Individual birch trees may assume dominance when young (Fowells 1965) but soon become overtopped by conifers (Antos 1977). As a dense canopy develops above, growth slows and the birch diminishes. Typically, more tolerant species replace the birch after one generation (Fowells 1965). Some birch may persist within 150 year old stands in canopy gaps or under thin stands of larch (Antos 1977).

**Regeneration Ecology**

In their study of the Swan Valley grand fir forests, Antos and Habeck (1981) found that historically the frequency of fire prevented most stands from reaching climax. After high-intensity fires, larch or lodgepole pine (*Pinus contorta*) becomes established. Larch establishment is favored by fires occurring in stands over 150 years of age (Antos and Habeck 1981).

The tree species which establish best in the first years following a fire are Douglas-fir and western whitepine (*Pinus monticola*) (Antos and Habeck 1981). Grand fir establishes and grows well after a fire (Antos 1977), though it invades and grows more slowly than Douglas-fir.
and western whitepine (Antos and Habeck 1981).

As a stand develops, dense shade and thick duff inhibit the regeneration of all species. Grand fir does not germinate well under its own shade in the Swan Valley stands. The high frequency of fire did not encourage the development of genotypes which can perpetuate in low light intensities. As the forest usually burned before the trees died from other causes, selection for invasion under a dense canopy had little chance to develop (Antos and Habeck 1981).

Most reproduction in these stands is limited to openings (Antos 1977, Antos and Habeck 1981). Grand fir dominates reproduction, being the species most successful at establishing in openings (Antos 1977). In large enough openings, Douglas-fir and western whitepine also establish and persist as minor forest components on drier sites (Antos 1977, Antos and Habeck 1981). Engelmann spruce also establishes itself in openings (Antos and Habeck 1981).
CHAPTER III
DESCRIPTION OF STUDY AREA

The grand fir forest under study is situated near Yellow Bay, an inlet located on the east shore of Flathead Lake. The five-hectare study site located within this forest extends north from the University of Montana Biological Station's entrance road and east from the lakeshore to Highway 35 (47° 53'N, 114° 02'W) (Figure 3).

The climate of the area is strongly influenced by moist maritime airmasses originating from the Alaskan Gulf and temperatures are moderated by Flathead Lake. The vegetation, both tree and undergrowth species, strongly reflects this Pacific climatic influence (Arno 1979). Many of the coastal species present, such as grand fir, are near their eastern range limits in this part of northwestern Montana.

An undulating topography and a southwest aspect (approximately 210° with a 3° slope) characterize the site. The elevation rises from 896 m at the southwest corner to 902 m at the north end of the study area. Underlying sediments, Quaternary and Tertiary valley fill deposits, were left by the Cordilleran glacier that carved the Flathead Lake basin during the last ice age (Alt and Hyndman 1972).

Grand fir is the potential climax dominant on this site, which classifies as an *Abies grandis* (grand fir)/*Clintonia uniflora* (queencup beadlily) habitat type (Pfister et al. 1977). Both seral and climax species (western larch, paper birch, ponderosa pine, Douglas-fir, Engelmann spruce and grand fir) are represented. Though actually a shrub, mountain maple (*Acer glabrum*) also plays an important role in
Figure 3. Study Area. Regional map modified from Antos (1977).
forest dynamics at this site. Its arborescent life form enables it to function as a small tree.

The western edge of the study area comes within a few hundred feet of the present day lakeshore. In the southern portion, lower terrain and greater site moisture influence plant community composition. Grand fir dominates the tree canopy which is of moderate density (about 75% canopy cover). The understory contains a diversity of mesic species.

On the upland portions of the forest, the tree canopy is more continuous (80-90% cover) and contains a greater proportion of Douglas-fir. Understory cover is sparse except within the intermittent canopy openings.

Under ownership of the University of Montana since 1906, the forest has remained relatively free of man-caused disturbances. The last ground fire occurred in 1905 (pers. comm. Habeck 1984). The completion of Kerr Dam in 1936 raised the level of Flathead Lake and probably, the water table under the forest. Though the study area has never been logged, a few trees were removed from its eastern edge for a dock built in the early 1950's. In 1947, the draining of a swamp located at the southwest corner of the study area initiated the change of that area from a hydric to a more mesic environment. In the late 1960's, the construction of a trailer site, a gravel pit and a fire road destroyed portions of the north edge of the forest.

The major disturbances affecting the forest today are insect infestations and disease. Most of the pole-sized larch have been damaged or killed by the casebearer (*Coleophora laricella* [Hubner]) in the last decade and grand fir have been seriously weakened or killed by heart rot (*Echinodontium tinctorium*). Dwarfmistletoe (*Arceuthobium* spp.)
has weakened larch and Douglas-fir. The Douglas-fir beetle (*Dendoc
tonus pseudotsugae* Hopk.) has killed some of the Douglas-fir in recent years (Tunnock et al. 1984). The falling and defoliation of these insect- and disease-killed trees has created canopy openings scattered throughout the forest.

Late in the 1940's, twelve acres of the Yellow Bay forest were surveyed into a series of 50 by 50 ft units to facilitate mammal and bird censuses. In 1951, Jacqueline Arthur, a summer student, randomly selected fifteen of these plots for a vegetational study. Arthur's original data (plot maps) were preserved in the University of Montana's departmental files where they were discovered in 1983. These data provide the basis for this study of "real-time" succession.
CHAPTER 4
METHODS

Sampling Methods

In 1951, Arthur collected tree population data from 15 randomly chosen plots in the Yellow Bay inventory grid. Figure 4 illustrates the location of these plots within the grid. The total area sampled accounted for 7.65% of the grid. Arthur mapped the location of each tree, recording its species, vigor and size class. Size classes were divided as follows: 0-1 in, 1-3 in, 3-6 in, 9-12 in ... and so on. Arthur also recorded the shrubs and herbs present in the grid. A high correspondence between Arthur's maps and the current locations and sizes of trees indicated the 1951 data were of suitable quality for a long-term study.

Tree and shrub data also were available for 128 of the gridded plots for 1967. Eleven of the 128 plots were from the original set of permanent plots. Only six plots, however, had exact locations of trees mapped. As the 1967 maps did not correspond well to either the 1951 or the 1984 maps, these data were not used.

Numbered wooden stakes placed at 50 ft intervals throughout the grid and Arthur's original maps permitted the relocation of the 15 plots during the summer of 1984. If the stakes marking plot corners had been moved or lost, they were replaced. Plot corners were relocated by measuring from adjacent stakes. Arthur's maps helped to pinpoint locations by illustrating which trees were and were not in a plot. Also, many of the plots had corner trees that had been blazed and engraved with the
Figure 4. Successional study grid. Shaded squares represent location of permanent plots.

Total area equals 12.86 acres (5.20 ha)
stake number. Since many of the corner stakes were broken or hard to find, bright yellow, numbered stakes were driven into the corners of the resampled plots.

The numbering of stakes begins at the southeast corner of the grid area. Numbers run west for 15 stakes and then east for 15 stakes up to stake 255. Plot numbers follow the same pattern with plots 1 through 14 in row one, plots 15 through 28 in row two, etc.

Only 14 plots were resampled as one plot had been destroyed by the construction of a fire road at the north end of the grid. Using a dbh (diameter at breast height) tape, tree diameters were remeasured to the nearest .1 in. Present day maps of each plot were constructed to record each tree's location, diameter, and vigor. The presence of seedlings below breast height also was noted. The data are listed along with their x-y coordinates in the appendix.

Sampling included taking increment cores at breast height of healthy conifers of various sizes. Xylem rings were counted on cores to estimate the tree's age. Representative saplings, from outside the plots, were cut near the ground to determine age. The diameters of all trees and saplings were recorded to determine age-size relationships, if any existed.

Each vascular understory species on each plot was assigned one of the following cover classes (Pfister et al. 1977, as modified from Daubenmire 1959): ' + ' = a species in the stand, but not in the plot, T = 0-1%, 1 = 1-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-95%, and 6 = 95-100%.

Forest overstory density was measured using a spherical densiometer. Four overstory readings; facing north, east, south and west;
were taken from the center of each plot's four quarters. The average of these 16 values determined the overstory density for each plot.

Site moisture stress was evaluated by measuring pre-dawn xylem potentials with a portable pressure bomb (PMS Instrument Co., Corvallis, OR). This technique accounts for the three factors influencing plant moisture stress: soil moisture stress, atmospheric stress, and the plant's ability to control water loss (Waring and Cleary 1967). To measure the tension that a plant's vascular system is under—an indicator of internal water stress—a severed twig is placed in the chamber with its cut end protruding and pressure is exerted on the leaves until moisture rises to the cut surface. The pressure at which moisture is first observed is equal in magnitude to the tension which was initially in the plant's vascular system (Waring and Cleary 1967).

Five grand fir were sampled for moisture stress on each plot. The average size of the trees sampled was 14 cm (dbh). One branchlet was clipped from each tree at 1.2 to 2.4 m height and its xylem potential measured. Grand fir were selected because individuals with accessible branches occurred on all plots. To maximize moisture stress, the fourteen plots were sampled after a two to three week mid-summer dry period. To minimize change in moisture stress, a sampling session was aborted if it rained before the session was complete. Once these requirements were met, sampling took three nights (8/19/84-8/21/84), working between 0200 M.S.T. and dawn.
Methods of Data Analysis

Demographic Changes

Tree population data were used to calculate species recruitment, growth and mortality since 1951. Data were presented as absolute numbers of, e.g., recruitments and mortalities, and as rates, i.e., as a proportion of the number recruited or dead in relation to the 1951 total. The above calculations were made using number and basal area of individuals. Total basal area growth included basal area of recruited trees (ingrowth) and growth of trees alive since 1951. The net change in numbers (absolute and rates) of each species was calculated by subtracting mortalities from recruitments. Net basal area change was calculated as the total basal area growth minus the basal area lost to mortality.

These values, calculated for each species, were computed at the forest level (all plots combined), for each of the two successional pathways (plots separated into two groups) and for each plot individually.

The thirty-three year birth/growth rates were converted to ten-year birth/growth rates (for easier comparison to other studies) using the following compound interest formula:

\[ B_{10} = \left(1 + B_{33}\right)^{10/33} - 1 \]

where \( B_{10} \) is the 10-year birth/growth rate and \( B_{33} \) is the 33-year birth/growth rate.

Ten-year mortality rates were calculated from the 33-year rate.
using a negative compound interest formula (McCune and Cottam 1985):

\[
Q_{10} = 1 - (1 - Q_{33})^{10/33}
\]

where \(Q_{10}\) is the 10-year mortality rate and \(Q_{33}\) is the 33-year mortality rate.

Ordination

**Introduction.** Ordination is a valuable tool in understanding plant succession and has been used to display basic successional trends (Huschle and Hironaka 1980). Through ordination, samples (or species) are arranged in abstract ecological space based on one or more attributes, e.g. species composition (Beals 1984). The closeness of two samples in space directly relates to the similarity of the samples (Gauch 1982). By reducing the dimensionality of ecological space and by finding major axes of variation through the cluster of samples, ordination clarifies major patterns of variation (Beals 1984).

To interpret patterns of variation, environmental variables are superimposed on the ordination. Environmental factors, however, may be highly correlated to each other and the influences of each difficult to separate. The ordination itself reflects these integrated environmental factors, as well as biotic and historical factors, as the community responds to them (Beals 1984).

Although the original Bray-Curtis (1957) technique has been criticized, the current form incorporates many improvements and options, making it "one of the most successful and appropriate means of multivariate analysis of phytosociological data" (Beals 1984).
Detrended correspondence analysis (DCA) is an eigenvector ordination technique (Hill and Gauch 1980) which has been successfully used to evaluate successional pathways occurring in stands (Hann 1982).

**Methodology.** Both Bray-Curtis (1957) ordination and detrended correspondence analysis, as presented in the computer programs BCORD (W. Post unpublished program) and DECORANA (Hill 1979), respectively, were used in this study. Both programs offer a variety of options for constructing an ordination. Dominance of tree species was used to ordinate samples because it is a better predictor of indicators of tree productivity, such as leaf area (McCune and Allen 1985).

In the Bray-Curtis (1957) ordination, plot totals were relativized to 100 to reduce the effect of total amount of vegetation on the ordination pattern. Dissimilarity between plots was calculated using Sorenson's coefficient: \(1 - \frac{2W}{A+B}\), where \(A\) = the sum of values for one plot, \(B\) = the sum of values for the other plot, and \(W\) = the sum of the lower value for each attribute common to both plots. Kessell and Whittaker (1976) found this coefficient performed better than the other tested distance measures. Axis endpoints were selected using variance-regression (Beals 1984). Of all endpoint-selection techniques using real samples as endpoints, variance-regression is the most satisfactory and tends to give more interpretable results (Beals 1984). In the detrended correspondence analysis, plot totals were also relativized to 100, axes were rescaled, and 26 segments were used in detrending.

Four sets of ordinations were constructed with the 1951 and the 1984 data. Three ordinations were based on (1) the dominance of all sizes of trees, (2) the dominance of trees in the understory (1-6" dbh) and (3) the dominance of trees in the overstory (greater than 6" dbh).
Although a tree does not necessarily enter the overstory when it reaches six inches in diameter, this dividing point allows the comparison of vegetation dynamics in the smaller size classes with those in the larger size classes. The fourth ordination compared 1951 understory and 1984 overstory compositions to see if vegetational trends might have been predicted from the 1951 understory composition.

In all ordinations, species dominance was correlated to axes and was superimposed on the ordination to determine if dominant species occupied distinct parts of ecological space. Pearson product-moment correlation and Kendall's rank-order correlation were used for dominance data. Environmental and community variables were correlated to the ordination axes using Pearson product-moment correlation. These variables included site moisture stress; birth, growth, and mortality rates; and maximum grand fir size on each plot.

As aging of the large grand firs by increment coring was not possible due to extensive heart rot, the diameter of the largest grand fir was used to approximate a plot's successional age. Grand fir, the only tree species present on all the plots, was the prime candidate for measurement of this parameter. Though size has been shown to have a limited relationship to age, a graded series of sizes does have some successional significance (Daubenmire 1968).

The ordination of 1951 and 1984 data together allowed the construction of successional vectors (sensu Goff and Zedler 1972). A successional vector connected each 1951 sample point with its corresponding 1984 sample point. Each vector illustrates a compositional shift in species dominance on a plot over the 33-year period. These vectors were examined to determine which plots are converging on the same point in ecological space, i.e., the same species composition.
Discriminant Analysis

Introduction. Discriminant analysis was used to distinguish between groups of plots which seemed to be following two different successional pathways, i.e., heading towards one of two points in species composition.

Discriminant analysis, a parametric statistical technique, weights and linearly combines the discriminating variables to make groups of cases as distinct as possible. This technique can be used to determine if two subjectively chosen groups are indeed statistically different, to study the spatial relationship among groups and to predict to which group a case belongs (SPSS 1983). Groups can be discriminated among by species composition or environmental data (McCune 1983).

Methodology. Two groups, following two distinct successional pathways, were apparent from the ordination results. These two pathway groups were differentiated on the basis of species dominance for 1951 and 1984, for all size classes combined and for understory and overstory separately. Environmental data were also used to differentiate between groups in 1984 (all size classes combined). The variables used to distinguish groups were entered directly to compare the discriminating power of the attributes (McCune 1983).

The degree of group differentiation for the year-size classes was compared using canonical correlations and the significance of the $\chi^2$. The relative contribution of each species to the function was determined by its standardized discriminant function coefficient and the significance of its F-ratio (Nie et al. 1975).
T-Tests

To further analyze differences between the two groups of plots t-tests were used. Group means of site moisture, species dominances and various community factors were compared and the significance of the differences were tested. As Student's $t$ was used to test the null hypothesis that the group means for each variable were equal, two-tailed probabilities were calculated. When variances for the two groups were equal ($P > .05$), $t$ was based on pooled variances. For unequal variances, $t$ was calculated using separate variances (Nie et al. 1975).
CHAPTER V
RESULTS

Forest-level Dynamics

Forest-level analyses indicated each species' relative success at establishment and growth since 1951 and suggested how each species might influence future forest dynamics. The total number of trees and basal area for each species in 1951 and 1984 suggested the relative importance of each species and how that has changed (Table 1). Changes in species' densities and dominances were compared using rates of change (Table 2). Rates indicate how a species' population or total basal area has changed relative to the initial number or amount. Birth, ingrowth, growth and mortality rates were calculated to determine the cause of a species' net increase or decrease in importance. Net population growth rates are calculated from recruitment and mortality rates and are based on numbers of individuals. Net basal area growth rates are the sum of ingrowth, growth and mortality rates.

From 1951 to 1984, forest tree density decreased and total basal area increased. All tree species except grand fir decreased in density, though grand fir increased only slightly. Four species—grand fir, Douglas-fir, maple and spruce—increased in dominance while the other five—ponderosa pine, larch, birch, willow and alder—diminished. Grand and Douglas-fir led the species in increases in relative dominance while larch suffered the greatest losses (Table 1).
Table 1. Forest-level changes in species numbers and basal areas. Values listed under 'Total Number of Trees' and 'Total Basal Area' are sums for the total area sampled (.8035 acres).

<table>
<thead>
<tr>
<th>Species</th>
<th>Total Number of Trees</th>
<th>Total Basal Area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1951</td>
<td>1984</td>
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<tr>
<td>Grand fir</td>
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<tr>
<td>Maple</td>
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<tr>
<td>Spruce</td>
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<td>18</td>
</tr>
<tr>
<td>Willow</td>
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<td>9</td>
</tr>
<tr>
<td>Alder</td>
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<td>6</td>
</tr>
<tr>
<td>Larch</td>
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<td>4</td>
</tr>
<tr>
<td>Ponderosa pine</td>
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<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1106</td>
<td>746</td>
</tr>
<tr>
<td>Species</td>
<td>Recruitment Rate</td>
<td>Mortality Rate</td>
</tr>
<tr>
<td>-----------------</td>
<td>------------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Grand fir</td>
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<td>.19</td>
</tr>
<tr>
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<tr>
<td>Ponderosa pine</td>
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<td>.42</td>
</tr>
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</table>

Table 2. Forest-level demography. Values are a proportion of the number of trees or amount of basal area present in 1951. Rates are adjusted to a 10-year basis.
Grand fir had the greatest recruitment rate and lowest mortality rate of the species present. In terms of basal area, it had the greatest net growth rate. Although grand fir's ingrowth rate (.03) was below that of maple, willow and birch, its net growth surpassed these species' because of growth and mortality rates. The growth rate of existing grand firs (.24) was the highest of all species and their mortality rate (.07) was one of the lowest. These recruitment and net growth rates indicate that grand fir will continue to be a major component of reproduction and small size classes and a major influence in the forest.

Douglas-fir reproduced very little since 1951. Most individuals belong to larger size-classes. Douglas-fir had the third highest net population growth of the species. Its success was due to its longevity—it had the second lowest mortality rate (.30)—not to its recruitment rate. Only two new stems, both recent recruits under one inch diameter, have survived since 1951. The growth rate of existing Douglas-firs (.20) and their low mortality rate (.07) accounted for Douglas-fir's net basal area growth rate (.13)—the second highest. If the standing Douglas-firs are not replaced, size-class structure will shift to larger and larger classes and Douglas-fir's role in the forest will diminish as these older trees die.

Maple, with the greatest rate of basal area ingrowth, was a stable component of the forest community. In terms of numbers of trees, maple had the fourth highest net population growth rate (-.32). Relative to the other species, maple had moderate recruitment (.07) and mortality (.39) rates. After grand fir and Douglas-fir, maple had the next greatest net growth rate in basal area. Maple's healthy ingrowth rate (.28)
reflects its ability to resprout and grow in low light levels. The high rate of ingrowth combined with a moderate growth rate (.18) and an average mortality rate (.33) ensures maple a continuing role in forest dynamics.

The spruce population consists mostly of older, persisting trees. Though some reproduction has occurred, only six new stems have survived since 1951 and two of these were less than one inch diameter. In spite of its low recruitment rate (.04), spruce's low mortality rate (.31)—relative to the other species—resulted in the third highest net population growth rate. Its net basal area growth rate is the fourth highest. Spruce's growth rate (.22) was second only to grand fir and its mortality rate (.16) was relatively low. Low ingrowth and recruitment indicate that spruce will persist only in scattered occurrences, if the current disturbance regime continues.

Larch and ponderosa pine experienced high mortality with no recruitment. Neither species produced any surviving new stems since 1951. Larch's net rate of basal area growth (-.37) was a function of its mortality rate (.38) and its nominal growth rate (.01). An outbreak of larch casebearer caused larch's unexpectedly high mortality rate. Though ponderosa pine had greater net growth (-.11), its growth rate (.11) was due to the growth of only one remaining pine. In the absence of a major disturbance, the larches and the ponderosa pine will soon cease to play a role in forest dynamics, except for their roles in creating canopy gaps for the regeneration of other species.

Birch, with a low recruitment rate (.02) and a high mortality rate (.43), had a net population growth rate of -.41. Relative to the other species, its ingrowth rate was average (.05), its growth rate low (.10)
and its mortality rate high (.38). These rates of change in basal area reflect birch's short longevity and shade intolerance and indicate that birch will enter into forest dynamics infrequently and for only short periods of time.

Willow and alder, very short-lived species, had the lowest net population growth rates (-.87 and -.89, respectively). Their relatively high recruitment rates (.13 and .11) were a function of the small number of stems that were present in 1951 (9 of willow and 6 of alder). Both have mortality rates of 1.00. As no individuals survived over the 33-year period, all basal area growth was due to ingrowth. With 100% mortality, these short-lived species persist only briefly in the course of succession.

Plot-level Dynamics

Ordination of Data for all Size Classes

1951 and 1984 Ordination. By ordinating 1951 and 1984 species dominances of the fourteen plots, plot compositions were compared and their differences related to environmental and community variables (Figure 5). In the ordination of tree dominance for 1951 and 1984, the first two axes extracted 76.49% of the information in the data matrix. Construction of a third axis extracted little additional information from the data matrix (12.08%) and separated only plot 35 from the other plots. This axis was highly correlated to ponderosa pine ($r^2 = .67$, tau = .43)—a species present only on plot 35. As the variation along the axis related to a single event—the establishment of a ponderosa pine—and not a major vegetational trend, two axes give the best
Figure 5. Ordination of plot compositions for 1951 and 1984. Plot positions are based on relative dominances of species.
ordination of the 14 plots. The first axis of the ordination of 1951 and 1984 data represents a moisture gradient. When moisture stress data (available only for 1984 plots) were correlated to the position of the 1984 plots in the ordination, moisture stress accounted for 38% (P<.01) of the variation in species composition.

Axis one related to Douglas-fir (r^2 = .47, tau = -.63) (Figure 6), paper birch (r^2 = .79, tau = .56) and Engelmann spruce (r^2 = .43, tau = .59) (Figure 7) dominances. Douglas-fir was associated with the drier end, birch and spruce with the moister end of the moisture gradient.

Tree mortality (r^2=.64 (+), P<.01) and net growth (r^2 = .44, (-), P<.01) rates, calculated using basal areas, were also correlated to the first axis. Species associated with wetter sites, e.g. birch, alder and willow, have shorter lifespans than other species present, and thus greater mortality rates. Net growth (growth + ingrowth - mortality) rates were greater on the drier plots where the mortality rate was lower.

Axis two was correlated with grand fir (r^2 = .75, tau = -.77) and Douglas-fir (r^2 = .43, tau = .40) dominances (Figure 6). Grand fir was associated with the older end and Douglas-fir with the younger end of this axis.

The second axis of the ordination represents an age gradient. Maximum tree (Abies grandis) size on each plot was correlated to this axis for 1951 (r^2 = .39 (-), P<.01) and for 1984 (r^2 = .57 (-), P< .001). Plot 182, at the "young" end of this axis, underwent a massive dieback of trees since 1951 and now contains much tree regeneration and lush undergrowth in the resultant gap. Plot 182 has the lowest overstory canopy density (65%) of all the study plots. Plot 59, at the
Figure 6. Overlay of Douglas-fir (A) and grand fir (B) relative dominances on plot ordination.
Figure 7. Overlay of birch (A) and spruce (B) relative dominances on plot ordination.
"older" end of the axis, is characterized by a dense tree canopy (90%) and sparse understory. Plot 59 is the only plot to have not produced any surviving new recruits of any species since 1951.

Basal area growth rate was negatively correlated to this axis ($r^2 = .45, P<.01$) (1951); ($r^2 = .39, P<.01$) (1984), which can be partially explained by its correlation to maximum tree diameter ($r^2 = .40, P<.01$). Larger trees, more prevalent on older plots, add more basal area per unit of diameter gained than smaller trees, under similar environmental conditions.

DECORANA did not give significantly different results from BCORD. Though the axes chosen were arranged differently in species space, the relationship between plots remained the same. As stand dispersal was slightly better in BCORD, only BCORD was used in these analyses.

The two-dimensional ordination (Figure 5) illustrates compositional differences of the fourteen plots. In the following description, plot numbers include a plot's composition in both 1951 and 1984 unless one year is specified, e.g. plot 13-1951. Most of the plots located in the northern, drier portion of the study site (69, 91, 99, 113, 117-1981, 173, 188) are grouped in the ordination because they all contain moderate amounts of Douglas-fir and grand fir (Figure 6). The driest plot (182) is found slightly above the other dry plots in the ordination due to its greater dominance of Douglas-fir. Plots 1, 11-1984, 59, 117-1951 and 122, all high in grand fir dominance and moderate in site moisture, are grouped in the lower, central portion of the ordination. Alone near the center of the ordination, plot 35 is distinguished by its ponderosa pine dominance. The plots located on the wetter (11-1951) and wettest (13) portions of the study area are grouped by their birch dominance at
Compositional differences of the plots relate to moisture and age gradients. The driest plots had the greatest dominance of Douglas-fir and the wettest plots had the greatest birch dominance. Grand fir dominance peaked in the intermediate moisture range. In terms of successional age, the "youngest" plots (11-1951, 13, 182), located in the western, more open portion of the study area, contained greater amounts of less tolerant seral species—either birch or Douglas-fir. In contrast, the "oldest", i.e., the least recently disturbed, plots (1, 59, 117, 122) contained more grand fir and were located in the area of densest canopy cover.

**Successional Vectors.** Vegetational trends were evaluated by comparing plot composition between 1951 and 1984. Successional vectors identified the direction of vegetation change in each plot, in terms of increasing or decreasing species compositions. Each successional vector originated at a plot's ordination position in 1951 and ended at the same plot's position in 1984. (Figure 8).

The vectors of eight plots (69, 91, 99, 113, 117, 173, 182, 188) converge at the left center section of the ordination, an area of similar grand fir and Douglas-fir relative dominance. Species dominance on most of these plots increased in grand fir [\(\bar{X}\) (mean change) = .065, \(N = 8\)] and Douglas-fir [\(\bar{X} = .11, N = 8\)] relative dominances. The only decreases in relative dominance of these species were very small.

The vectors of the other six plots are more widely dispersed, but still converge at a point in the lower center of the ordination. These plots generally increased in grand fir dominance and decreased slightly in Douglas-fir dominance.
Figure 8. Successional vectors. Vectors originate at a plot's species composition in 1951 and end at its composition in 1984. Species codes indicate regions high in relative dominance: ABGR = Abies grandis, PSME = Pseudotsuga menziesii, BEPA = Betula papyrifera, PIEN = Picea engelmannii.
These two groups of plots, each converging on a different area in species space, were assigned to two potential pathway groups. Group A includes the six moist, southern plots converging toward high grand fir dominance and group B includes the eight dry, northern plots converging toward Douglas-fir and grand fir codominance (Figure 4).

These analyses reveal the major compositional differences between the two groups of plots to be in Douglas-fir and spruce relative dominances. As the recruitment of both of these species has been very low, it hardly seems that they will be discriminating factors in the future.

**Convergence.** If the vegetation in the fourteen study plots is converging towards one or two common compositions, the similarity among plots should be higher in 1984 than in 1951. In the plot ordination (Figure 5), the 1951 plots are more widely dispersed than the 1984 plots. A closer look at Figure 5 reveals the greatest dissimilarity along the first axis to be between 1951 plots. As site moisture stress explains over one-third of the variation along this axis, the movement of vectors (Figure 8) toward the axis' center indicates that a shift toward more mesophytic species accompanied the convergence in species composition. Since the second axis relates to an age/size gradient, the greatest dissimilarity along this axis is between a 1951 and a 1984 plot.

**Discrimination of Pathway Groups for All Size Classes**

Discriminant analysis (DA) and t-tests were used to quantify compositional, environmental and community differences between the two groups of plots. The fourteen plots were assigned to one of two "pathway" groups as described in the ordination results. DA tested the
significance of the difference between these two groups and identified the factors most important in separating groups.

Using data combined for all size classes, discriminant analysis was only marginally successful in separating groups (Table 3). Douglas-fir and spruce were the most powerful variables in separating the groups at both sampling times (Table 4). The greater significance of group separation in 1984 over 1951 suggests that the fourteen plots may indeed be converging toward two regions of species composition space—one of grand fir dominance and one of grand fir—Douglas-fir codominance.

In addition to the compositional differences determined by DA, t-tests revealed significant differences in moisture stress (excluding plot 35), in birch growth and in overall tree mortality (Table 5). Because of the small number of plots in each group, only strong differences were significant at the .05 level. Therefore the difference in moisture stress of the two groups (P=.10) may be due to an actual difference rather than chance. Excluding plot 35 from the analysis increased the significance of the difference to .03. Plot 35 was removed because it had the most ambiguous group membership.

The t-test results indicated that group B plots were located in drier regions of the study area than group A plots. Compositional differences of the two groups support this moisture difference. Birch, typical of moister areas, grew better on group A plots (P=.08). Spruce, also favoring moist sites, had greater relative dominance and recruitment on group A plots. Douglas-fir, typical of drier sites, had greater dominance and growth on group B plots. In addition, group A plots suffered a greater average number of overall mortalities, possibly because more of the short-lived species, e.g., birch, willow and alder, grew on the moister plots.
Table 3. Discriminant analysis of two pathway groups, 1951 and 1984. A higher canonical correlation indicates greater group separation.

<table>
<thead>
<tr>
<th>Year</th>
<th>Canonical Correlation</th>
<th>$x^2$</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1951</td>
<td>.83</td>
<td>9.75</td>
<td>.2032</td>
</tr>
<tr>
<td>1984</td>
<td>.89</td>
<td>12.85</td>
<td>.1170</td>
</tr>
</tbody>
</table>

Table 4. Standardized discriminant function coefficients for separating pathway groups. F-ratios indicate species' relative contributions to group separations.

<table>
<thead>
<tr>
<th>Species</th>
<th>Function 1 '51</th>
<th>Function 1 '84</th>
<th>F-Ratio '51</th>
<th>F-Ratio '84</th>
<th>Significance '51</th>
<th>Significance '84</th>
</tr>
</thead>
<tbody>
<tr>
<td>Douglas-fir</td>
<td>1.49</td>
<td>2.69</td>
<td>10.63</td>
<td>32.07</td>
<td>.0068</td>
<td>.0001</td>
</tr>
<tr>
<td>Spruce</td>
<td>.11</td>
<td>0.45</td>
<td>3.33</td>
<td>7.76</td>
<td>.0929</td>
<td>.0165</td>
</tr>
</tbody>
</table>
Table 5. T-test results for comparison of two pathway groups

<table>
<thead>
<tr>
<th>Category</th>
<th>Variable</th>
<th>Group</th>
<th>n</th>
<th>Group Mean</th>
<th>Std. Error</th>
<th>t</th>
<th>Prob-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site Moisture</td>
<td>All Plots</td>
<td>A</td>
<td>6</td>
<td>150.50</td>
<td>11.14</td>
<td>-1.76</td>
<td>.10</td>
</tr>
<tr>
<td>Stress (p.s.i.)</td>
<td></td>
<td>B</td>
<td>8</td>
<td>169.75</td>
<td>4.61</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Without</td>
<td>A</td>
<td>5</td>
<td>143.80</td>
<td>10.90</td>
<td>-2.53</td>
<td>.03</td>
</tr>
<tr>
<td>Stress (p.s.i.)</td>
<td></td>
<td>B</td>
<td>8</td>
<td>169.75</td>
<td>4.61</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douglas-fir 1984</td>
<td>Rel Dom</td>
<td>A</td>
<td>6</td>
<td>.06</td>
<td>.04</td>
<td>-5.89</td>
<td>.00</td>
</tr>
<tr>
<td>Douglas-fir 1984</td>
<td></td>
<td>B</td>
<td>8</td>
<td>.48</td>
<td>.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total BA 1951</td>
<td></td>
<td>A</td>
<td>4</td>
<td>151.29</td>
<td>71.61</td>
<td>-2.81</td>
<td>.02</td>
</tr>
<tr>
<td>(in²/plot)</td>
<td></td>
<td>B</td>
<td>8</td>
<td>460.73</td>
<td>68.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce 1984</td>
<td>Rel Dom</td>
<td>A</td>
<td>6</td>
<td>.09</td>
<td>.03</td>
<td>3.13</td>
<td>.03</td>
</tr>
<tr>
<td>Spruce 1984</td>
<td></td>
<td>B</td>
<td>8</td>
<td>.001</td>
<td>.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total BA 1951</td>
<td></td>
<td>A</td>
<td>4</td>
<td>170.81</td>
<td>50.07</td>
<td>3.15</td>
<td>.05</td>
</tr>
<tr>
<td>(in²/plot)</td>
<td></td>
<td>B</td>
<td>1</td>
<td>13.20</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>New</td>
<td></td>
<td>A</td>
<td>3</td>
<td>2.00</td>
<td>.57</td>
<td>3.46</td>
<td>.07</td>
</tr>
<tr>
<td>New</td>
<td></td>
<td>B</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>New BA 1951</td>
<td></td>
<td>A</td>
<td>3</td>
<td>5.81</td>
<td>.97</td>
<td>6.02</td>
<td>.03</td>
</tr>
<tr>
<td>(in²/plot)</td>
<td></td>
<td>B</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birch</td>
<td>BA Growth</td>
<td>A</td>
<td>5</td>
<td>102.64</td>
<td>31.82</td>
<td>2.26</td>
<td>.08</td>
</tr>
<tr>
<td>(in²/plot)</td>
<td></td>
<td>B</td>
<td>5</td>
<td>27.74</td>
<td>9.16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree 1951</td>
<td>Number Lost</td>
<td>A</td>
<td>6</td>
<td>64.00</td>
<td>7.34</td>
<td>2.26</td>
<td>.04</td>
</tr>
<tr>
<td>Mortality</td>
<td></td>
<td>B</td>
<td>8</td>
<td>43.25</td>
<td>5.74</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Relative Dominance
2Basal Area

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The major differences in species composition of the two groups were in total numbers of individuals and total amounts of basal area of a species, not in rates of change. Species ingrowth, growth and mortality rates were not significantly different in the two groups. Due to the small number of plots in each group, many subtle or even moderate differences between the two groups may not be substantiated by statistical tests. Further comparison of species’ demographics and basal area dynamics revealed additional information (Table 6).

From 1951 to 1984, group A plots had greater net growth of grand fir while group B plots had much greater net growth of Douglas-fir. Grand fir's advantage on A plots came mostly from the growth of existing trees. A higher growth and lower mortality rate for Douglas-fir accounted for Douglas-fir's greater net growth rate on B plots. Group A plots demonstrated a much higher net growth rate of grand fir compared to Douglas-fir. On B plots, the net growth rates of the two species were similar, suggesting a codominant relationship.

Ordination of Data by Size Class, 1951 and 1984

Though the understory may indicate the future composition of a forest, this information can not be attained from an ordination combining all size classes. The contribution of large trees to species dominance overshadows that of small trees. To see how vegetational trends in the understory might differ from those in the overstory, successional vectors were constructed for understory and overstory dominance data separately.
Table 6. Pathway demography. Rates are adjusted to a 10-year basis.

<table>
<thead>
<tr>
<th>Pathway</th>
<th>Numbers</th>
<th>Basal Area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Recruitment Rate</td>
<td>Mortality Rate</td>
</tr>
<tr>
<td>Grand fir</td>
<td>0.18</td>
<td>0.11</td>
</tr>
<tr>
<td>Maple</td>
<td>0.05</td>
<td>0.08</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>0.00</td>
<td>0.01</td>
</tr>
<tr>
<td>Birch</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Spruce</td>
<td>0.04</td>
<td>--</td>
</tr>
</tbody>
</table>
Overstory Ordination. The ordination of overstory dominance data was not appreciably different from the ordination of all size classes together (Figure 9). This ordination did, however, clarify plot relationships as species dominances, maximum tree size and site moisture stress had stronger correlations to the axis scores.

Site moisture stress \(r^2 = .40, P = .009\) and Douglas-fir dominance \(r^2 = .49, \tau = -.62\) had slightly higher correlations to the first axis. Also, the position of group A plots along the first axis was significantly different from the position of group B plots, both in 1951 \((t = 3.03, P = .03)\) and in 1984 \((t = 4.07, P = .01)\). The second axis of the ordination was more strongly correlated to grand fir dominance \(r^2 = .83, \tau = .76\) and less correlated to Douglas-fir dominance \(r^2 = .39, \tau = -.41\). Successional age showed a stronger correlation to the second axis of the overstory ordination \(r^2 = .66 (+), P < .001\) compared to that of the ordination of all size classes together.

Successional vectors for the overstory data converged in two regions of species space. Five of the six plots in group A \((1, 11, 35, 59, 122)\) converged in an area characterized by high grand fir dominance. The influence of the other species on the overstories of these plots is diminishing. Plot 13, the sixth plot, increased in birch dominance. This plot, located in the southwest corner of the ordination, is part of a former marsh. Grand fir is currently invading the plot from the adjacent forest, but none has yet entered the plot's overstory. Birch comprises the entire overstory. The successional vectors of group B plots converge in a region of dominance shared between grand fir and Douglas-fir. The overstory ordination suggested that 13 of the 14 plots are converging towards one of two species.
Figure 9. Ordination of plots using overstory dominance. Vectors connect 1951 species composition with 1984 composition. Species codes indicate regions high in relative dominance: ABGR = *Abies grandis*, PSME = *Pseudotsuga menziesii*, BEPA = *Betula papyrifera*, PIEN = *Picea engelmannii*. 
compositions—grand fir dominance or dominance equally divided between grand fir and Douglas-fir. The fourteenth plot (13) is in a relatively early stage of development compared to the other plots and therefore is not yet converging toward a similar species composition.

**Understory Ordination.** Ordination of understory dominance data (Figure 10) revealed successional trends not evident from the ordination of all size classes combined.

The first axis of the ordination was correlated to grand fir \((r^2 = .76, \tau = -.68)\) and to birch \((r^2 = .85, \tau = .78)\) dominance. Though the left endpoint on this axis (plot 13-1951) had the lowest moisture stress, this axis is not significantly correlated to site moisture stress \((r^2 = .19, P = .06)\). This axis separated out those plots having birch dominant. High birch dominance occurs in three plots in 1951 but only in one (plot 13) in 1984.

The second axis separated plots mainly on the basis of their larch \((r^2 = .81, \tau = .46)\) and Douglas-fir \((r^2 = .84, \tau = .53)\) dominances. The only plots with appreciable amounts of these species in their understory were 1951 plots. This axis did not relate to any of the measured environmental or community variables.

The third axis was highly correlated to maple dominance and succeeded in separating 1984 plots 1 and 182 from the rest of the plots. Over the 33-year period, these two plots increased in maple relative dominance by .44 and .65 respectively.

Most of the successional vectors, regardless of group membership, converge in the left bottom corner of the ordination. This area is strongly dominated by grand fir. The vectors of three plots (1, 99, 117) point away from this region. Plots 99 and 117 increased in birch
Figure 10. Ordination of plots using dominance of trees in the understory. Vectors connect 1951 species composition with 1984 composition. Species codes indicate regions high in relative dominance: ABGR = Abies grandis, PSME = Psuedotsuga menziesii, BEPA = Betula papyrifera, LAOC = Larix occidentalis.
dominance by .24 and .20 respectively and plot 1 increased in maple dominance. Maple and birch are surviving in the understory in isolated cases. Thus, the major successional trend is toward an increase of grand fir dominance in the understory, regardless of pathway group.

**Discrimination of Pathway Groups in Size Classes**

The ordinations of understory and overstory data indicated that groups A and B displayed distinctly different vegetational trends in the overstory, but not in the understory. Discriminant analysis (DA) of the two groups for each of the combinations of stratum and year quantified the relative degrees of group separation. The degree of separation in 1984 versus that in 1951 indicated whether or not the two groups of plots were converging toward two different species compositions. DA also quantified the relative importance of each species in 1951 and 1984 group separations.

Group separation was significant in both the 1951 and the 1984 overstories and in the 1951 understory (Table 7). In the discriminant analysis of the 1984 understory, the separation of the two pathway groups was not successful.

The 1984 overstory displayed the greatest difference in species composition of the two groups. Douglas-fir and spruce were the key variables in discriminating groups, both in the 1951 and the 1984 overstories. The separating power of these two species, as expressed by the significance of their F-ratios, was greater in 1984 (Table 8).

Species compositions of the two pathway groups were the most similar in the 1984 understory. The power of species to discriminate the plots into two distinct groups decreased (Table 9). Maple contri-
Table 7. Discriminant analysis of two pathway groups by year- and size-class. A higher canonical correlation indicates greater group separation.

<table>
<thead>
<tr>
<th>Year</th>
<th>Canonical Correlation</th>
<th>$\chi^2$</th>
<th>Significance</th>
<th>Canonical Correlation</th>
<th>$\chi^2$</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>.95</td>
<td>20.49</td>
<td>.0023</td>
<td>.71</td>
<td>6.21</td>
<td>.3998</td>
</tr>
</tbody>
</table>
buted to group separation in 1951 but had become ubiquitous by 1984. Larch had disappeared from the understory by 1984, and so, ceased to be an influence in separating groups.

DA indicated that the separation of plots into two pathway groups hinged on the differential dominance of Douglas-fir and spruce in the two groups. The growth of the large, long-lived Douglas-fir increased group separation in the overstory from 1951 to 1984. Analysis of the 1984 understory indicated that compositional differences between the two groups may diminish.

Douglas-fir did not impact group separation in the understory in 1951 or in 1984. Since 1951, only two Douglas-firs were successfully recruited. Both still small and vulnerable, they have little chance of survival. Spruce contributed the most to group separation in both years. Even though spruce became established only in group A, its numbers were too few to affect group separation significantly.

Although the grand fir-dominated understory suggests that group separation will eventually diminish as the overstory Douglas-firs are replaced, the Douglas-fir codominance on group B plots may continue for a couple hundred years. The oldest Douglas-firs on these plots were about 170 years old. Douglas-firs live up to 400 years in western Montana (pers. comm. Habeck 1986). In lieu of any disease or insect outbreak directed toward Douglas-fir, Douglas-fir could predictably separate group A from group B plots for 230 more years. If a major disturbance opens the dry end of stand, Douglas-fir recruitment might also perpetuate Douglas-fir—grand fir codominance.
Table 8. Standardized discriminant function coefficients for separating pathway groups in overstory dominance data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Function 1</th>
<th>F-Ratio</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>'51 '84</td>
<td>'51 '84</td>
<td>'51 '84</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>1.42 2.09</td>
<td>19.98 32.91</td>
<td>.0008 .0001</td>
</tr>
<tr>
<td>Spruce</td>
<td>-.21 -.04</td>
<td>4.16 10.33</td>
<td>.0641 .0074</td>
</tr>
</tbody>
</table>

Table 9. Standardized discriminant function coefficients for separating pathway groups in understory dominance data. F-ratios indicate species contributions to group separation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Function 1</th>
<th>F-Ratio</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>'51 '84</td>
<td>'51 '84</td>
<td>'51 '84</td>
</tr>
<tr>
<td>Spruce</td>
<td>.23 -.02</td>
<td>3.23 2.70</td>
<td>.0975 .1265</td>
</tr>
<tr>
<td>Maple</td>
<td>.11 3.66</td>
<td>2.67 .0005</td>
<td>.1279 .9818</td>
</tr>
<tr>
<td>Larch</td>
<td>5.60 --</td>
<td>1.35 --</td>
<td>.2685 --</td>
</tr>
<tr>
<td>Grand fir</td>
<td>3.95 4.43</td>
<td>1.17 .56</td>
<td>.2999 .4697</td>
</tr>
</tbody>
</table>
Successional Trends: Inferred vs. Actual

To determine if understory composition could be used to predict successional trends, species dominances of the 1951 understory were compared to those of the 1984 overstory. This comparison was illustrated with Bray-Curtis ordination using a pair of successional vectors for each plot (Figure 11). Both vectors of a pair originate at the 1951 overstory dominance. One vector leads to 1951 understory dominance (representing inferred change) and the other leads to 1984 overstory dominance (representing actual change). The length and direction of the two vectors were compared for the 14 plots. Vector length indicates the relative rate of change in species composition. The direction of a vector indicates differences in species compositions. Interpretation of a vector's direction was based on the correlation of species dominances to the axis scores. The first axis was correlated to grand fir dominance ($r^2 = .69$, $\tau = -.64$) and to Douglas-fir dominance ($r^2 = .62$, $\tau = .61$). The second axis was strongly correlated to birch dominance ($r^2 = .82$, $\tau = .65$).

The vector pairs of seven of the eight plots in group B show similar characteristics. Vectors connected to the 1951 understory are longer than the vectors connected to the 1984 overstory. The shorter overstory vector suggests that the rate of compositional change was less than predicted from the 1951 understory composition. In contrast, plot 182 underwent greater change in species composition in 33 years than predicted by its 1951 understory composition. Most of these vectors point left, toward the area of the ordination dominant in grand fir. The longer understory vector reflects the greater amount of grand fir in the 1951 understory compared to the 1984 overstory. Two of the over-
Figure 11. A comparison of predicted (inferred) vs. actual change in species composition. Plot positions are based on relative dominances of species.
story vectors point right, indicating an increase in Douglas-fir since 1951. Except for plot 182, understory vectors point slightly upward and overstory vectors point slightly downward. Since the second axis was strongly correlated to birch dominance, the difference in direction of the two vectors indicates that birch present in the understory may never be expressed in the overstory. Birch was not present on plot 182 in 1951 or in 1984, which explains why both of this plot's vectors point the same direction.

The vectors of group A plots display a greater variety of patterns. The understory and overstory vectors of plots 1 and 122 follow the directional pattern of group B plots, but are more similar in length. The overstory vector of plot 11 is much longer than the understory vector, indicating greater compositional change in the overstory than predicted. In accordance with the general trend, plot 11 did contain less birch in its 1984 overstory than in its 1951 understory. On plot 13, both vectors point upward and are the same length. The vectors of plot 59 were similar in length, but the overstory vector points upward indicating more birch in the overstory. On plot 59, birch dominance in the 1984 overstory was relatively low but was higher than that of the 1951 understory from which birch was absent.

Analysis of the fourteen pairs of successional vectors indicated that the rate of change in species compositions was generally lower than predicted. The major compositional difference between the 1984 overstory and the 1951 understory was in birch dominance. Generally, the overstory contained less birch than the understory. Birch, a small-sized, short-lived tree, requires much light for all stages of development. Once overtopped by conifers, birch stems die. The birch stems
will sprout or regenerate only in large gaps. Birch's size, longevity and light-requirements explain why this species plays a greater role in the forest understory than in the overstory.

Of the three plots which differed from the general pattern displayed in the ordination, two (11 and 13) were located in the wettest and one (182) in the driest region of the study area. These three plots had the lowest overstory canopy densities of the fourteen plots in 1984. As explained in the section on the overstory ordination, plot 13, the wettest site, differed from the other plots as it is in an earlier stage of development. Plot 11, also located in the moister region of the study area, has reached the successional stage where its once dominant birches are dying as the conifer canopy closes above them. Because the birches are in a senescent phase, actual compositional change was greater than predicted. Somewhat parallel to the situation on plot 11, plot 182 suffered a dieback of its seral species—larch. Plot 182 also changed more in species composition than predicted. Grand fir recruits filled the gaps created by the dead trees on both plots. In 1951, grand fir was absent from these plots' overstories and present in only small amounts in their understories. Thus, increased mortality of overstory trees, regardless of its source, may cause an unpredictable stochastic change in species composition.

Though understory compositions in these Yellow Bay Forest plots may suggest general successional trends, they can not be used to directly predict future overstory composition. Because of the longevity of many species, the rate of compositional change in the overstory is generally slower than that of the understory. Direction of compositional change may also vary over time. Given the complexity of forest dynamics, some
biotic or environmental factor, e.g., differential mortality or disturbance rate, will eventually change in frequency or intensity. A change in the disturbance regime results in a change in the rate and direction of succession. As the degree and type of disturbance vary within a forest, so may the pathway of succession vary within a forest.
Disturbance and Forest Dynamics

Since the turn of the century, the disturbance regime of Yellow Bay Forest has changed. As rates, distribution (in time and space) and severity of a disturbance affect species composition and structure of a forest (Runkle 1985), a change in any of these factors will have important consequences on forest dynamics. In the Yellow Bay Forest, fire occurring at long intervals was the major disturbance shaping forest development until 1905. After this time fires were suppressed and eventually, insects and disease became the major agents of disturbance.

The change in patterns of mortality at Yellow Bay had a profound influence on forest dynamics and species composition. Previously, the deaths from fire of groups of trees suddenly released large amounts of previously limited resources, e.g. light, space and nutrients. Newly exposed soil provided an optimal seed bed for many species. In the absence of periodic fire, disturbances were less intense and usually smaller. Resources became available in smaller quantities.

Without fire to periodically open portions of the forest canopy, most of the forest's canopy closed. Even grand fir, which establishes well in moderate shade could not reproduce or grow in the dense shade. The previous regularity of fire was not conducive to the development of shade tolerance as the forest usually burned before such traits were selected (Antos 1977). The increased senescence of trees increases
their susceptibility to insects and disease. Insects and disease, biotic agents of change, speed the demise of senescing trees, create openings in the canopy and allow the recruitment of new stems (Mueller-Dombois et al. 1983).

Gap phase dynamics, the process by which growth continues in the canopy openings of dense stands, characterizes species dynamics in the Yellow Bay forest. Most of the gaps are small, formed by the death of one or two trees. The larger gaps are formed by the death of a group of trees, such as the larch which suffered high losses to the larch casebearer. Windstorms hastened the rate of gap formation by felling disease-weakened and standing dead trees.

The change in disturbance regime strongly affected species dynamics. Under the periodic fire regime, faster-growing, less tolerant species were able to reestablish themselves. Larch seedlings establish well on bare mineral soil after a fire and mature larches are highly resistant to fire. With greater light intensity, the fast-growing Douglas-fir compete well with grand fir. As the canopy closed, these less shade tolerant species were lost from the understory.

Most of the Yellow Bay Forest now has a dense canopy cover with intermittent and small canopy openings. Under these conditions, the more shade tolerant species, grand fir and maple, dominate the understory. Grand fir's ability to persist in a suppressed state under a dense canopy and to respond well to release from suppression gives it a crucial advantage in the gaps. Grand fir also establishes well by seed in gaps. Grand fir's high net basal area growth rate and low mortality rate reflect its shade tolerance and other adaptations to current forest conditions. Maple, though not as common as grand fir, is a ubiquitous
component of forest gaps. Maple's very high ingrowth rate indicates that this shrub resprouts well under gap conditions. In spite of maple's ability to tolerate shade, its successional role is limited by its shorter life span and its smaller size compared to the forest trees. Engelmann spruce, though moderately shade tolerant, was rarely successful in colonizing gaps. Spruce's low density is characteristic of spruce in the grand fir forests of the Swan Valley (Antos 1977).

While small canopy openings favor the more tolerant species, larger openings allow less tolerant species such as Douglas-fir to become established. The one large gap present on the study plots was located in the dry northwest region of the forest. All of the larch that were present on this plot in 1951 have since died. Though two Douglas-fir seedlings were recently recruited, no Douglas-firs survived into larger size classes. The understory, still fairly open, was dominated by young grand firs and maples.

The southwest portion of the study area was not yet influenced by gap phase dynamics. Formerly a marsh, this area still had a moderately open canopy with many grand firs and a few spruces thriving in the understory.

**Compositional Trends**

Successional vector ordinations of plot overstories revealed distinct compositional trends in group A as opposed to group B plots. Group A plots increased in only grand fir while group B plots increased in grand fir and Douglas-fir.

The increasing dominance of grand fir on five group A plots
resulted from the high growth and low mortality rates of grand fir concomitant with the loss of other species. The short-lived species, maple and birch, had high mortality. Only a few Engelmann spruces and no Douglas-firs were recruited, leaving little competition for grand fir.

One of the six group A plots increased in birch rather than grand fir dominance. This plot, also the moistest plot, was located on the site of a marsh drained in the 1960's. In 1984, birch was the only tree species in the overstory. Grand fir moved into the understory from the adjacent forest edge as the site became drier but had not reached the overstory by 1984.

The eight plots of group B increased in Douglas-fir and grand fir dominance. The net growth rate of Douglas-fir was similar to that of grand fir on these drier plots. Growth and mortality rates were similar for the two species. Grand fir recruitment, however, was greater than that of Douglas-fir. Douglas-fir and grand fir dominances increased at the expense of the short-lived species—maple and birch—and the insect-killed larch.

Successional vector ordinations revealed similar compositional trends in the understories of the two groups of plots. The two groups differed in what species were lost, but in both, grand fir dominated recruitment. More birch was lost from group A plots while more Douglas-fir and larch were lost from group B plots. Grand fir and maple had the greatest rates of ingrowth. A few plots increased more in maple than in grand fir, but grand fir will eventually overtop and replace this short-lived species.

Thus, both groups became less diverse compositionally between 1951
and 1984. An analysis of overstory dominance indicates a convergence toward two species compositions: (1) grand fir dominance and (2) grand fir—Douglas-fir codominance. An analysis of understory dominances in both groups indicates convergence toward grand fir dominance.

Site characteristics partially explain compositional changes of the two groups of plots. Grand fir, typical of moister areas compared to Douglas-fir, dominated the moister group A plots. On the drier group B plots, Douglas-fir and grand fir established equally well after the last replacement burn opened the canopy and cleared the ground of litter. The oldest overstory trees of both these species are around 170 years of age. Site conditions changed as the canopy dominated by Douglas-fir and grand fir closed. Less light was available for the establishment of new trees favoring the more shade-tolerant grand fir. The closed canopy created moister conditions due to reduced evapotranspiration, decreasing Douglas-fir's competitive advantage. Most reproduction became limited to small gaps beneath the canopy opening, also favoring the more tolerant grand fir which can survive suppression and can respond to release from suppression soon after the canopy opens.

Species life history characteristics also partially explain group dynamics from 1951 to 1984. Birch diminished in the overstory due to its short longevity, small stature and low shade tolerance. Maple's shade tolerance and ability to resprout explain its high rate of ingrowth. Grand fir's greater longevity and size account for its advantage over maple. Douglas-fir's longevity and size allow its continued codominance in the north end of the forest. The main event not explained by species characteristics was the insect-caused dieback of larch. The larches, with potential lifespans of 700 years, were not

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in a senescent phase. The oldest larch was about 270 years old and most were 75 to 200 years old. The larch casebearer unpredictably hastened the death of the larches.

**Short-term Projections of Forest Dynamics**

The increasing homogeneity of the smaller size classes of the two groups of plots may indicate a convergence of the two groups into one grand fir-dominated group as the overstory Douglas-firs at the north end of the forest senesce and die. However, these healthy Douglas-firs could live another 230 years, in which time a major disturbance most likely will occur. If the primary form of disturbance continues to be the creation of small gaps from the death of one or two canopy trees, grand fir will continue to dominate regrowth in both groups of plots. A massive dieback of trees, however, could change the course of succession. Theoretically, a large gap created by a dieback of canopy trees in the dry region of the forest would allow for the replacement of the Douglas-firs. However, Douglas-fir recruitment was not very successful in the one large gap present at the northwest corner of the study area created from the death of several larches. Two first-year Douglas-fir seedlings were present, but no seedlings from previous years had survived. Thus, the successful establishment of Douglas-fir may be limited by factors other than light availability. Lush understory herbs and shrubs compete for space as well as light. The falling of trees or the death of trees that remain standing do not remove the thick litter or rapidly release stored nutrients, making seedling establishment more difficult. A more intense disturbance such as a fire would remove this
litter and would release large quantities of nutrients. Also, the forest soil may have increased in available moisture since 1951, thereby favoring the grand fir. The dam at the south end of Flathead Lake began raising the lake level in 1936. A rise in the water table underneath the forest accompanied the rise in the lake level. The lake level now fluctuates depending on water discharge of the dam. Thus, a rising water table may have increased water availability of the soil, thereby decreasing the ability of Douglas-fir's seedlings to compete with those of grand fir.

Evidence Supporting the Various Succession Models

The Relay Floristics Model

The only area of the Yellow Bay forest possibly undergoing a stage-by-stage process of succession is the moist southwest corner. Here, birch, willow and alder were present in 1951. The willow and alder died by 1984, appearing to be associated with an early seral stage. In 1984, birch remained in the overstory and grand fir was invading from the adjacent woods. Though birch and grand fir also are associated with stages, these stages are overlapping, not discrete. In addition, the relay floristics model does not fit well as primarily allogenic—not autogenic—forces drive successional change. The draining of this wet marshy area had a more drastic effect on site characteristics than did the plants themselves.
Initial Floristics Composition

Initial floristics composition seems a more appropriate model of forest dynamics at Yellow Bay. Egler (1954) suggested that any species present on a site can colonize the site in its early developmental stages and that shifts in species dominances are a function of the species' life history characteristics. Aging of trees indicated that grand firs, Douglas-firs and spruces all colonized the study area 150 to 200 years ago. In the southern end of the forest, dominance shifted from birch to grand fir due to grand fir's greater size and longevity. On the north end of the forest, Douglas-fir's initially higher growth rate and its greater longevity has allowed it to codominate with the more shade-tolerant grand fir.

Tolerance Model. Connell and Slatyer (1977) suggested that species assume dominance later in the successional sequence because they tolerate the reduced level of resources. Grand fir, the most tolerant species, has benefited from reduced light levels at the expense of the less tolerant species. Although no species grow much under the dense forest canopy, grand fir and maple germinate and grow well under small canopy openings.

Inhibition Model. The inhibition model explains shifts in dominance from short- to long-lived species. Grand fir and maple establish well in gaps, inhibiting the invasion of other species. Even if the species establish equally, the shorter-lived maple is more often replaced than the longer-lived grand fir. This produces a sequence from maple and grand fir to only grand fir in the gaps.
Multiple Pathway Model

A multiple pathway model of succession proves most useful in describing events at the Yellow Bay Forest. Such a model would incorporate tolerance and inhibition pathways and would emphasize life history characteristics. Yellow Bay Forest is a patchwork of vegetation in various stages of disturbance and recovery from disturbance. As the intensity, type, and frequency of disturbance as well as physical terrain and initial composition vary throughout the forest, a multiple pathway model is necessary to explain the variation.

The cone model, a multiple pathway model, illustrates forest dynamics on the two groups of plots at Yellow Bay. The timespan of the long-term data fits into the mid-to-late seral stages of the cone model (Figure 2). In 1951, the plots were in the slightly overlapping mid-seral stage. The groups were, for the most part, distinct, but a few plots did not fit clearly into either group. By 1984, the two groups were distinct—represented by the non-overlapping, late seral stage. Plots formerly intermediate in composition between the groups became more similar to one of the groups. The more moist group of plots is increasing in grand fir dominance while the more dry group is increasing in grand fir and Douglas-fir. The tips of the two cones, however, will not be climax communities in the classical sense. Douglas-fir is not replacing itself in the understory so it is not considered a "climax" species. Because of its longevity and size, Douglas-fir will continue to codominate with the shorter-lived grand fir for perhaps 230 years. If current conditions continue, the two cone tips will merge into one
when the Douglas-firs die. Of course, a change from the present disturbance regime could hasten the demise of the Douglas-fir, or it could rejuvenate the Douglas-fir population—keeping the tips of the two cones distinct.

**Some Management Implications**

Information gained from long-term data, such as those from Yellow Bay Forest, may be useful in forest management as it relates to timber and wildlife and environmental problems.

As forest management has increased in sophistication, so has competition for forest resources increased. A better understanding of the ecological processes involved in forest dynamics and the development of forest models can minimize negative impacts and can reduce conflicts between timber, wildlife, recreation and research interests. Long-term data provide information on forest species and communities and help in developing and validating models. Forest managers may attempt to mimic natural forest conditions, such as those found at Yellow Bay Forest, because these are the conditions to which species are best adapted.

With models, foresters simulate the effects of different management practices or various types of disturbance on forest development, using the results to decide how to manage a stand for the desired goals. Because of the amount of time necessary to observe forest dynamics, long-term data are essential in developing and improving forest models.

Long-term vegetation data, in combination with data on habitat
preferences of wildlife species, can aid in managing forests for wildlife. Changes in forest structure and diversity affect wildlife diversity and abundance. An understanding of forest development under natural conditions allows managers to manipulate the forest to improve its suitability for selected wildlife species.

The widespread damage of trees by man-caused disturbances has forced foresters to study environmental stresses and their effects on tree decline and dieback. The data from Yellow Bay, a relatively undisturbed site, provide a norm against which disturbed grand fir forests can be compared. These data also provide a baseline for future studies at the Yellow Bay Forest if environmental stresses increase.

By increasing our understanding of forest processes under natural conditions, the data from Yellow Bay may help foresters make better management decisions and may provide a baseline for measuring the effects of environmental stresses on forest dynamics.
LITERATURE CITED


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APPENDIX

Long-term Data for Yellow Bay Forest, Montana

SPSSX Command File

FILE HANDLE OUTPUT /NAME = 'FOR2 FIL'
FILE HANDLE INPUT /NAME = 'FOR1 DTA'
DATA LIST FILE = INPUT
/ TRID 1-4
PLOT 7-9
SPEC 11-12
DC51 15-16
DBH51 19-22
VG51 25
DBH67 28-31
DBH84 34-37
VG84 40
XCOR 43-45
YCOR 48-50

VARIABLE LABELS
TRID 'Tree Identification Number'
PLOT 'Plot Number'
SPEC 'Tree Species'
DC51 'Diameter Class in 1951'
DBH51 'Diameter in 1951'
VG51 'Vigor in 1951'
DBH67 'Diameter in 1967'
DBH84 'Diameter in 1984'
VG84 'Vigor in 1984'
XCOR 'X Coordinate'
YCOR 'Y Coordinate'

VALUE LABELS
SPEC 1 'Abies grandis'
2 'Acer glabrum'
3 'P. menziesii'
4 'Betula papyrifera'
5 'Picea engelmannii'
6 'Larix occidentalis'
7 'Pinus ponderosa'
8 'Salix bebbiana'
10 'Alnus tenuifolia'

DC51 1 '0-1 inches'
2 '1-3 inches'
3 '3-6 inches'
4 '6-9 inches'
5 '9-12 inches'
6 '12-15 inches'
7 '15-18 inches'
8 '19-21 inches'
9 '21-24 inches'
10 '24-27 inches'
11 '27-30 inches'
12 '30-33 inches'

VG51 0 'dead'
1 'alive'

VG84 0 'dead'
1 'alive, but stunted'
2 'alive and growing'

MISSING VALUES DC51, DBH51, DBH67 (99) VG84 (9)

SAVE OUTFILE= OUTPUT

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